EXAMINING EVOLUTIONARY TRENDS IN *EQUUS* AND ITS CLOSE RELATIVES FROM FIVE CONTINENTS

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EXAMINING EVOLUTIONARY TRENDS IN *EQUUS* AND ITS CLOSE RELATIVES FROM FIVE CONTINENTS

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Evolution of the horse has been an often-cited primary example of evolution, as well as one of the classic and important stories in paleontology for over a century and a half, due to their rich fossil record across 5 continents: North America, South America, Europe, Asia and Africa. The recent horse has served a profound role in human ancestry, including agriculture, commerce, sport, transport, warfare, and in prehistory, for the subsistence of humans. Many studies have examined the evolution of the Equidae and chronicled the striking changes in skulls, dentition, limbs, and body size which have long been perceived to be a response to environmental shifts through time. Most comprehensive studies heretofore have: (1) focused on the "Great Transformation"- changes that occurred in the early Miocene, (2) involved tracking long-term diversity or paleoecological trends on a single continent or within a geographical locality, or (3) concentrated on the 3-toed hipparions.

The Plio–Pleistocene evolutionary stage of horse evolution is punctuated by the great climatic fluctuations of the Quaternary beginning 2.6 Ma which influenced Equus evolution, biogeographic dispersion and adaptation on a nearly global scale. The evolutionary biology of Equus evolution across its entire range remains relatively poorly understood and often highly controversial. Some of this lack of understanding is due to assumptions that have arisen because of the relatively derived craniodental and postcranial anatomy of Equus and its close relatives which has seemed to imply that that these forms occupied relatively homogenous and narrow dietary and locomotor niches - notions that have not been adequately addressed and rigorously tested. Other challenges have revolved around teasing apart environmentally-driven adaptation versus phylogenetically defined morphological change. Geochronologic age control of localities, geographic provinces and continents has improved, but in no way is absolute and can be reexamined in our proposed volume. Temporal resolution for paleodietary, paleohabitat and paleoecological interpretations are also challenging for understanding the evolution of Equus. Our proposed volume attempts to assemble a group of experts who will address multiple dimensions of Equus' evolution in time and space.

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The Role of Grass vs. Exogenous Abrasives in the Paleodietary Patterns of North American Ungulates

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Equids have often been discussed regarding tooth morphological change due to the evolution of highly hypsodont teeth over time, the hyper-grazing habits of modern horses, and an older view that the acquisition of hypsodonty and the widespread appearance of grasslands were synchronous. Many more recent studies, however, have reported asynchrony in the origin of hypsodonty and the widespread appearance of grasslands and have considered exposure to exogenous grit as important evolutionary drivers of hypsodonty in ungulates. We tracked changes in crown height (hypsodonty index), relative abrasion (mesowear), and food and grit scar topography on dental enamel (microwear) to examine the relative contributions of grass vs. grit as a driving force in ungulate tooth changes during the evolution of North American Equidae compared to four North American ruminant artiodactyl families (Camelidae, Antilocapridae, Dromomerycidae, and Merycoidodontidae). We mirror other studies by finding that the overall pattern of the timing of the attainment of hypsodonty is inconsistent with grazing as the main impetus for the "Great Transition" within equids nor within the artiodactyl families as highly hypsodont ungulates post-date the spread of widespread grasslands. Mesowear closely mirrored hypsodonty trends in all families. Microwear patterns, particularly high degrees of enamel pitting (particularly large pits) and unusually coarse scratch textures in all five families, are consistent with exposure to exogenous grit as the main driver of hypsodonty acquisition prior to the consumption of significant levels of grass. Equidae exhibited a wider array of dietary behavior than the other families through most of their evolutionary history. Even so, grass was a much more common dietary item for equids than for the other families, and when combined with exogenous grit, which was more accelerated from the early Miocene onward based on more pitting and coarser scratch textures, may explain the more extreme acquisition of hypsodonty in equids compared to the artiodactyl families studied and set the stage for the Equidae alone to become hypergrazers in the Recent.

Keywords: ungulates, microwear, mesowear, hypsodonty, paleodiet

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INTRODUCTION

Horse evolution has often been presented as a standard example of evolution. This proclivity is not surprising given: (1) well-documented evolutionary changes, particularly in the late early Miocene, (i.e., greater body size, somewhat higher-crowned cheek teeth, and more cursorially-adapted limbs) that have been perceived for a long time to echo higher-latitude environmental shifts through time (i.e., adaptations to shifts from living in tropical forests to eventual occupation of open grasslands) (Janis, 2007) and (2) the expansive fossil record of North American horses (especially in the Miocene) where the bulk of horse evolution and diversification (Equidae) occurred despite several successive dispersals to the Old World (MacFadden, 1992; Janis, 2007). Despite these dispersals to the Old World, the Equidae apparently evolved in isolation in North America from the middle of the Eocene through the late Oligocene (MacFadden, 1992). During the mid-Cenozoic, horses were very widespread in North America—reaching their maximum diversification and abundance in the late Miocene with individual fossil localities often accommodating up to eight equid species (MacFadden, 1992; Hulbert, 1993).

Because food acquisition is so imperative to an animal's survival, paleontologists have long been interested in adaptations that facilitate acquiring and comminuting food items as well as those that help to deal with an enhanced rate of tooth wear induced by food that is abrasive (e.g., grass) or due to exogenous substances possibly adhering to food (e.g., grit). Hummel et al. (2011) tested the relationship of total silica ingested (from plant phytoliths and exogenous grit) and hypsodonty by investigating the correlation between fecal silica content and hypsodonty and demonstrated a considerable influence of ingested silica on hypsodonty in large herbivores. The evolution of high-crowned teeth (i.e., hypsodonty) has particularly intrigued paleontologists (Osborn, 1910; Stirton, 1947; Simpson, 1953; White, 1959; Webb, 1983; Fortelius, 1985; Janis, 1988; Solounias et al., 1994; MacFadden, 2000a,b; Williams and Kay, 2001; Mihlbachler and Solounias, 2006; Strömberg, 2006; Jardine et al., 2012; Lucas et al., 2014). The potential correlation of crown height with habitat, climate, and dietary shifts has also been the subject of intensive study (Webb, 1983; Janis, 1988, 2008; Janis et al., 2000, 2002, 2004; Williams and Kay, 2001; Semprebon and Rivals, 2010; Mihlbachler et al., 2011) as the obtainment of high crowned dentitions had been considered generally as a potential response to a shift in foraging from closed habitats to more open ones and/or from feeding on browse to feeding on grass in the early Miocene (Osborn, 1910; Scott, 1937; Simpson, 1944; Stirton, 1947; Webb, 1977, 1983; Stebbins, 1981; Janis, 1984, 1993; Webb and Opdyke, 1995). Thus, hypsodonty was in the past mostly associated with grass consumption because of the large number of silica-rich phytoliths found in grasses which were presumed to impose accelerated wear of mammalian teeth.

Two important caveats have been considered in recent studies when evaluating the veracity of this old evolutionary "story": Firstly, was the appearance of hypsodonty in the Miocene truly synchronous with the appearance of grasslands? Secondly, is dietary preference operating alone in determining the degree of hypsodonty acquisition? Recent studies have revealed a lack of synchronicity between the appearance of hypsodonty in the Miocene and the appearance of grasslands. Some of the latest evidence comes from recent research on phytoliths (Strömberg, 2004, 2005, 2011; Strömberg et al., 2016) that has revealed that grass was available for forage in the North American Great Plains region by ∼22 million years ago (earliest Miocene), but possibly by even about 26 million years ago (latest Oligocene–Strömberg, 2011) about 6 million years before the appearance of the genus *Merychippus*. *Merychippus* represents the first hypsodont horse even though some members of the genus *Parahippus* showed a slight enhancement in crown height and evidence of profound dental wear (MacFadden and Hulbert, 1988; Strömberg, 2006; Damuth and Janis, 2011; Mihlbachler et al., 2011). *Merychippus* represents an important milestone in the evolution of horses due to its relatively high crowned cheek teeth, but also due to the first appearance of well-developed cementum between lophs and with the similar positioning of its tooth cusps to modern horses. A change in the shape of the angle of the jaw, indicating a more horizontally-oriented angle of insertion of the masseter muscle was also seen in *Merychippus* (Stirton, 1947; Simpson, 1951; Turnbull, 1970; MacFadden and Hulbert, 1988; Bernor et al., 1989, 1997; Prothero and Schoch, 1989; Hulbert and MacFadden, 1991; MacFadden, 1992; Spaan et al., 1994). Even so, highly hypsodont equines did not appear until about 14 Ma (late middle Miocene), well after the apparent availability of open grasslands (Damuth and Janis, 2011), a trend echoed by certain artiodactyl clades such as antilocaprids (pronghorns) and camelids that also developed hypsodonty in the late middle Miocene. In addition, a moderate amount of hypsodonty was attained by some artiodactyls in the Oligocene and many families of mostly burrowing rodents at least 7 million years earlier (Jardine et al., 2012). However, these hypsodont artiodactyls (stenomyline camelids, leptauchinine oreodonts, and hypisodine hypertragulids) went extinct in the late Oligocene/early Miocene not giving rise to later hypsodont artiodactyls.

Another important factor to consider is that researchers have suspected for some time that grass phytoliths may not have been the only evolutionary driver in the development of tooth morphological change [e.g., Janis (1988) and Fortelius et al. (2002)]. Janis (1988) has long hypothesized that grit consumption might also be an evolutionary driver through her observations that the degree of hypsodonty in ungulates might be more due to habitat preferences than to dietary preferences. Janis (1988) showed that ground-feeding ungulates in open habitats are significantly more hypsodont than closed habitat ungulates regardless of their preferences for food (see **Figure 1**). Janis (1988) also noted that ungulates that feed on dicotyledonous material above ground have the lowest hypsodonty values and suggested that dust and grit which accumulates on food consumed in open habitats is more important for determining hypsodonty in ungulates than dietary fiber levels. Others have also considered grit and soil as possibly more important agents of abrasion than grass phytoliths (Stirton, 1947; Janis, 1988;

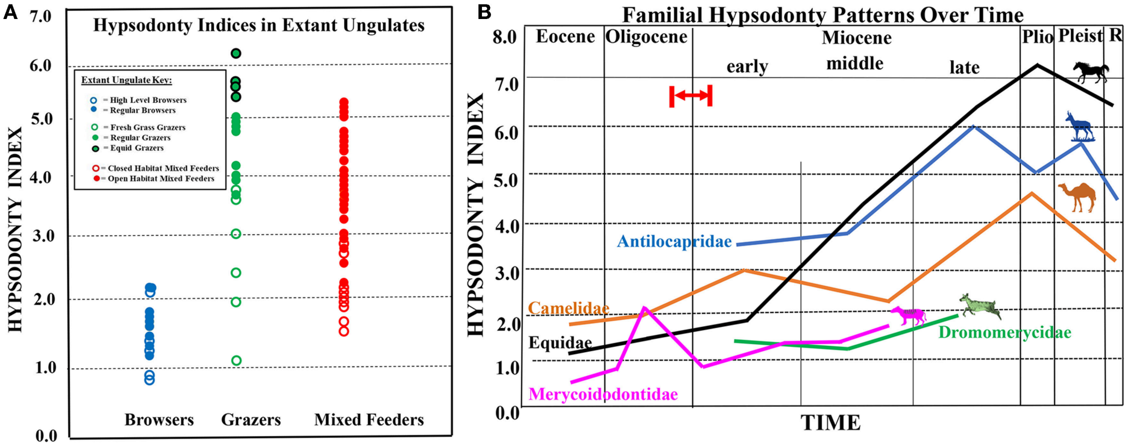

FIGURE 1 | (A) Extant ungulate m3 hypsodonty indices (data from Janis, 1988; modified from Semprebon and Rivals, 2010). Extant ungulates are represented by circles (closed circles = regular browsers, grazers, and mixed feeders; closed circles with black outlines represent equid grazers; open circles = high-level browsers, fresh grass grazers, and closed habitat mixed feeders). **(B)** Composite figure showing hypsodonty trends through time for equids (black line), antilocaprids (blue line), camelids (orange line), dromomerycids (green line), and oreodonts (pink line). Red arrow and red lines indicate probable timing of first availability of grass in the North American Great Plains Region by ∼22 million years ago (earliest Miocene), but possibly by even about 26 million years ago (latest Oligocene) based on phytolith data from (Strömberg, 2011). Please note that hypsodont equids will likely always have higher hypsodonty indices than ruminants on a similar diet, due to differences in digestive physiology and ingestive mastication.

Williams and Kay, 2001; Janis et al., 2002) or ingested soil (Damuth and Janis, 2011).

Hoffman et al. (2015) examined the possibility of a "grit effect" experimentally and highlights as supporting evidence: (1) the asynchronous timing of the expansion of grasslands in North America and the acquisition of hypsodonty in Glires and ungulates (Jardine et al., 2012), (2) the coincidence of the finding of more hypsodonty and hypselodonty (ever-growing teeth) in herbivorous mammals from South America from the middle Eocene (40 Ma) to the early Miocene (20 Ma) with an interval of dry and open environments which lacked grasslands but were exposed to recurrent volcanic ashfall (Strömberg et al., 2013; Dunn et al., 2015), and (3) exogenous grit as an agent to producing microwear in ungulates like the extant *Antilocapra americana, Camelus bactrianus*, *Camelus dromedarius*, and *Vicugna vicugna* which live in semi-arid or arid habitats have been reported to have coarser microwear scars (i.e., coarse scratch textures, higher average pit numbers and gouging) relative to their counterparts in more humid places (Solounias and Semprebon, 2002). Hoffman et al. (2015) assessed the contribution of exogenous grit to enamel microwear by using a new technique for molding live animals representing the first ungulate controlled feeding experiment (*in-vivo*) using abrasives of different sizes. This study (2015) found a significant "grit effect" with medium sized silica particles (i.e., an increased abundance of pits [but not more scratches] which resulted from fracturing of sand grains through masticatory movements). Smaller particles of the fine sand treatment proved harder to break apart in this study and did not show a significant grit effect.

Jardine et al. (2012) carried out a study of crown height changes in herbivorous species (i.e., Glires and large mammals) of the Great Plains region of the United States to better understand the importance of grass vs. grit as drivers of the attainment of hypsodonty. This study focused on examining when hypsodonty evolved in these forms relative to the spread of grasslands and determining how widely distributed hypsodonty was among taxa. Jardine et al. (2012) found that the timing of the expansion of grasslands in North America was asynchronous with the timing of the acquisition of hypsodonty in Glires and ungulates. Jardine et al. (2012) also documented that many artiodactyl and perissodactyl families were exclusively low-crowned with the exception of the Antilocapridae (pronghorns), Camelidae (camels), Merycoidodontidae (oreodonts), Equidae (horses), and Rhinocerotidae (rhinoceroses) which were the only families that attained hypsodont or highly hypsodont dentitions. They also reported that these high-crowned families (except for pronghorns which appeared in the early Miocene as immigrants) have molars that change from brachydont to hypsodont or highly hypsodont and range through most of the time series. They (2012) describe: (1) a "first wave" of high-crowned taxa represented by leptauchenine oreodonts and stenomyline camelids in the Oligocene (with hypertraguline traguloids showing some degree of hypsodonty), (2) the appearance of the first highly hypsodont ungulate in the early Miocene (He1) (e.g., the latest surviving stenomyline camelids, and (3) a "second wave" of hypsodonty in the early Miocene (He1) in horses, rhinos, and pronghorns, but highly hypsodont taxa not appearing until the late middle Miocene (Barstovian) (including the first of the hypsodont later camelids).

In this study, we examine the relative contributions of grass vs. grit as a driving force in ungulate tooth evolutionary changes using a combination of dietary proxies (hypsodonty index, mesowear, and microwear) with different temporal resolution capabilities to investigate the amounts of different levels of abrasion imposed on molar teeth over evolutionary time and the potential causes of this abrasion. For example, hypsodonty is an evolutionary adaptation developed over deep time which makes a tooth more durable as an adaptation to resist augmented tooth wear incurred during mastication (Janis and Fortelius, 1988). Thus, a hypsodont tooth is not worn away as quickly because there is more tooth material present (Janis, 1988). Thus, hypsodonty is a reflection of selective pressures over time imposed by high levels of dental abrasion incurred by a species' lineage (Damuth and Janis, 2011).

Mesowear assesses gross molar wear by assessing lateral cusp shape and involves ecological time, in that, dental wear that accumulates on molars during an individual's lifespan is explored. Thus, mesowear should be sensitive to intrinsic, abrasive elements in plants but also to grit encountered on food or during the process of feeding (but does not tease apart relevant contributions of each).

Microwear examines shorter-term microscopic tooth wear imposed upon dental enamel by the last meals partaken by these animals just before dying, and as such, can elucidate daily, seasonal, or regional alterations in diet not possible with hypsodonty, mesowear or other gross craniodental methods. Importantly, microwear (Hoffman et al., 2015) shows a habitat effect (i.e., grit signature) as well as dietary food discrimination. In particular, dietary discrimination of modern ungulates using microwear is dependent upon relative numbers of scratches whereas scratch textures (i.e., widths) and degree of large pitting have been shown to track relative dietary abrasion regardless of dietary category (Semprebon, 2002; Solounias and Semprebon, 2002; Semprebon et al., 2004; Hoffman et al., 2015). Thus, browsers subsisting on relative soft foods such as leaves that occupy arid and open habitats show higher levels of pitting (especially large pits) and coarser scratch textures than leaf browsers that occupy relatively closed habitats (Semprebon, 2002). Coarser scratches are found in modern grazers that consume dry grass as opposed to fresh or moist C3 grass (and more large pits and gouges) and closed habitat and moist C3 grass mixed feeders have finer scratches and fewer large pits and gouges than open habitat mixed feeders (Semprebon, 2002). Solounias and Semprebon (2002) and Semprebon et al. (2004) have reported that those extant ungulate taxa that either encounter exogenous abrasives or consume fruit have large percentages of individuals displaying large pits in their enamel. However, frugivory produces large pits that are crater-like, deeply etched into the enamel and with very symmetrical, and well defined, and round border outlines. Exogenous abrasives produce a more superficial chipping effect on enamel where large pits are relatively shallow and with irregular borders.

The purpose of this work is twofold: (1) to examine the changing paleodiet of Eocene to Recent Quaternary equids from North America using three different dietary proxies with different temporal resolutions (hypsodonty, mesowear, and microwear) and (2) to compare this pattern to that of four North American artiodactyl families to gain insight as to the impact of differing amounts of dietary abrasion encountered by food and grit on shaping these families through time.

MATERIALS AND METHODS

Data from North American equids ranging from the Eocene (early Uintan) through the Pleistocene (Rancholabrean) were obtained from (Semprebon et al., 2016) (microwear; $N = 1203$) and (Mihlbachler et al., 2011) (mesowear; $N = 6498$). These data were compared to published microwear data on extant ungulates (Solounias and Semprebon, 2002) and microwear and mesowear data from North American Miocene through Pleistocene antilocaprids (data from Semprebon and Rivals, 2007), Eocene through Pleistocene camelids (data from Semprebon and Rivals, 2010), early Miocene through late Miocene dromomerycids (microwear and mesowear data Semprebon et al., 2004), and early Miocene through late Miocene merycoidodontids (unpublished microwear and mesowear "score" data from GS; published mesowear and hypsodonty data from Mihlbachler and Solounias, 2006). Unpublished hypsodonty data was obtained for all five fossil families from Christine Janis. Details regarding taxa and localities represented may be found in the above publications. These data were evaluated to compare the paleoecology of these North American through time.

All microwear data was obtained by a single, trained observer (G.S.) using a light stereomicroscope at 35× magnification following technique regime of Semprebon (2002) and Solounias and Semprebon (2002) and Semprebon et al. (2004). The tooth and area studied were the same for all families. The average number of pits (rounded features) vs. average number of scratches (elongated features) per taxon were counted within a 0.16 mm^2 area using an ocular reticle. Results were compared to an extensive extant ungulate database (Semprebon, 2002; Solounias and Semprebon, 2002) to determine browser vs. grazer dietary categories. Large pits were scored as either present (i.e., more than four large pits per microscope field) or absent (within the 0.16 mm^2 area) and if gouges were present and the percentage of individuals within each taxon with these variables was calculated. Scratch textures were qualitatively recorded as being either mainly fine, mainly coarse, or a mixture of fine and coarse textural types following procedures for recognizing these textural differences outlined in Solounias and Semprebon (2002) and Semprebon et al. (2004). A scratch width score (SWS) was attained by ascribing a score of 0 to molars with mostly fine scratches, 1 to molars possessing a mix of fine and coarse textures, and 2 to those with mostly coarse scratches. An average of individual scores for a taxon was obtained to arrive at the average scratch width score. Mixed feeders were distinguished from browsers and grazers based on calculations of the percentage of raw scratches per taxon falling into a low raw scratch range of 0–17 scratches as discriminating patterns are discernible among these three extant trophic groups (Semprebon, 2002; Semprebon and Rivals, 2007).

Mesowear for all families was obtained by modifying the mesowear technique of Fortelius and Solounias (2000) which examines attritional tooth wear due to tooth-on-tooth contact wear vs. abrasional wear due to food-on-tooth contact (i.e., mesowear). As in the traditional mesowear method, mesowear data was collected by observing molar cusps macroscopically in buccal view and assessing cusp sharpness (i.e., sharp, round, blunt) and degree of occlusal relief (high or low) (Fortelius and Solounias, 2000). However, because cusp shape and occlusal relief are not independent variables and also because assigning tooth wear into mesowear categories is dependent upon an individual observer's judgment without standardization of actual boundaries defining various shape categories, mesowear was treated as a single variable and cusp apices were assigned to stages along a continuum ranging from the sharpest cusps with the highest relief to the bluntest cusps with the lowest relief comparing fossil teeth to a mesowear "ruler" (Mihlbachler et al., 2011) which was devised using seven modern *Equus* tooth cusps, representing a range from sharp cusps with high relief (stage 0) to blunt cusps and no relief (stage 6). Stage 7 was assigned when cusps had a negative relief (i.e., the apex of the cusp was convex). A mesowear score was determined by calculating the average mesowear value from each fossil tooth sample. With this scoring technique, higher scores reflect relatively more abrasion vs. attrition. Lower scores reflect more attrition vs. abrasion. An individual with mostly high relief and sharp cusps would have a score near 0 (e.g., low abrasion browsers), whereas, an individual with blunt cusps and low relief such as extreme grazers with high abrasion diets would have a score of 6. Other individuals would have scores falling in between these two extremes (e.g., coarser browsers, mixed feeders, and non-extreme grazers).

Extant ungulate data for hypsodonty was obtained from Janis (1988) and fossil merycoidodontids from Mihlbachler and Solounias (2006). Unpublished data for fossil equids were provided to us from Christine Janis. Hypsodonty was measured as the crown height (distance from the base of the crown to the tip of the protoconid) divided by the labio-lingual width of the third, lower and unworn molar provided the crown height ratio (m3 ratio). Molar width was measured between the protoconid and the entoconid (occlusal surface). Mihlbachler and Solounias (2006), however, used upper third molars for merycoidodontids.

RESULTS

Figure 1A shows extant ungulate m3 hypsodonty indices (data from Janis, 1988) which will serve as a comparative framework and context for understanding fossil indices. Extant ungulate hypsodonty indices are represented by circles (for extant browsers: open circles represent high-level browsers (i.e., those browsers that invariably feed above ground level), whereas closed circles represent regular browsers (those browsers that feed both above the ground and at ground level); for extant grazers: open circles represent fresh-grass grazers, whereas closed circles represent regular grazers and closed circles with a black outline represent equid grazers; for extant mixed feeders: open circles represent closed habitat mixed feeders, whereas closed circles represent open habitat mixed feeders). **Figure 1A** shows that lower crown heights are found in those extant taxa that either feed less close to the ground, on fresh grass, or in closed habitats. This underscores the likely influence that exposure to grit has played on tooth crown height over time.

Figures 2, **3** and 1B show graphical representations of hypsodonty indices through time in five North American ungulate families. **Figure 2A** shows that North American basal Eocene equids (hyracotherines) and Eocene and Oligocene *Mesohippus* and *Miohippus* have low crowned teeth (i.e., are brachydont)—at the level of extant regular browsers (**Figure 1A**). A slight increase in crown height (i.e., mesodonty) is observed in the early Miocene in some parahippine-grade taxa but

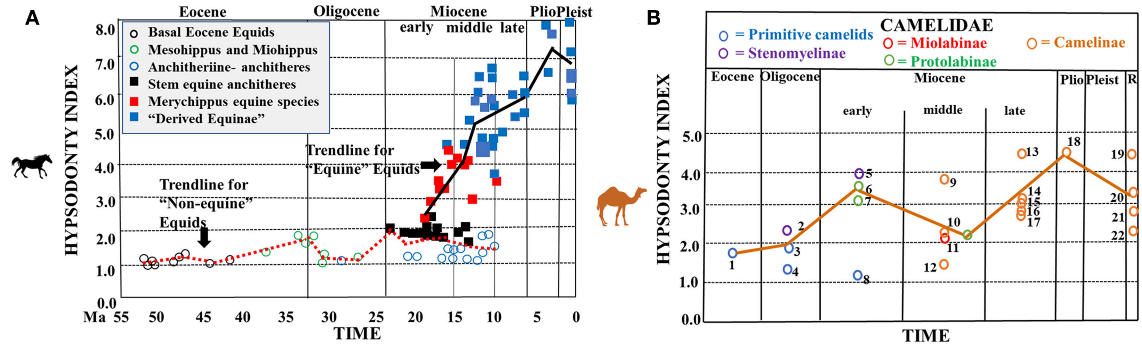

FIGURE 2 | Hypsodonty indices of fossil equids and camelids. **(A)** Hypsodonty indices of North American fossil equids and Recent Old World equids (modified from Figure 2 in Damuth and Janis, 2011). Key to taxa: open circles = basal Eocene equids (*Epihippus*, *Hyracotherium*, *Orohippus*); *Mesohippus* and *Miohippus*, and Anchitherini; (*Anchitherium*, *Hypohippus*, *Kalobatippus*, *Megahippus*); squares = stem equine anchitheres (*Archaeohippus*, *Desmatippus*, *Parahippus*); *Merychippus* equine species; and "Derived Equinae." Average modern (Recent) *Equus* hypsodonty indices from Janis (1988). The red, dotted line represents the hypsodonty index trendline for non-equine equids; the black, solid line represents the hypsodonty index trendline for equine equids **(B)**. Hypsodonty indices of North American fossil camelids through time (brown, solid line represents the trendline through time -modified from **Figure 4A** in Semprebon and Rivals, 2010). Key to taxa: blue circles = primitive camelids (1 = *Poebrotherium eximus*, 3 = *Poebrotherium wilsoni*, 4 = *Poabromylus kayi*, 8 = *Paratylopus cameloides*); purple circles = Stenomyelinae (2 = *Pseudolabis dakotensis*, 5 = *Stenomylus hitchcocki*); red circles = Miolabinae (11= *Miolabis longiceps*); green circles = Protolabinae (6 = *Protolabis* sp., 7 = *Michenia* sp.); orange circles = Camelinae (9 = *Procamelus* sp., 10 = *Aepycamelus* sp., 12 = *Aepycamelus stocki*, 13 = *Procamelus occidentalis*, 14 = *Megatylopus gigas*, 15 = *Procamelus* sp., 16 = *Hemiauchenia* sp., 17 = *Aepycamelus* sp., 18 = *Camelops mexicanus*, 19 = *Lama vicugna*, 20 = *Lama guanicoe*, 21 = *Camelus bactrianus*, 22 = *Camelus dromedaries*) Locality information for numbered taxa as in Table 1 in Semprebon and Rivals (2010). Please note that hypsodont equids will likely always have higher hypsodonty indices than ruminants on a similar diet, due to differences in digestive physiology and ingestive mastication.

Merychippine-grade and "Derived Equinae" begin a relatively progressive increase in hypsodonty level in the middle Miocene (consistent with the crown heights of some closed- and open-habitat mixed feeders), the latter continuing that trend through the Pliocene and Pleistocene when they finally attain crown heights similar to extant open-habitat mixed feeders and regular grazers.

Figure 2B shows that camels appear in the Eocene and Oligocene (e.g., *Poebrotherium*) with hypsodonty indices that are somewhat greater than equids from those time periods and similar to those of either extant browsers or closed-habitat mixed feeders. Crown height increased in the early Miocene (particularly in stenomylines) to the level of some extant fresh grass grazers and open habitat mixed feeders. Crown heights were lower in the middle Miocene due to the extinction of some of the more hypsodont earlier forms (e.g., stenomylines) but then were higher beginning in the late Miocene in the camelines (no Pleistocene m3 hypsodonty data were available) only to decrease slightly in the Recent. The highest hypsodonty levels were attained by the stenomylines and camelines—often approaching that of extant open-habitat mixed feeders and regular grazers.

Figure 3A shows that the cheek teeth of antilocaprids were relatively hypsodont even in the earliest immigrant forms that appear in the late early Miocene—the "merycodontines"—and more hypsodont than the early Miocene camels, dromomerycids, and equids (**Figure 1B**)—at the level of some extant open-habitat mixed feeders and fresh-grass grazers. Like all three other North American families studied here, pronghorns show an increase in hypsodonty level in the late Miocene (**Figure 1B**). Hypsodonty levels remain high through the Pleistocene but decreased in the Recent.

Figure 3B shows that dromomerycids appear in North America in the early Miocene. While the more derived and cursorial aletomerycines appear with mesodont crown heights at this time almost at the level of some parahippine-grade equid taxa, the majority of dromomerycines (Dromomerycini and early Cranioceratini) have low-crowned teeth (similar to modern browsers) from the early-middle Miocene. Crown height decreases slightly in the middle Miocene and then increases (though not significantly) in later Cranioceratini to the level of some extant closed-habitat mixed feeders until they go extinct (in the early Pliocene). Hypsodonty data may be found in **Supplementary Table 1**.

Figure 3C shows that Merycoidodontids ("oreodonts") appear in North America in the Eocene (Oreonetinae and Merycoidodontinae) with low molar crown heights typical of extant regular browsers. As in fossil equids and camelids, the oreodonts begin to increase their crown height in the Oligocene [though the highly hypsodont *Sepsia nitida* (Leptaucheniinae) and the somewhat hypsodont *Leptauchenia major* (Leptaucheniinae) skew the trend curve up in **Figure 3C** as other merycoidodontids are not highly hypsodont at this time]. In the early Miocene, the dip in the graph (**Figure 3C**) is due to the extinction of the hypsodont leptauchinine clade followed by a small trend toward increasing crown height into the middle Miocene. Hypsodonty data for merycoidodontids is from Mihlbachler and Solounias (2006).

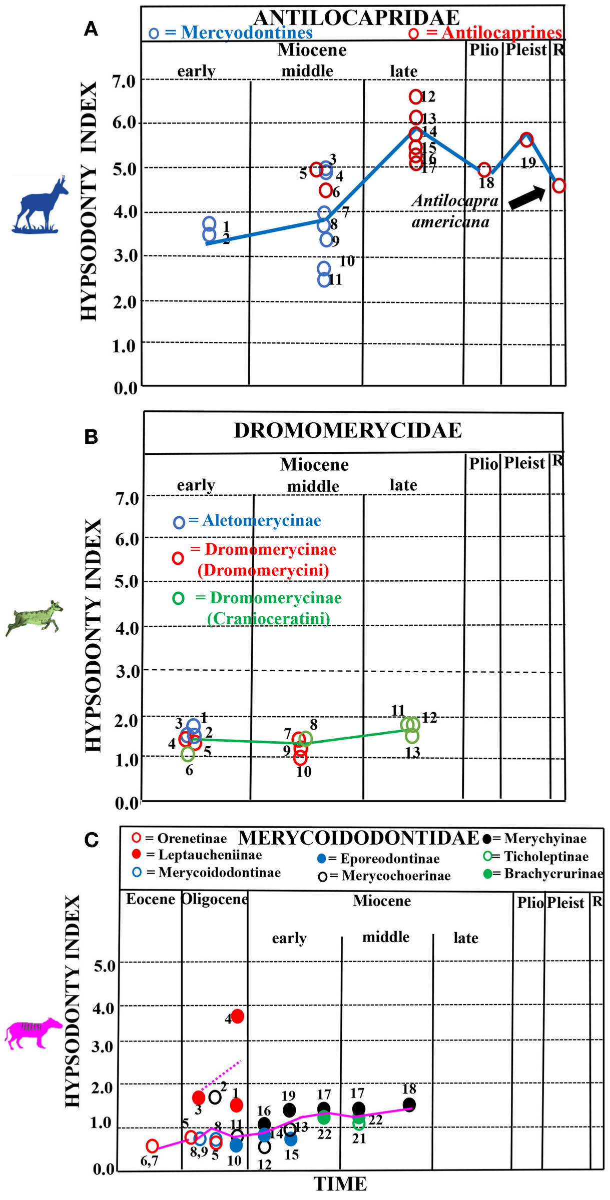

FIGURE 3 | Hypsodonty indices of fossil pronghorns, dromomerycids and oreodonts through time. **(A)** North American fossil pronghorns through time. Key to taxa: blue circles = merycodontines (1 = *Paracosoryx wilsoni,* 2 = *Paracosoryx alticornis,* 3 = *Cosoryx furcatus,* 4 = *Cosoryx cerroensis*, 7 = *Meryceros nenzelensis,* 8 = *Ramoceros ramosus,* 9 = *Ramoceros* sp., 10 = *Merycodus sabulonis*, 11 = *Merriamoceras coronatus*); red circles = antilocaprines 12 = *Hexabelomeryx* sp., 13 = *Ilingoceros* sp., 14 = *Texoceros guymonensis,* 15 = *Osbornoceras osborni*, 16 = *Plioceras dehlini*, 17 = *Hexabelomeryx* sp., 18 = *Capromeryx* sp., 19 = *Stockoceros* sp., 20 = *Antilocapra americana* (Recent)]. Blue solid line = hypsodonty index trendline. Unpublished fossil data from Christine Janis; Recent data from Janis (1988). **(B)** Hypsodonty indices of North American fossil dromomerycids through time (Unpublished fossil data from Christine Janis). Key to taxa: blue circles = Aletomerycinae (1 = *Aletomeryx marslandensis*, 2 = *Aletomeryx scotti*, 3 = *Sinclairomeryx riparius*); red circles = Dromomerycinae (Dromomerycini) (4 = *Subdromomeryx scotti,* 5 = *Barbouromeryx trigonocorneus,* 7 = *Dromomeryx whitfordi,* 9 = *Rakomeryx sinclairi,* 10 = *Drepanomeryx* sp.); green circles = Dromomerycinae (Cranioceratini)

(Continued)

FIGURE 3 | (6 = *Procranioceras skinneri,* 8 = *Bouromeryx* sp., 11 = *Pediomeryx hemphilliensis,* 12 = *Pediomeryx hamiltoni*, 13 = *Cranioceras granti*). Green, solid line = hypsodonty index trendline. **(C)** Hypsodonty data from North American fossil oreodonts through time (modified from **Figure 2** from Mihlbachler and Solounias, 2006). Key to taxa: closed red circles = Leptaucheniinae (1 = *Leptauchenia major,* 2 = *Leptauchenia decora,* 3 = *Leptauchia* sp., 4 = *Sespia nitida*); open red circles = Orenetinae (5 = *Oreonetes gracilis,* 6 = *Oreonetes chadronensis*, 7 = *Merycoidodon culbertsoni*, 8 = *Merycoidodon major*); open blue circles = Merycoidodontinae (9 = *Merycoidodon bullatus*); solid blue circles = Epororeodontinae (10 = *Eporeodon occidentalis,* 14 = *Merycoides harrisonensis,* 15 = *Merycoides longiceps*); open black circles = Merychochoerinae (11 = *Merychochoerus superbus,* 12 = *Merychochoerus chelydra*, 13 = *Merychochoerus* sp.); solid black circles = Merychyinae (16 = *Merychyus crabilli,* 17 = *Merychyus relictus*, 18 = *Merychyus medius*, 19 = *Merychyus elegans*; open green circles = Ticholeptinae (20 = *Ticholeptis zygomaticus*); solid green circles = Brachycrurinae (22 = *Brachycrus laticeps*. Locality information for numbered taxa as in Table 1 in Mihlbachler and Solounias, 2006). Pink, solid line = hypsodonty trendline for non-leptauchinines; dotted, pink line represents the trend for the relatively hypsodont leptauchinines.

Figure 1B displays relative hypsodonty trends through time of all five North American fossil ungulate families studied. **Figure 1B** shows that merycoidodontids and dromomerycids never attained levels of hypsodonty approached by antilocaprids, camelids and equids with the exception of *Sepsia nitida* (merycoidodontid). Also, equid hypsodonty eventually (in the late Miocene) far surpasses camelids and antilocaprids and equids alone remain at the crown height level of regular grazers from the late Miocene to the Recent.

Figures 4, **5** represent familial mesowear and microwear patterns plotted along a time axis. Symbols used to represent mesowear scores specify the dietary category assigned to each taxon based on microwear analysis (circles = leaf-dominated browsers, stars = regional or seasonal mixed feeders, squares = grazers).

EQUIDAE

Mesowear

Figure 4A shows that basal equids start off in the Eocene with slightly rounded cusps, but cusp apices gain in sharpness as the Eocene progresses. Mesowear values were lowest in the earliest Oligocene, suggesting very low abrasion feeding behavior at that time although this is followed by a change in the mesowear trend toward increased abrasion—however, abrasion is still fairly low. In the early Miocene, there is an increase in abrasion (higher mesowear values) and this increased abrasion sustained the progression toward a higher level of abrasion which started after the Eocene–Oligocene Transition. This trend toward greater abrasion continued into the Pliocene and Pleistocene. These mesowear results are mostly consistent with microwear dietary assignments. However, *Miohippus obliquidens* (Eocene), *Mesohippus bairdii* (Oligocene), *Mesohippus* sp. (Oligocene) and *Kalobatippus* sp. (middle Miocene) have unimodal, high scratch counts typical of extant grazers yet low mesowear scores typical of relatively low abrasion. When equid mesowear is compared to that of the other ungulate families studied (**Figure 6**), it is apparent that of those taxa that survived beyond the Miocene (i.e., equids, camelids, and antilocaprids), only the equids continued the trend toward higher dietary abrasion into the Pleistocene and Recent.

Microwear

The most basal early Eocene equids have microwear consistent with frugivory (e.g., many large, symmetrical puncture-like pits, scratch textures coarser than extant leaf browsers, as well as somewhat rounded gross cusp morphology) but a shift toward more leaf browsing and relatively fine scratch textures (**Figure 7**) (and sharper cusps) in the middle Eocene correlates with mesowear which shows less of a degree of dietary abrasion incurred toward the approach of the Eocene-Oligocene boundary. Microwear results in the early Miocene are consistent with the mesowear trend toward more abrasion at this time [i.e., scratch textures became coarser and gouging and large pitting in dental enamel increased (**Figure 8**)—even in browsing forms]. Microwear also shows grazing or mixed feeding in parahippine-grade taxa at this time which would add to the increased abrasion trend.

Unlike the camels, pronghorn, and dromomerycids (**Figure 6**), equid mesowear continued the trend in the middle Miocene toward greater abrasion that began after the Eocene-Oligocene Transition. The percentages of large pits in enamel (**Figure 8**) remained at a level seen in most extant grazers from the early Miocene onward. Most of this greater abrasion seen in the middle Miocene was due to the dietary patterns of the derived Equinae which were mostly grazing on more abrasive grasses with coarser scratch textures (**Figure 7**), whereas the merychippine-grade taxa were mostly mixed feeders on relatively low abrasion grasses and the Anchitherinae *sensu stricto* (e.g., *Archaeohippus*, *Hypohippus*, *Kalobatippus*, and *Megahippus*) had low abrasion browsing patterns. In the late Miocene, the relatively rare Anchitherinae *sensu stricto* continued their low abrasion browsing, while the derived Equinae continued coarser mixed-feeding or grazing and showed more pitting in dental enamel compared to the middle Miocene. This trend toward feeding on a coarser type of food persisted into the Pliocene as microwear shows a continuation of grazing as well as mixed feeding although total pit counts were higher than at any other time and scratch textures (**Figure 7**) were generally coarser. These results concur with the increased mesowear scores (higher abrasion) observed in mesowear at this time.

The trend toward higher microwear pit counts, that began in the late Miocene and Pliocene continued into the Pleistocene, with the greatest amount of pitting in Pleistocene species which is concordant with the high abrasion patterns seen in mesowear at this time although most *Equus* taxa exhibited dietary flexibility—alternating between browse and grass and scratch textures diminished slightly (**Figure 7**) and pitting of enamel surfaces decreased in the Recent.

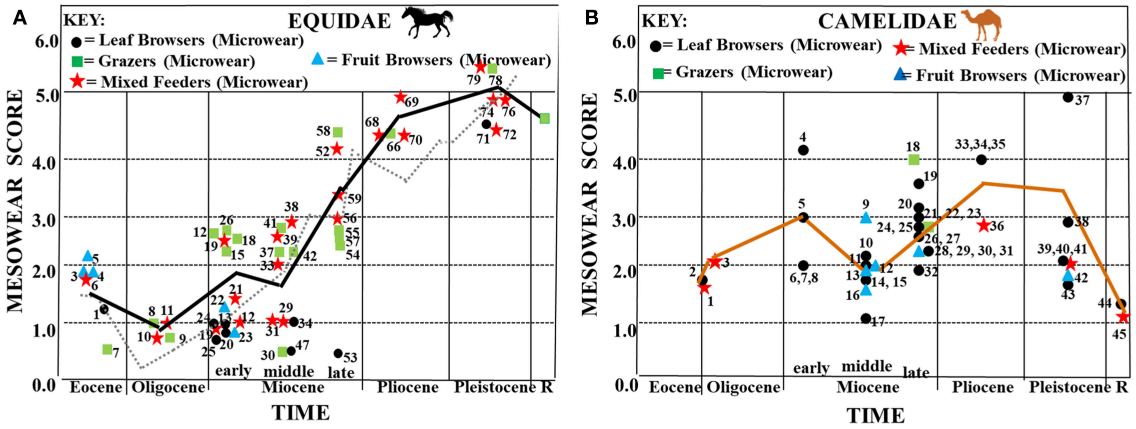

FIGURE 4 | Synthesis of mesowear and microwear results for fossil equids (A) and camelids (B) plotted along a time axis. **(A)** Average mesowear scores for each equid taxon (mesowear scores from Mihlbachler et al., 2011) are shown plotted along a horizontal axis representing geological time. Symbols used for each mesowear score represent dietary assignment assessed via microwear (data from Semprebon et al., 2016). Key to microwear dietary assignment: circles = browsers, squares = grazers, stars = seasonal or regional mixed feeders. Black trend line = mesowear trend line using the same taxa from the same localities that had both mesowear and microwear data available (*N* = 72). Gray dotted line = mesowear trend line for those taxa with only mesowear scores available (*N* = 6,498). Key to taxa: 1 = Basal Eocene equid—Species A, 2 = Basal Eocene equid—Species B, 3 = Basal Eocene equid—Species C, 4 = Basal Eocene equid—Species D, 5 = Basal Eocene equid—Species E, 6 = *Mesohippus* sp., 7 = *Miohippus obliquidens*, 8 = *Mesohippus bairdii*, 9,11 = *Mesohippus* sp., 10 = *Mesohippus westoni*, 12, 16, 17 = *Parahippus nebrascensis*, 13 = *Kalobatippus agatensis*, 14 = *Kalobatippus* sp., 15, 18, 30, 31 = *Parahippus* sp., 19 = *Parahippus leonensis*, 20, 21 = *Parahippus pawniensis*, 22 = *Archaeohippus blackbergi*, 23 = *Archaeohippus penultimus*, 24 = *Hypohippus* sp., 25 = *Kalobatippus* sp., 26 = *Merychippus primus*, 27 = *Acritohippus tertius*, 28 = *Parahippus avus*, 29 = *Parahippus integer*, 32, 33, 53 = *Hypohippus* sp., 34, 35, 43 = *Megahippus* sp., 36 = "*Merychippus*" *goorisi*, 37 = *Merychippus insignis*, 38 = *Scaphohippus intermontanus*, 39 = *Acritohippus isonesus*, 40 = *Acritohippus tertius*, 41 = *Calippus proplacidus*, 42 = *Protohippus perditus*, 44, 45 = "*Merychippus*" *calamarius*, 46 = *Cormohipparion quinni*, 47 = *Megahippus matthewi*, 48 = *Pseudhipparion retrusum*, 49 = *Protohippus supremus*, 50 = *Cormohipparion occidentale*, 51, 54 = *Calippus martini*, 52 = *Pseudhipparion hessei*, 55 = *Cormohipparion occidentale*, 56 = *Hipparion tehonense*, 57, 60 = *Dinohippus leidyanus*, 58 = *Dinohippus* sp., 59 = *Dinohippus interpolatus*, 61 = *Dinohippus* sp., 62 = *Nannipus aztecus*, 63 = *Pseudhipparion simpsoni*, 64 = *Neohipparion eurystyle*, 65 = *Cormohipparion emsliei*, 66, 67 = *Equus simplicidens*, 69, 71, 72, 74, 78 = *Equus* sp., 70 = *Nannipus peninsulatus*, 73 = *Equus* (*Hemionus*) sp. "B," 75 = *Equus calobatus*, 76 = *Equus complicatus*, 77 = *Equus fraternus*, 79 = *Equus pacificus*. Key to localities as in Semprebon et al. (2016) Table 1. **(B)** Synthesis of mesowear and microscopic microwear results for fossil camelids plotted along a time axis. Average mesowear scores for each taxon are shown plotted along a horizontal axis representing geological time. Symbols used for each mesowear score represent dietary assignment assessed via microwear (microwear and mesowear data from Semprebon and Rivals, 2010). Key for microwear dietary assignment: circles = browsers, squares = grazers, stars = seasonal or regional mixed feeders. Orange trend line = mesowear trend line using the same taxa from the same localities that had both mesowear and microwear data available (*N* = 45). Key: 1, 2 = *Poebrotherium* sp., 3 = *Poebrotherium wilsoni*, 4 = *Stenomylus hitchcocki*, 5, 9, 15, 16 = *Aepycamelus* sp., 6 = *Michenia* sp., 7, 8, 17 = *Protolabis* sp., 10 = *Paramiolabis singularis*, 11 = *Aepycamelus proceras*, 12, 13, 20, 26, 27, 29 = *Procamelus* sp., 14 = *Miolabis princetonianus*, 18, 19, 21, 22, 33, 34 = *Megatylopus* sp., 23 = *Machaerocamelus* sp., 24 = *Procamelus occidentalis,* 25, 30, 31, 32, 36 = *Hemiauchenia* sp., 28 = *Megacamelus* sp., 35 = *Gigantocamelus spatula*, 37, 38, 39 = *Camelops* sp., 40 = *Hemiauchenia macrocephala*, 41 =*Camelops nevadanus*, 42, 43 = *Palaeolama mirifica,* 44 = *Camelus dromedarius*, 45 = *Lama vicugna.* Key for localities as in Semprebon et al. (2016)—Table 1.

CAMELIDAE

Mesowear

Figure 4B shows increasing mesowear scores (a rise in abrasion) from the late Eocene/early Oligocene to the early Miocene. Camelid dietary abrasion decreased in the middle Miocene but then changed to more abrasion through the late Miocene, Pliocene and most of the Pleistocene. In the late Pleistocene, a large shift toward less abrasion occurred that continued into the Recent. When camelids are compared to the other ungulate fossil families studied (**Figure 6**), the relatively high abrasion pattern begun in the late Miocene (which is equivalent to many extant mixed feeders and grazers) is reversed toward relatively low abrasion in the later Pleistocene into the Recent (unlike the pattern in equids).

Microwear

Unlike equids, that begin the Eocene as browsers in closed habitats, late Eocene-early Oligocene camels show microwear evidence of some mixed feeding and significantly more pitting. This is congruent with camelids occupying relatively more open habitats than the equids at this time, a pattern consistent with the much longer legs and higher mesowear scores found in early camels than in the other families studied here. Scratch textures in the Eocene-Oligocene camelids are also relatively coarse (**Figure 7**) contributing to the relatively high abrasion indicated by heavy pitting and fairly high mesowear scores.

Early Miocene fossil camels have microwear results indicating browsing but with heavy enamel pitting consistent with the higher mesowear scores at this time (especially *Stenomylus hitchcocki*). Scratch textures (**Figure 7**) become finer (decreased scratch widths) in the early Miocene which is consistent with a switch from some grass consumption in the Eocene/Oligocene to pure browsing in the Early Miocene. A somewhat lower abrasion browsing pattern (fewer pits overall) is seen in the middle Miocene which correlates with the decrease in mesowear seen then—although scratch textures increase slightly (**Figure 7**). The increased mesowear scores in the late Miocene are accompanied

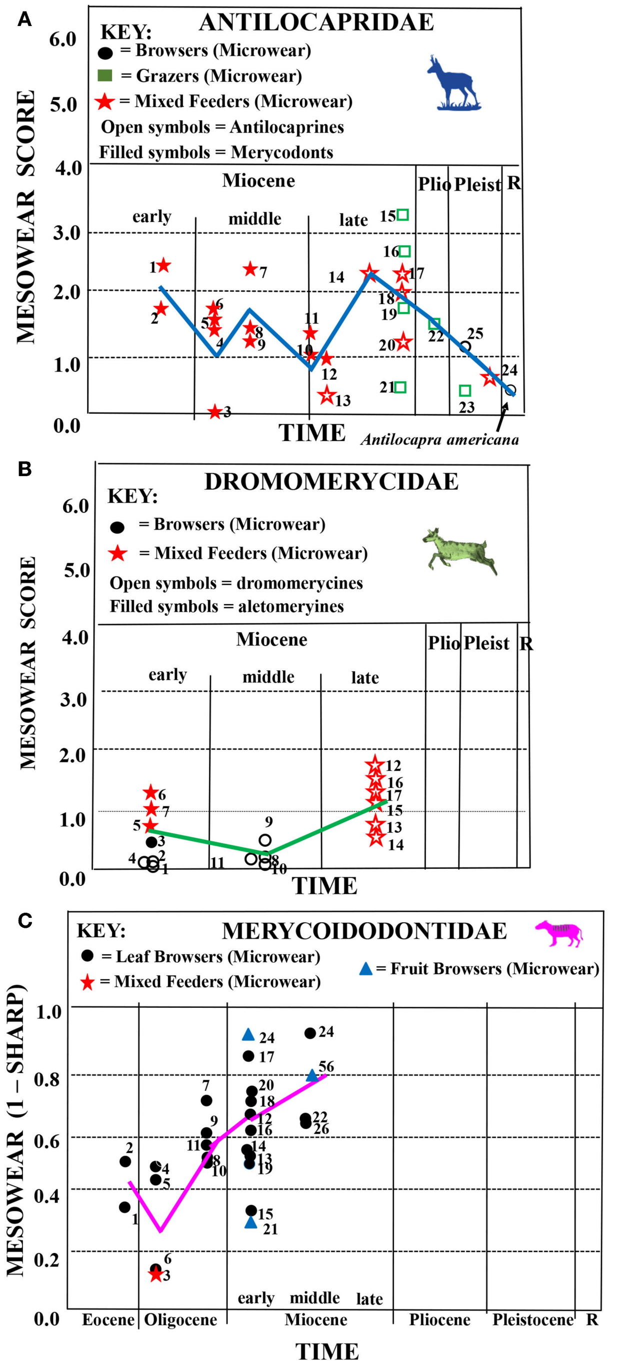

FIGURE 5 | Synthesis of mesowear and microscopic microwear results for fossil antilocaprids, dromomerycids and merycoidodontids plotted along a time axis. **(A)** Antilocaprids: average mesowear scores for each taxon are shown plotted along a horizontal axis representing geological time. Symbols used for each mesowear score represent dietary assignment assessed via microwear (microwear and mesowear data from Semprebon and Rivals, 2007). Key for microwear dietary assignment: circles = browsers, squares = grazers, stars = seasonal or regional mixed feeders. Blue trend line = mesowear trend line using the same taxa from the same localities that had both mesowear and microwear data available (*N* = 26). Key: *"Merycodontinae"*—1 = *Paracosoryx dawesensis*, 2 = *Paracosoryx wilsoni*, 3, 4 = *Merriamoceros coronatus,*

(Continued)

FIGURE 5 | 5 = *Paracosoryx alticornis*, 6 = *Merycodus sabulonis*, 7 = *Meryceros joraki*, 8 = *Ramoceros* sp., 9 = *Paracosoryx alticornis*, 10, 11 = *Cosoryx furcatus,* 12 = *Cosoryx cerroensis*. *Antilocaprinae*—13 = *Proantilocapra platycornea*, 14 = *Plioceros dehlini*, 15 = *?Hexobelomeryx,* 16 = *Ilingoceros alexandrae*, 17 = *Osbornoceros osborni*, 18 = *Texoceras guymonensis*, 19 = *"Plioceros" texanus*, 20 = *cf. Sphenophalos*, 21 = *Ilingoceros alexandrae*, 22 = *Tetrameryx* sp., 23 = *Hayoceros falkenbachi*, 24 = *Stockoceros onusrosagris*, 25 = *Capromeryx furcifer*. Key to localities as in Semprebon and Rivals (2007)—Table 2. **(B)** Dromomerycids: synthesis of mesowear and microscopic microwear results for fossil dromomerycids plotted along a time axis. Average mesowear scores (previously unpublished) for each taxon are shown plotted along a horizontal axis representing geological time. Symbols used for each mesowear score represent dietary assignment assessed via microwear (microwear data from Semprebon et al., 2004). Key for microwear dietary assignment: circles = browsers, squares = grazers, stars = seasonal or regional mixed feeders. Green trend line = mesowear trend line using the same taxa from the same localities that had both mesowear and microwear data available (*N* = 14). Key: 1= *Barbouromeryx* sp., 2 = *Bouromeryx pawniensis*, 3 = *Dromomeryx* (*Subdromomeryx*) *scotti*, 4 = *Procranioceras skinneri*, 5 = *Aletomeryx gracilis*, 6 = *Aletomeryx scotti*, 7 = *Sinclairomeryx riparius*, *Dromomeryx whitfordi*, 9, 10 = *Drepanomeryx* (*Matthomeryx*) sp., 11 = *Rakomeryx sinclairi*, 12 = *Cranioceras clarendonensis*, 13 = *Cranioceras unicornis*, 14 = *Pediomeryx hamiltoni*, 15,16 = *Pediomeryx hemphilliensis*, 17 = *Pediomeryx* (*P.*) sp. **(C)** Merycoidodontids: synthesis of mesowear and microscopic microwear results for fossil merycoidodontids plotted along a time axis. Mesowear is represented as the proportion of cusps in a taxon that are not sharp (i.e., are rounded or even blunt) and were obtained from Mihlbachler and Solounias (2006) and derived in this study be subtracting the proportion of sharp cusps from 1.00. Mesowear for each taxon is plotted along a horizontal axis representing geological time. Symbols represent dietary assignment assessed via microwear (unpublished microwear data from GS). Key for microwear dietary assignment: circles = browsers, squares = grazers, stars = seasonal or regional mixed feeders. Pink trend line = mesowear trend line using the same taxa from the same localities that had both mesowear and microwear data available (*N* = 26). Key: 1 = *Orenetes chadronensis* (Oreonetinae), 2 = *Merycoidodon culbertsoni* (Merycoidodontinae), 3 = *Leptauchenia* sp. (Leptaucheniinae) *(L. decora)*, 4 = *Merycoidodon bullatus* (Merycodoidodontinae), 5 = *Merycoidodon major* (Merycodoidodontinae), 6 = *Orenetes gracilis* (Oreonetinae), 7 = *Sepsia nitida* (Leptaucheniinae), 8 = *Leptauchenia major,* (Leptaucheniinae), 9 = *Eporeodon occidentalis* (Eporeodontinae), 10 = *Merycochoerus superbus superbus* (Merycochoerinae), 11 = *Merycochoerus superbus* (Merycochoerinae), 12 = *Hypsiops breviceps breviceps* (Merycochoerinae), 13 = *Merychyrus crabilli* (Merychyinae), 14 = *Merycoides harrisonensis harrisonensis* (Eporeodontinae), 15 = *Merycochoerus chelydra carrikeri* (Merycochoerinae), 16, 17 *Merychyus elegans arenarum* (Merychyinae), 18 = *Merychochoerus* sp. (Merycochoerinae), 19 = *Merychyus* sp. (Merychyinae), 20 = *Merychyus relictus* (Merychyinae), 21 = *Brachycrus laticeps buwaldi* (Brachycrurinae), 22 = *Merychyus relictus* (Merychyinae), 23 = *Brachycrus laticeps buwaldi* (Brachycrurinae), 24 = *Ticholeptus zygomaticus* (Ticholeptinae), 25 = *Brachycrus laticeps siouense* (Brachycrurinae), 26 = *Merychyus medius medius* (Merychyinae).

by microwear results indicating a shift toward some mixed feeding and occasional grazing in addition to browsing with heavy pitting of enamel. The relatively high mesowear scores in the Pliocene and Pleistocene camels match the heavy enamel pitting found in the browsing, mixed feeding and grazing taxa from this time period as well as an increase in scratch widths (**Figure 7**). The modern camelids (Recent) have lower mesowear scores than the fossil camelids even though hypsodonty levels are different (i.e., *Lama vicugna* has more hypsodont dentition than *Camelus dromedarius* but both have similar mesowear

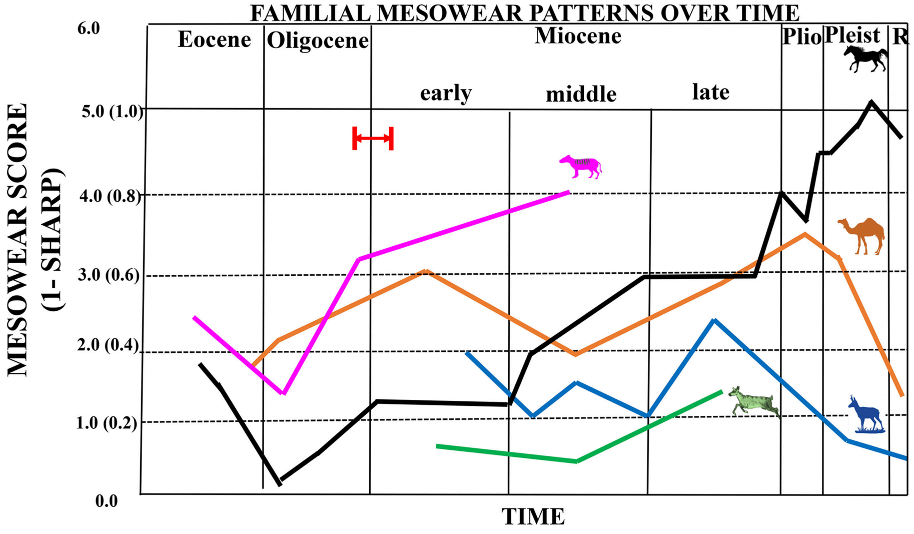

FIGURE 6 | Composite figure showing mesowear trends through time for equids (black line), antilocaprids (blue line), camelids (orange line), dromomerycids (green line), and oreodonts (pink line). Equid, camelid, antilocaprid, and dromomerycid trends reflect a graphical display of average mesowear scores (scores that combine cusp shape with occlusal relief) for taxa in a particular time period (0–6); merycoidodontid trend reflects cusp shape only (i.e., the proportion of cusps that are not sharp, 0–1.0). Red arrow and red lines indicate probable timing of first availability of grass in the North American Great Plains Region by ~22 million years ago (earliest Miocene), but possibly by even about 26 million years ago (latest Oligocene) based on phytolith data from Strömberg (2011).

scores), suggesting that fossil camels have a more abrasive diet than the modern camels studied. Scratch widths (**Figure 7**) also decrease in the Recent further substantiating that modern camels encounter less abrasion in their diets than fossil forms. Interestingly, camelids display many individuals in each taxon with large pits in their enamel (**Figure 8**) for most of their evolutionary history only declining in the Pleistocene and Recent even though most of them have microwear patterns similar to modern dirty browsers (i.e., a grit effect).

ANTILOCAPRIDAE

Mesowear

Figure 5A shows that antilocaprids begin the Miocene with somewhat rounded cusps and then shift toward higher mesowear scores indicating more abrasive diets starting in the late Hemphillian (late Miocene–Pliocene). After this, they reverse toward a less abrasive diet starting in the Pliocene and continuing through the Pleistocene into the Recent. Antilocaprids (like camelids) had relatively long legs and were rather hypsodont when they first appeared and were well-suited to exploit open habitats. When antilocaprids are compared to the other fossil ungulate families studied here (**Figure 6**), it is apparent that they followed a similar pattern to that seen in fossil camelids in terms of reducing overall abrasion as they moved into the Recent [although pronghorns apparently reduced their level of abrasion a bit earlier (i.e., in the Pliocene)] than camelids.

Microwear

Like the camelids but unlike equids, the earliest and more primitive merycodonts have microwear results consistent with browsing and grazing on a seasonal or regional basis but with far less pitting overall than camelids and finer scratch textures (narrower scratches) (**Figure 7**) which explains the relatively low mesowear scores in antilocaprids (less abrasion) at this time. Like the other families studied here, overall abrasion increased (**Figure 6**) in the late Miocene (i.e., mesowear) when the more derived antilocaprines apparently engaged in more grass consumption although scratch textures (**Figure 7**) indicate a diet that was not highly abrasive. As seen in the camelids and dromomerycids (but not in equids), antilocaprids decreased dietary abrasion (**Figure 6**) in the Pliocene and Pleistocene into the Recent (the modern *Antilocapra americana* eats mostly low-level browse in an open habitat). This decrease in abrasion is consistent with the decrease in scratch widths in the Recent seen in **Figure 7**. Interestingly, like camelids, antilocaprids have relatively large numbers of individuals per taxon that display large pits in their enamel (**Figure 8**), about the level of extant grazers, for most of their evolutionary history regardless of dietary assignment via microwear.

DROMOMERYCIDAE

Mesowear

Figure 5B shows that the dromomerycids have relatively low abrasion mesowear scores in the early Miocene which dip down further in the middle Miocene and then begin to climb in the late Miocene to the level of some extant mixed feeders. Dromomerycids experienced the lowest levels of abrasion throughout their evolutionary history when compared to abrasion levels (mesowear) in the other families studied here (**Figure 6**).

Microwear

The early Miocene low abrasion mesowear results parallel microwear results as the earliest dromomerycids

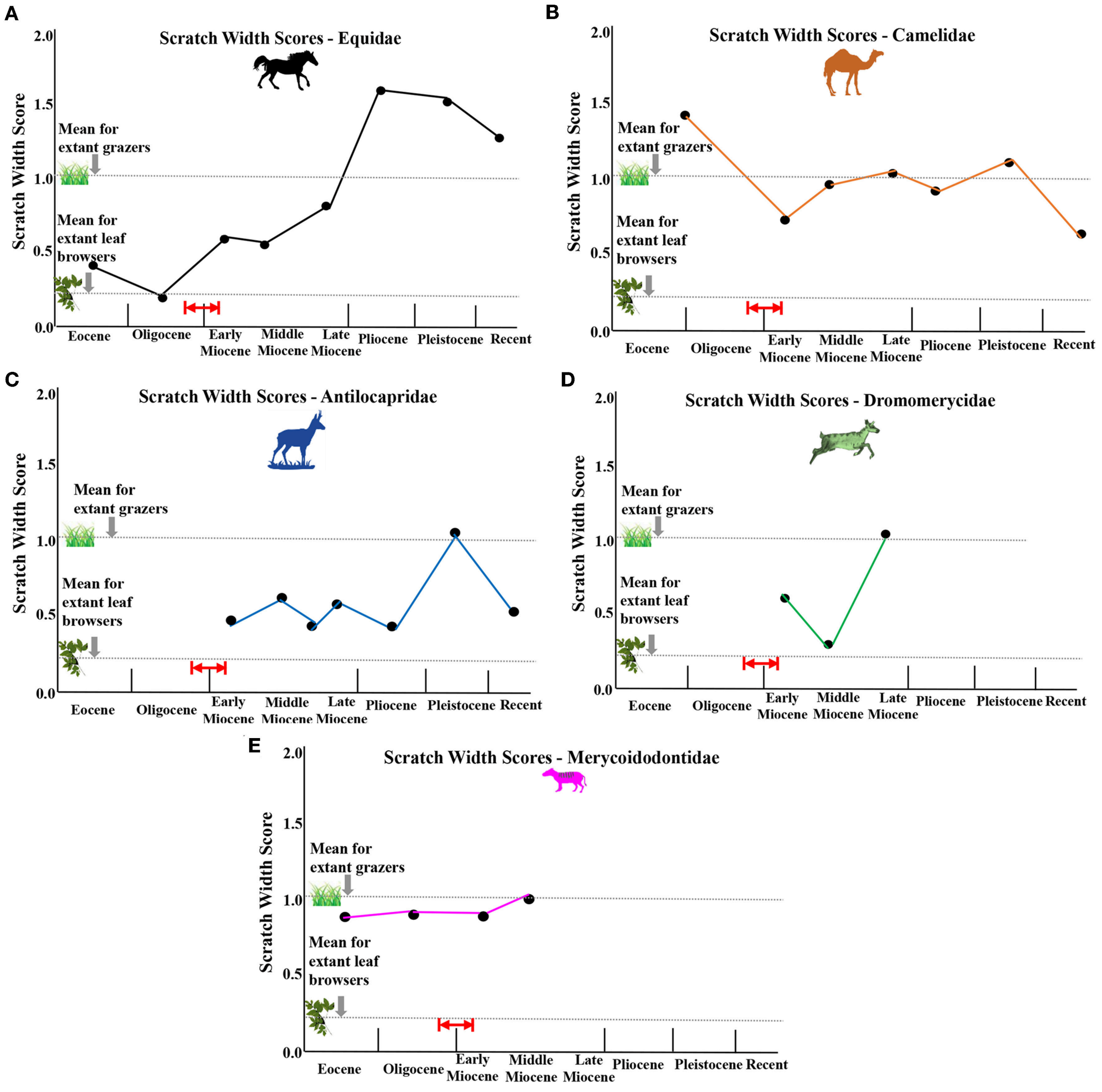

FIGURE 7 | Average scratch width scores (sws) for each fossil family plotted over evolutionary time. **(A)** equids, **(B)** camelids, **(C)** antilocaprids, **(D)** dromomerycids, **(E)** merycoidodontids. Red arrow and red lines indicate probable timing of first availability of grass in the North American Great Plains Region by ∼22 million years ago (earliest Miocene), but possibly by even about 26 million years ago (latest Oligocene) based on phytolith data from Strömberg (2011).

(Dromomerycinae—Dromomerycini) have microwear similar to fine browsers [i.e., many finely-textured scratches and relatively few pits (including little or no large pits)]. In the late early Miocene, the Aletomerycinae appear with limb proportions suggestive that they occupied open/ecotonal habitats and microwear indicating seasonal or regional mixed feeding. Aletomyerycinae start off in the late early Miocene with fairly high scratch textures. The relatively large percentages of individuals displaying large pits (**Figure 8**) in the late early Miocene are confined to the more open country and mesodont Aletomerycinae. From the early-middle Miocene, the majority of dromomerycids were low abrasion browsers (scratches were also relatively fine and narrow—**Figure 7**) but in the late Miocene, increased mesowear scores are mirrored by the more derived Cranioceratini (subfamily Dromomerycinae) which show evidence of alternating between browsing and grazing but with many individuals displaying large pits (**Figure 8**) and a prodigious level of enamel surface gouging as well many coarse scratches (**Figure 7**) compared to what is typically found in extant mixed feeders (i.e., a grit effect).

MERYCOIDODONTIDAE

Mesowear

Figure 5C shows mesowear trends through time in fossil merycoidodontids. Mesowear was obtained from Mihlbachler and Solounias, 2006. In this study, mesowear was graphically

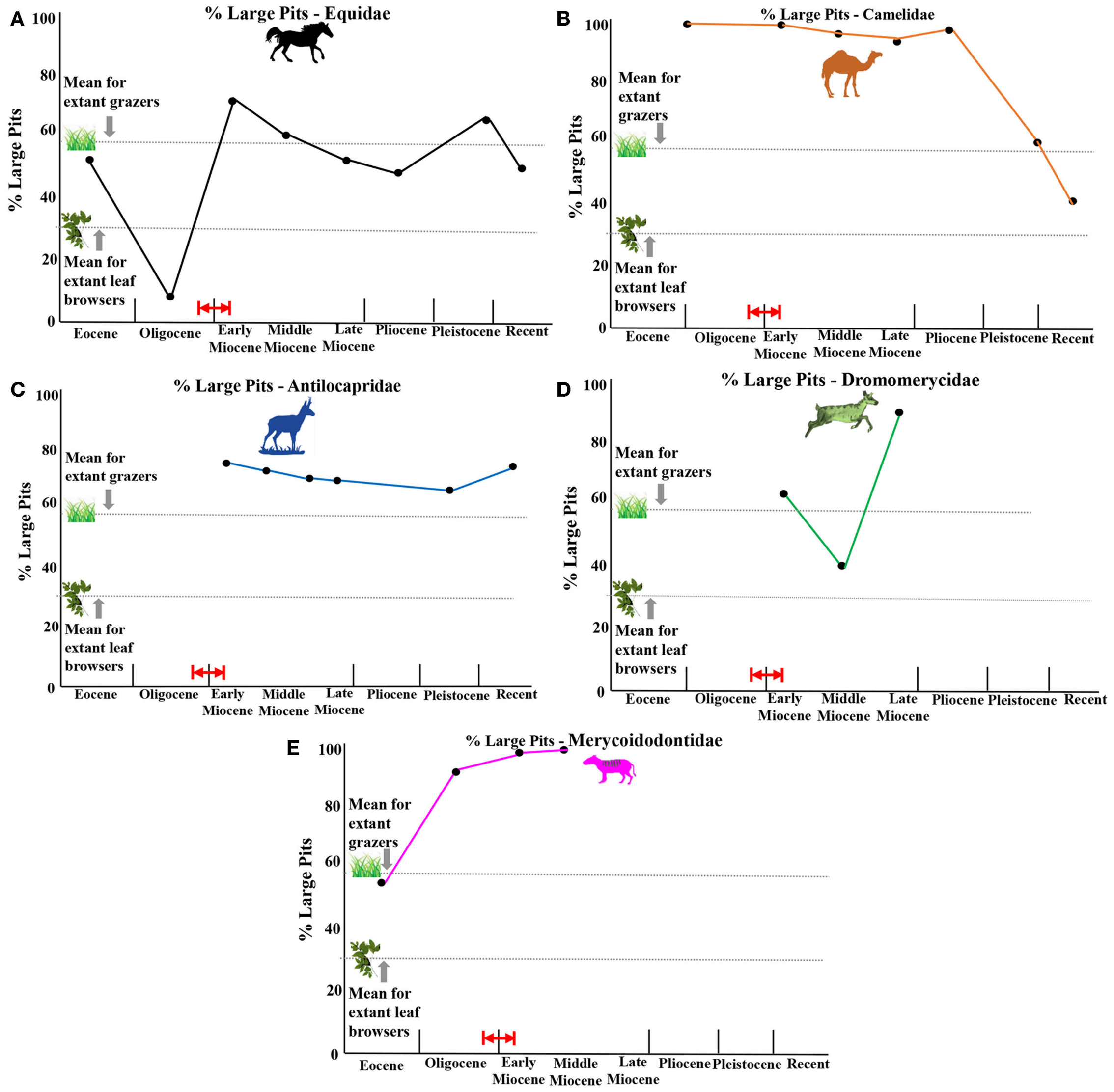

FIGURE 8 | Average percentages of individuals per taxa in each time period that display large enamel pits (averages for extant ungulates from Semprebon, 2002). **(A)** equids, **(B)** camelids, **(C)** antilocaprids, **(D)** dromomerycids, **(E)** merycoidodontids. Red arrow and red lines indicate probable timing of first availability of grass in the North American Great Plains Region by ∼22 million years ago (earliest Miocene), but possibly by even about 26 million years ago (latest Oligocene) based on phytolith data from Strömberg (2011).

portrayed as the inverse proportion of sharp cusp apices (1-sharp) rather than via comparison with the mesowear ruler which gives a mesowear score that is a combination of cusp shape and occlusal relief. Even so, higher values represent more abrasion wear and can be used to demonstrate changes in abrasion over evolutionary time. **Figure 5C** demonstrates that early merycoidodontids (Eocene and early Oligocene) display low abrasion (similar to extant browsers) but this trend reverses beginning in the late Oligocene and continues as an increasing abrasion trend into the middle Miocene with some taxa showing abrasion similar to that of extant mixed feeders and some non-extreme grazers. It is not possible to compare merycoidodontid mesowear in terms of magnitude of abrasion to other fossil ungulate families studied herein (**Figure 6**) because mesowear scoring systems were somewhat different although overall relative similarities and differences in trends can be discerned.

Microwear

Figure 5C shows that merycoidodontids relied mainly on a browsing dietary strategy throughout their evolutionary time. Even so, scratch textures (**Figure 7**) and percentages of individuals displaying large pits in their enamel (**Figure 8**) are well above typical modern leaf browsers. The higher crowned Leptauchiniinae (**Figure 3C**) are interesting in that *Leptauchenia decora* (early Oligocene) apparently engaged in seasonal or regional mixed feeding while the highly hypsodont *Sepsia nitida* apparently browsed (late Oligocene). Miocene merycoidodontids (most taxa) have microwear patterns that demonstrate committed leaf browsing or an alteration between leaves and fruit (*Brachycrus* species).

Figure 8 depicts a summary of the average percentage of large pits found in the enamel of the five fossil ungulate families relative to each other through evolutionary time shown in relation to the mean score for extant browsers (typically with low percentages of large pits) and extant grazers (typically with higher percentages of large pits). A preponderance of large pits reflects either an increased amount of fruit and/or seed consumption (puncture-like, symmetrical large pits) or an increased exposure to grit coating food substances—the latter presumably due to feeding close to the ground (Solounias and Semprebon, 2002). Equidae (**Figure 8A**) begin the Eocene with increased large pits due mostly to frugivory (see **Figure 4A**) and then decrease the amount toward the Eocene-Oligocene transition as more leaf browsing and low abrasion grass consumption is apparent. During the early Miocene, large pitting increases to the level of extant ungulate grazers and remains at this relatively high level until the recent (grit effect).

The Camelidae (**Figure 8B**) display very high levels of large pits from the Eocene through the Pliocene (above the mean of extant grazers even though most of them are clearly browsing) and then show a rather precipitous decline. Antilocaprids (**Figure 8C**) show a very consistent level of large pitting (above the level of extant grazers—even though most of them are mixed feeding and eventually browsing). The dromomerycid large pit mean percentage is high in the early Miocene but this is mostly skewed high due to the large percentages of large pits found in the more open habitat, mixed feeding aletomerycines. The majority of dromomerycines (**Figure 8D**) (browsers) in the early Miocene have relatively low numbers of large pits. What is striking is the extreme level of large pitting encountered in the enamel of the late Miocene Cranioceratini before they go extinct in the Pliocene. The merycoidodontines (**Figure 8E**) show large percentages of individuals with large pits within taxa on average from their beginning in the Eocene and increasing to levels comparable to what is seen in the camelids.

Figures 9–13 summarize microwear average scratch vs. pit results for each family by plotting each family in the same time period and arranging results in chronologic order (data are shown in **Supplementary Tables 1,2**). Data in **Figures 9–13** are plotted using Gaussian confidence ellipses ($p = 0.95$) on the centroid as a reference for extant browser (B) and grazer (G) data which were also adjusted by sample size. Data are from Semprebon (2002) and Solounias and Semprebon (2002) . Dietary assignments given to mixed feeders which may fall within the browsing average scratch/pit ecospace (browse-dominant mixed feeders), grazing ecospace (grass-dominant mixed feeders), or in the gap between browsers and grazers (fairly equal browsing and grazing behavior) are based on raw scratch distributions as described in the relevant publications noted in figure captions from which data were obtained. The designation of fruit browser was based on percentages of large pits, puncture-like large pits, and coarser scratch textures than leaf browsers (see relevant publications noted in figure captions for details). **Figure 9** shows average pit vs. average scratch numbers for Eocene-Oligocene fossil equids, camelids, and merycoidodontids. Most fossil equids (**Figure 9A**) apparently engaged in both leaf and fruit browsing but *Miohippus obliquidens*, *Mesohippus bairdii*, and *Mesohippus* sp. displays unimodal and high scratch results (but finely textured unlike modern grazers) which is incongruent with the gross morphology of their teeth, their mesowear, and low overall rate of wear and may thus possibly reflect an abrasive element in their diet other than grass. Camelids and merycoidodontids were engaging in an unusual type of browsing and mixed feeding – exceptionally high pitting characteristic of open habitat "dirty" browsers and mixed feeders (i.e., significant grit effect).

For most time periods, the four families occupied mostly disparate niches with the exception of the late Miocene when all four families had a number of taxa engaging in varying levels of grass consumption—although the camelids (**Figure 9B**) were engaging in mainly browsing at this time as they apparently did for most of their evolutionary history. The camelids also were committed "dirty browsers" through most of their evolution—showing relatively extremely high total pit counts consistent with exposure to grit. None of the relatively low-crowned dromomerycids (**Figures 10B**, **11D**, **12D**) were pure grazers at any time in their past whereas the other families that had mesodont and hypsodont representatives engaged in grazing or alternating between grass and browse. In addition, equids appear to have consistently showed the greatest overall flexibility in their dietary behavior. Contrary to what is often assumed, Plio-Pleistocene equids were not restricted in their dietary regimes at this time but show a level of dietary breadth that may reflect more seasonal variation in diet.

Figure 10 shows average pit vs. average scratch numbers for early Miocene fossil equids, camelids, antilocaprids, dromomerycids, and merycoidodontids. Once again, equids (**Figure 10A**) show a diverse array of dietary behavior with some forms engaging in leaf browsing, some in fruit browsing, some alternating between browse and grass, and some grazing. Camelids (**Figure 10B**) and merycoidodontids (**Figure 10D**) continue mainly dirty browsing while antilocaprids (**Figure 10C**) are mixed feeders and dromomerycids (**Figure 10D**) are either leaf browsers or mixed feeders.

Figure 11 shows comparative average pit vs. average scratch numbers for middle Miocene fossil families. The equids (**Figure 11A**) show fairly balanced numbers of browsers, mixed feeders and grazers, while the camelids (**Figure 11B**) and merycoidodontids (**Figure 11E**) continue dirty browsing and some fruit browsing. Dromomerycids (**Figure 11D**) concentrated on pure browsing at this time, while antilocaprids were mostly alternating between browse and mixed feeding but also engaging in limited browsing and grazing.

Figure 12 shows average pit vs. average scratch numbers for late Miocene fossil families. All four families depicted in **Figure 12** show shifts toward more grass consumption than what was seen earlier in the Miocene. Only the camelids (**Figure 12B**) continue with mostly dedicated browsing (although high abrasion, dirty browsing). Equid (**Figure 12A**) mixed feeders are now closer to the grazing ecospace indicating more grass-dominated mixed feeding than antilocaprids (**Figure 12C**)

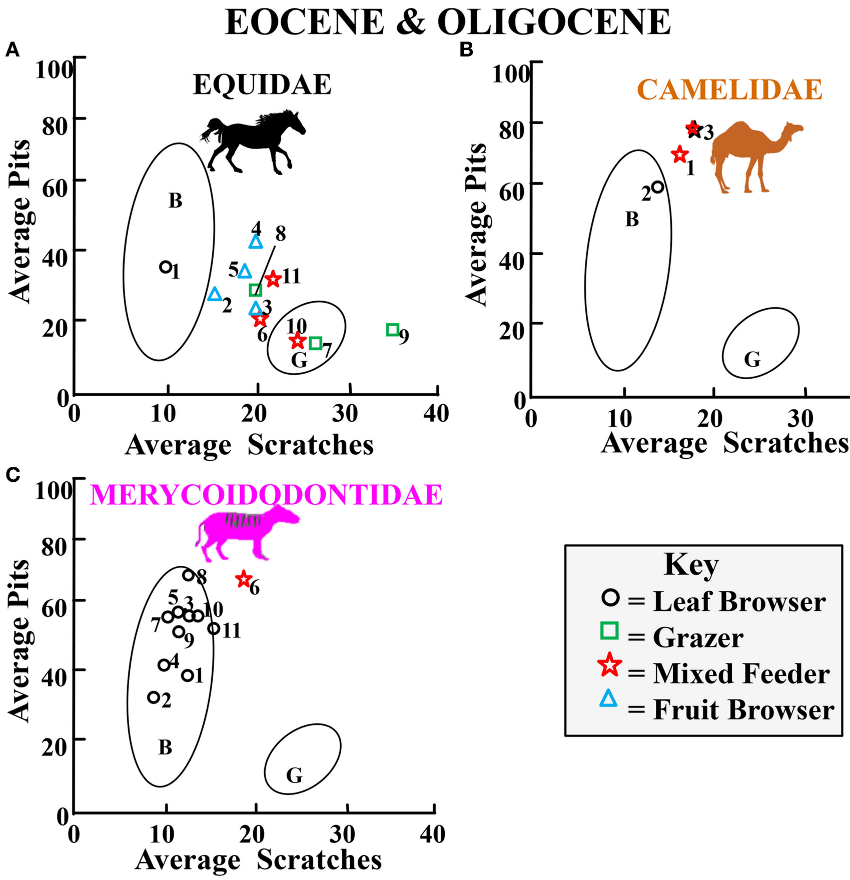

FIGURE 9 | Bivariate plot showing results for the average number of pits vs. the average number of scratches per taxon for Eocene and Oligocene fossil equids **(A)**, camelids **(B)**, and merycoidodontids **(C)** plotted in reference to extant leaf dominated ungulate browsers (B), and extant grazers (G) at 35 times magnification (extant comparative data from Semprebon, 2002 and Solounias and Semprebon, 2002). Gaussian confidence ellipses ($p = 0.95$) on the centroid are indicated for the extant leaf browsers and grazers (convex hulls) adjusted by sample size. Key to Equidae: (as in **Figures 3**, **4**) Semprebon et al. (2016)–1 = Species A, 2 = Species B, 3 = Species C, 4 = Species D, 5 = Species E, 6 = *Mesohippus* sp., 7 = *Miohippus obliquidens*, 8 = *Mesohippus bairdii*, 9 = *Mesohippus* sp., 10 = *Mesohippus westoni*, 11 = *Mesohippus* sp.. Key to Camelidae: 1,2 = *Poebrotherium* sp., 3 = *Poebrotherium wilsoni*. Key to Merycoidodontidae: 1 = *Orenetes gracilis chadronensis*, 2 = *Merycoidodon culbertsoni*, 3 = *Merycoidodon bullatus*, 4 = *Orenetes gracilis*, 5 = *Merycoidodon major*, 6 = *Leptauchenia decora*, 7 = *Sepsia nitida*, 8 = *Leptauchenia major*, 9 = *Eporeodon occidentalis*, 10 = *Merycochoerus superbus superbus*, 11 = *Merycochoerus superbus*.

or dromomerycids (**Figure 12D**). Also, equids and antilocaprid mixed feeders and equid mixed feeders and grazers show more pitting than earlier in the Miocene, indicating exposure to more grit during feeding.

Figure 13 shows average pit vs. average scratch numbers for Pliocene and Pleistocene fossil families. In the Pliocene and Pleistocene, there is a continuation of relatively high abrasion (i.e., heavy pitting) mixed feeding and grazing in equids (**Figures 13A,D**), high abrasion browsing and grazing in camelids (**Figures 13B,E**) and relatively lower abrasion browsing and grazing in antilocaprids (**Figures 13C,D**).

DISCUSSION

In this study, we examined the relative contributions of exogenous abrasives as a driving force in ungulate tooth evolutionary changes using a combination of dietary proxies (hypsodonty index, mesowear and microwear) with different temporal resolution capabilities to shed light on the amounts of different levels of abrasion imposed on molar teeth over evolutionary time and the potential causes of this abrasion.

The evolution of the Equidae has provided much fuel for the paleoecology fire. The rather dramatic craniodental and locomotory modifications of the late early Miocene radiation of horses (Equinae) prompted Simpson (1951) to call this the time of "the great transformation". Such changes (e.g., changes in craniodental proportions, cementum-covered, and hypsodont dentition, locomotory changes, and increased body size) were once considered as an indication that savannas spread during this time period, an hypothesis supported by the fact that crown height generally correlates with diet and habitat among extant ungulates.

To add to the growing body of knowledge that has been accumulating that challenges this historical hypothesis, we also investigated whether the appearance

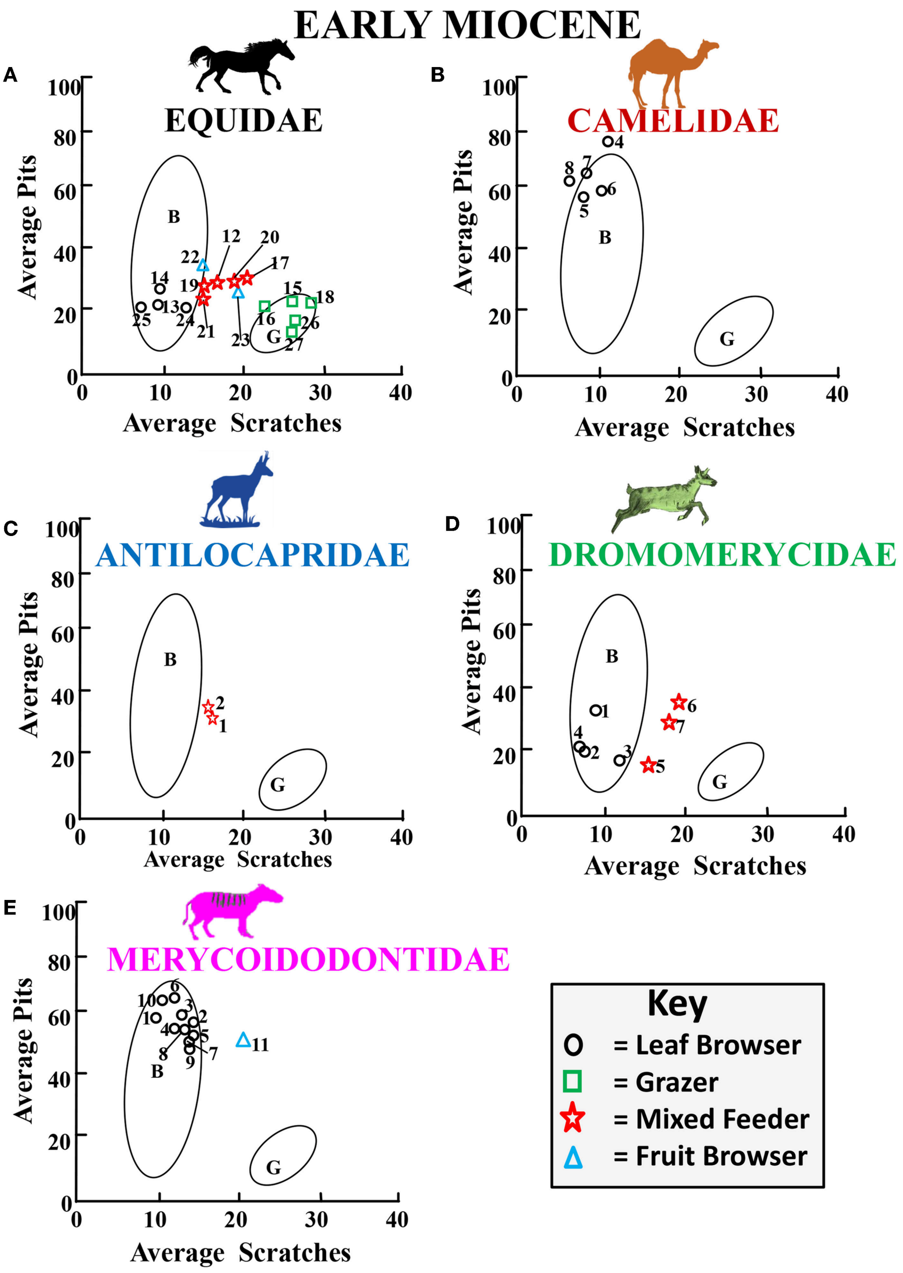

FIGURE 10 | Bivariate plot showing results for the average number of pits vs. the average number of scratches per taxon for Early Miocene fossil equids **(A)**, camelids **(B)**, antilocaprids **(C)**, dromomerycids **(D)** and merycoidodontids **(E)** plotted in reference to extant leaf dominated ungulate browsers (B), and extant grazers (G) at 35 times magnification (extant comparative data from Semprebon, 2002; Solounias and Semprebon, 2002). Gaussian confidence ellipses (p=0.95) on the centroid are indicated for the extant leaf browsers and grazers (convex hulls) adjusted by sample size. Key to Equidae: 12,16, 17 = *Parahippus nebrascensis*, 13 = *Kalobatippus agatensis*, 14, 25 = *Kalobatippus* sp., 15, 18 = *Parahippus* sp., 19, 21 = *Parahippus leonensis*, 20 = *Parahippus pawniensis*, 22 = *Archaeohippus blackbergi*, 23 = *Archaeohippus penultimus*, 24 = *Hypohippus* sp., 26 = *Merychippus primus*, 27 = *Acritohippus tertius*. Key to Camelidae: 4 = *Stenomylus hitchcocki*, 5 = *Aepycamelus* sp., 6 = *Michenia* sp., 7, 8 = *Protolabis* sp. Key to Antilocapridae: 1 = *Paracosoryx dawsensis*, 2 = *Paracosoryx wilsoni*. Key to Dromomerycidae: 1= *Barbouromeryx* sp., 2 = *Bouromeryx pawniensis*, 3 = *Dromomeryx* (*Subdromomeryx*) *scotti*, 4 = *Procranioceras skinneri*, 5 = *Aletomeryx gracilis*, 6 = *Aletomeryx scotti*, 7 = *Sinclairomeryx riparius*. Key to Merycoidodontidae: 1 = *Hypsiops breviceps breviceps*, 2 = *Merychyus crabilli*, 3 = *Merycochoerus chelydra carrikeri*, 4 = *Merycoides harrisonensis harrisonensis*, 5 = *Merychyus elegans arenarum*, 6 = *Merychyus elegans minimus*, 7 = *Merychyus elegans elegans*, 8 = *Merychochoerus* sp., 9 = *Merychyus* sp., 10 = *Merychyus relictus*, 11 = *Brachycrus laticeps buwaldi*.

of hypsodonty in the Miocene was truly synchronous with the appearance of grasslands and also whether exogenous grit could be a contributing factor to increased exposure to abrasion and subsequent crown height augmentation in fossil horses and other ungulates using three paleodietary techniques.

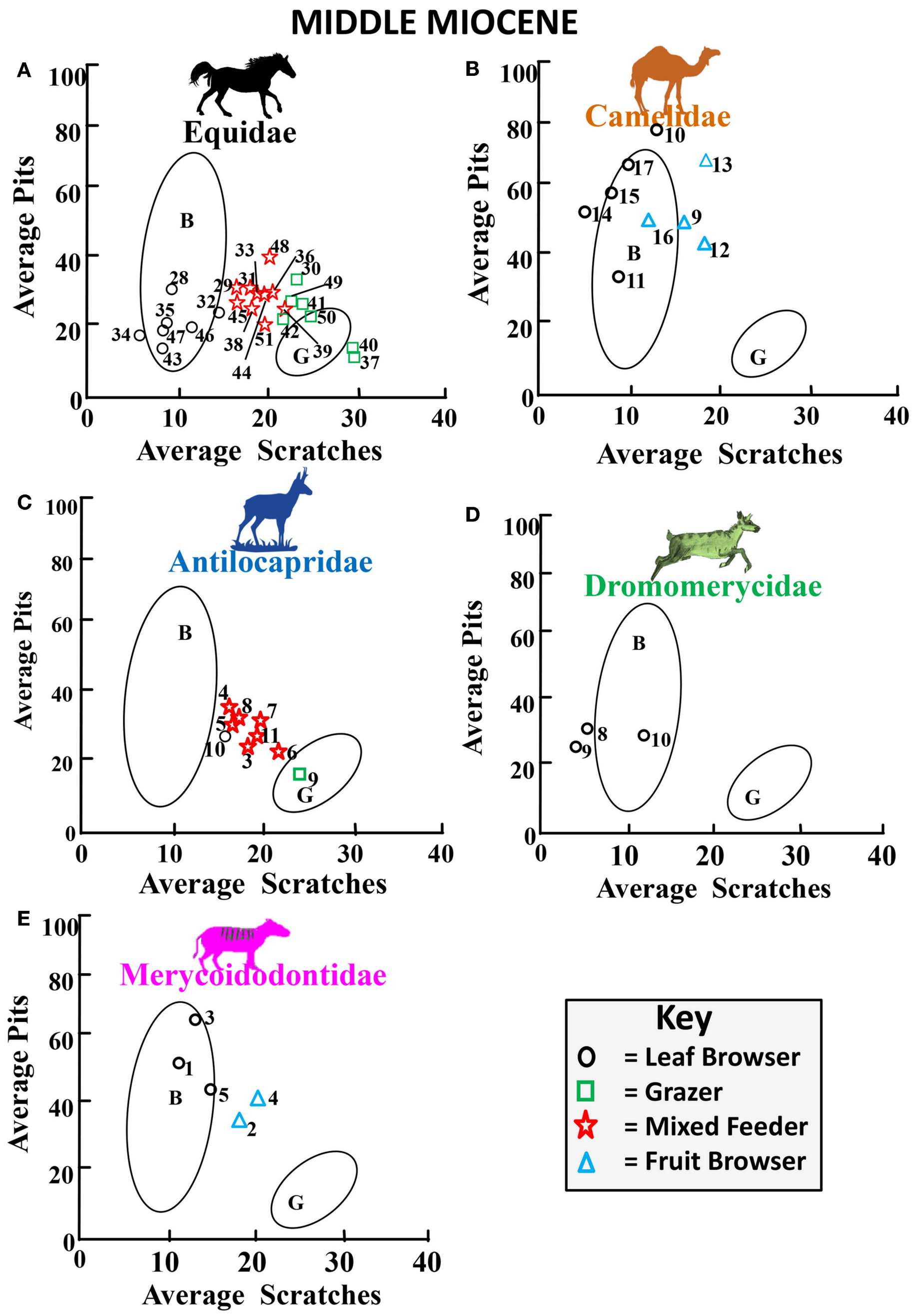

FIGURE 11 | Bivariate plot showing results for the average number of pits vs. the average number of scratches per taxon for Middle Miocene fossil equids **(A)**, camelids **(B)**, antilocaprids **(C)**, dromomerycids **(D)**, and merycoidodontids **(E)** plotted in reference to extant leaf dominated ungulate browsers (B), and extant grazers (G) at 35 times magnification (extant comparative data from Semprebon, 2002 and Solounias and Semprebon, 2002). Gaussian confidence ellipses (p=0.95) on the centroid are indicated for the extant leaf browsers (B) and grazers (G) (convex hulls) adjusted by sample size. Key to Equidae: 28 = *Parahippus avus*, 29 = *Parahippus integer*, 30, 31 = *Parahippus* sp., 32, 33 = *Hypohippus* sp., 34, 35, 43 = *Megahippus* sp., 36 = "*Merychippus*" *goorisi*, 37 = *Merychippus insignis*, 38 = *Scaphohippus intermontanus*, 39 = *Acritohippus isonesus*, 40 = *Acritohippus tertius*, 41 = *Calippus proplacidus*, 42 = *Protohippus perditus*, 44, 45 = "*Merychippus*" *calamarius*, 46 = *Cormohipparion quinni*, 47 = *Megahippus matthewi*, 48 = *Pseudhipparion retrusum*, 49 = *Protohippus supremus*, 50 = *Cormohipparion occidentale*, 51 = *Calippus martini*. Key to Camelidae: 9, 15, 16 = *Aepycamelus* sp., 10 = *Paramiolabis singularis*, 11 = *Aepycamelus proceras*, 12, 13 = *Procamelus* sp., 14 = *Miolabis princetonianus*, 17 = *Protolabis* sp. Key to Antilocapridae: 3, 4 = *Merriamoceros coronatus*, 5 = *Paracosoryx alticornis*, 6 = *Merycodus sabulonis*, 7 = *Meryceros joraki*, 8 = *Ramoceros* sp., 9 = *Paracosoryx alticornis*, 10, 11 = *Cosoryx furcatus*. Key to Dromomerycidae: 8 = *Dromomeryx whitfordi*, 9, 10 = *Drepanomeryx* (*Matthomeryx*) sp. Key to Merycoidodontidae: 1 = *Merychyus relictus*, 2 = *Brachycrus laticeps buwaldi*, 3 = *Ticholeptus zygomaticus*, 4 = *Brachycrus laticeps siouense*, 5 = *Merychyus medius medius*.

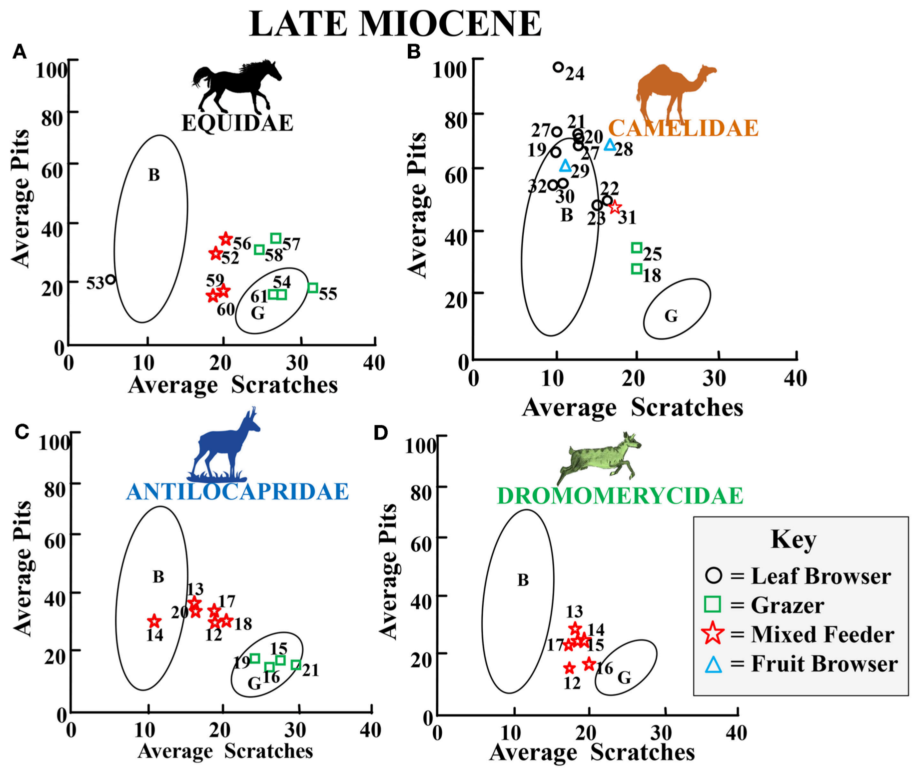

FIGURE 12 | Bivariate plot showing results for the average number of pits vs. the average number of scratches per taxon for Late Miocene fossil equids **(A)**, camelids **(B)**, antilocaprids **(C)**, and dromomerycids **(D)** plotted in reference to extant leaf dominated ungulate browsers (B), and extant grazers (G) at 35 times magnification (extant comparative data from Semprebon, 2002 and Solounias and Semprebon, 2002). Gaussian confidence ellipses ($p = 0.95$) on the centroid are indicated for the extant leaf browsers (B) and grazers (G) (convex hulls) adjusted by sample size. Key to Equidae: 52 = *Pseudhipparion hessei*, 53 = *Hypohippus* sp., 54 = *Calippus martini*, 55 = *Cormohipparion occidentale*, 56 = *Hipparion tehonense*, 57, 60 = *Dinohippus leidyanus*, 58, 61 = *Dinohippus* sp. 59 = *Dinohippus interpolatus*. Key to Camelidae: 18, 19, 21, 22 *Megatylopus* sp., 20, 27, 29 = *Procamelus* sp., 23 = *Machaerocamelus* sp., 24 = *Procamelus occidentalis*, 25, 30, 31, 32 = *Hemiauchenia* sp., 28 = *Megacamelus* sp. Key to Antilocapridae: 14 = *Plioceros dehlini*, 13 = *Proantilocapra platycornea*, 12 = *Cosoryx cerroensis*, 15 = ?*Hexobelomeryx* sp., 16, 21 = *Ilingoceros alexandrae*, 17 = *Osbornoceros osborni*, 18 = *Texoceras guymonensis* 19 = "*Plioceros* " *texanus*, 20 = cf. *Sphenophalos*. Key to Dromomerycidae: 12 = *Cranioceras clarendonesis*, 13 = *Cranioceras unicornis*, 14 = *Pediomeryx hamiltoni*, 15 = *Pediomeryx hemphilliensis* (Guymon Area), 16 = *Pediomeryx hemphilliensis* (Coffee Ranch), 17 = *Pediomeryx* sp.

To this end:

1. We tracked crown height (hypsodonty indices) through time for five North American families – Equidae, Camelidae, Antilocapridae, Dromomerycidae, and Merycoidodontidae.
2. We tracked level of abrasion incurred by individuals in each family through time via assessing cusp shape and occlusal relief (mesowear) and compared it to hypsodonty trends.
3. We reconstructed dietary behavior through time using enamel microwear to track grazing behavior and encroachment on food items by exogenous grit.

The older ideas regarding the correlation between the appearance of grasslands and hypsodonty in North America was fueled by the radiation of the genus *Merychippus* which represented a more hypsodont horse than earlier forms, as well as the earliest member of the subfamily Equinae which were highly hypsodont at around 17.5 Ma (late early Miocene) (Damuth and Janis, 2011), although a small increase in crown height was seen in the first appearance of *Parahippus* at about 23 Ma (Jardine et al., 2012). *Merychippus*, though more hypsodont than *Parahippus*, is not a highly hypsodont horse and plant phytolith evidence suggests that extensive grasslands were present in North America much earlier than the radiation of *Merychippus*.

Figure 1B shows that in equids, highly hypsodont equines appeared only about the late middle Miocene (roughly 14 million years ago), well after the projected availability of pervasive open grasslands by 22 Ma (earliest Miocene) (Strömberg, 2004, 2005) or even 26 Ma (latest Oligocene) (Strömberg, 2011), although many early Miocene forms were rather hypsodont. Antilocaprids and camelids also developed hypsodonty in the late middle Miocene. Merycoidodontids attained a modest degree of hypsodonty in the Oligocene. **Figure 1B** also shows that it is within the Equidae that the highest levels of hypsodonty were obtained through time of the families studied here.

Jardine et al. (2012) (Figure 21A) demonstrated with their regional-scale study of tooth height changes of US Great Plains fossil herbivores that both artiodactyls and perissodactyls show

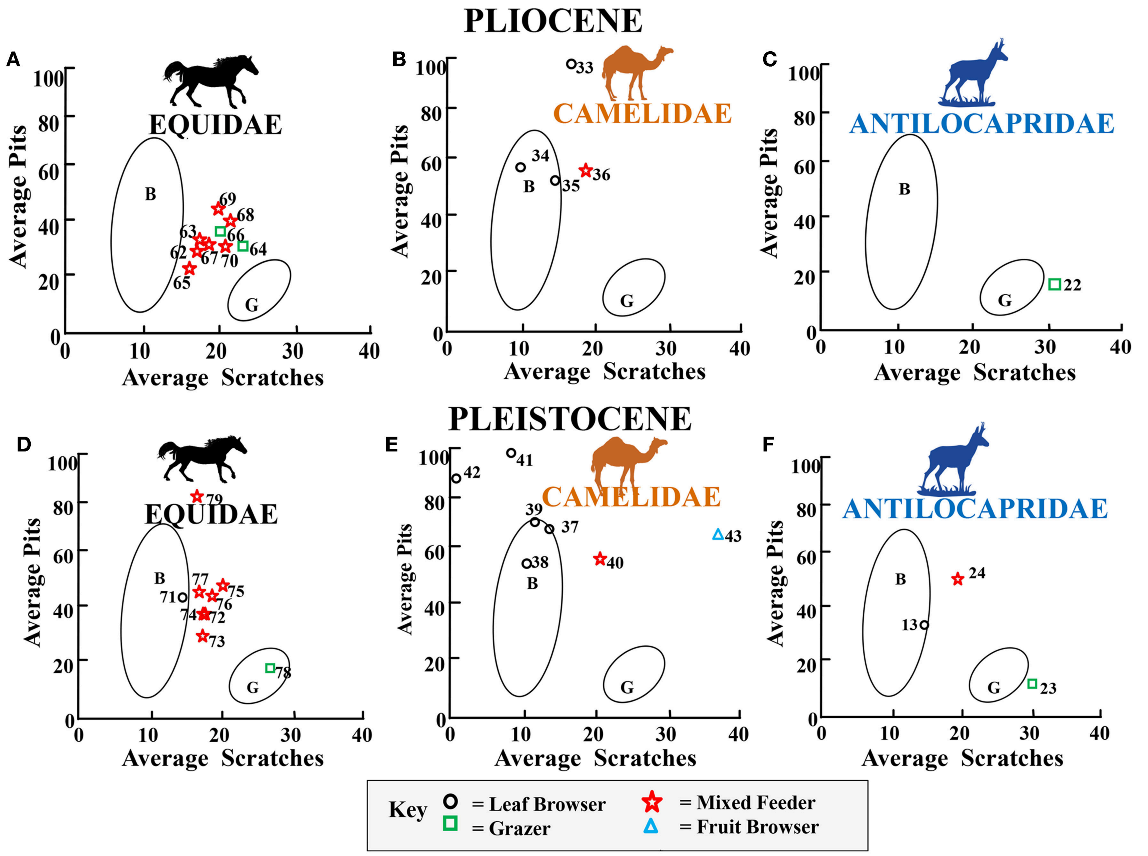

FIGURE 13 | Bivariate Plot showing results for the average number of pits vs. the average number of scratches per taxon for Pliocene and Pleistocene fossil equids **(A,D)**, camelids **(B,E)**, and antilocaprids **(C,F)** plotted in reference to extant leaf dominated ungulate browsers (B), and extant grazers (G) at 35 times magnification (extant comparative data from Semprebon, 2002 and Solounias and Semprebon, 2002). Gaussian confidence ellipses ($p = 0.95$) on the centroid are indicated for the extant leaf browsers (B) and grazers (G) (convex hulls) adjusted by sample size. Key to Pliocene Equidae: = 62 = *Nannipus aztecus*, 63 = *Pseudhipparion simpsoni*, 64 = *Neohipparion eurystyle*, 65 = *Cormohipparion emsliei*, 66, 67 = *Equus simplicidens*, 68, 69 = *Equus* sp., 70 = *Nannipus peninsulatus*. Key to Pliocene Camelidae: 33, 34 = *Megatylopus* sp., 35 = *Gigantocamelus spatula*, 36 = *Hemiauchenia* sp. Key to Pliocene Antilocapridae: 22 = *Tetrameryx* sp. Key to Pleistocene Equidae: 71, 74, 78 = *Equus* sp., 72 = *Equus* sp. A, 73 = *Equus* (*Hemionus*) sp. "B," 75 = *Equus calobatus*, 76 = *Equus complicatus*, 77 = *Equus fraternus*. Key to Pleistocene Camelidae: 37 = *Camelops* sp., 38, 39 = *Camelops* sp., 40 = *Hemiauchenia macrocephala*, 41 = *Camelops nevadanus*, 42, 43 = *Palaeolama mirifica*. Key for to Pleistocene Antilocapridae: 13 = *Capromeryx furcifer*, 23 = *Hayoceros falkenbachi*, 24 = *Stockoceros onusrosagris*.

a gradual changeover from brachydont to highly hypsodont forms, but that perissodactyls have a greater proportion of highly hypsodont taxa than artiodactyls. Jardine et al. (2012) also showed that within Perissodactyla, it is the Equidae rather than the Rhinocerotidae that make up a higher proportion of hypsodont forms, and only the Equidae that evolve highly hypsodont forms. Jardine et al. (2012) also found that many families of artiodactyls and perissodactyls were entirely low crowned (≤mesodont), and within the Artiodactyla, only antilocaprids (which appear as mesodont immigrants in the early Miocene), camelids and merycoidodontids attained hypsodont or highly hypsodont dentitions. The first artiodactyls to become hypsodont are the leptauchenine oreodonts and the stenomyline camelids (Jardine et al., 2012). The obvious question is why? Strömberg et al. (2016) investigated functions of phytoliths in vascular plants and rejected the traditional hypothesis that phytoliths in grasses evolved as part of a defense against large herbivorous mammals. Also, Müller et al. (2014) point out that although phytoliths abrade enamel, grit probably induces more wear on teeth in the habitats where most grazers seek food (Madden, 2014). Our results are consistent with these hypotheses as they indicate that a grit effect was likely an important first driver of the acquisition of hypsodonty in the families studied here. For example, very heavily pitted enamel surfaces with many large pits and relatively coarse scratch textures are found in leptauchenine oreodonts and stenomyline camels—results typical of modern ungulates today living in open and arid habitats and exposed to high levels of exogenous grit. Of the three leptauchenine oredonts studied here, two have microwear consistent with "dirty" browsing and *Leptauchenia decora* has microwear consistent with "dirty" seasonal or regional mixed feeding. Our microwear results for *L. decora* indicate that some forest fragmentation was most likely apparent in the Oligocene which is consistent with Retallack's research on plains paleosols (Retallack, 1992, 2004) that showed evidence of more open environments with the potential of feeding closer to the ground, as evidenced by mixed feeding in *L. decora* and the camelid *Probrotherium* sp.

Equids and antilocaprids also become somewhat hypsodont in the late early Miocene (Hemingfordian), and at this time both families experience high degrees of large pitting in their enamel and begin to show scratch textures regardless of dietary classification indicating heavy exposure to exogenous grit.

Our hypsodonty results (**Figure 1B**) are consistent with those of Jardine et al. (2012) that show that it is not until the middle Miocene (Barstovian) that highly hypsodont (HI >5) taxa first appear on the Great Plains. While some grass was likely consumed in the Oligocene based on our microwear results (e.g., early camels and pronghorns), the overall pattern in terms of timing of the attainment of hypsodonty is not congruent with a grass diet as the main impetus for the "Great Transition" in equids nor of crown height changes in the ungulate families studied here. Our results are more consistent with prior results that show that even after open grasslands became pervasive, forest cover was also available until the late Miocene and habitats remained heterogeneous (Strömberg, 2005; Strömberg and McInerney, 2011) – a finding consistent with the fact that most ungulates studied here were browsing or mixed feeding throughout the Miocene.

An excellent review of the evolution of grasses and grassland evolution was put forth by Strömberg (2011) where she pointed out that the evolution of hypsodonty was not synchronous with the spread of open and grass-dominated habitats and that in North America, hypsodonty appeared or became more prominent in faunas many million years after the expansion of open-habitat grasses (Strömberg, 2006; Strömberg et al., 2007). Our data confirm this assertion. Strömberg (2011) also confirmed that macrofossils demonstrate that while the earliest grasses on the North American continent are known from the earliest Eocene, the evolution of grasses in North America has proven to be a rather complex phenomenon in terms of how and when open and grass-dominant flora spread with different scenarios proposed by different lines of evidence.

These scenarios are summarized as follows: (1) Palynofloral and macrofossil data indicate that habitats that were mostly grass-free prevailed in the central parts of North America throughout the Oligocene, while habitats that were open and grass-dominated did not disseminate until the middle-late Miocene (e.g., Thomasson, 1990; Bolick et al., 1995). (2) Phytoliths (from the Great Plains region) reveal that some open-habitat type grasses permeated subtropical and closed forest by the earliest Oligocene but were minor elements there until the late Oligocene into the early Miocene when they began to expand. It was not until the latest Miocene that less patchy and more uniformly open grasslands seem to have spread based on work by Strömberg and McInerney (2011). (3) Paleosol data from studies by Retallack (1997, 2007) on the central Great Plains, northern Rocky Mountains, and Pacific Northwest suggests an expansion of more open habitats by the earliest Oligocene while C3-dominated grasslands were purported to have spread in the early Miocene in drier habitats.

Even so, Samuels and Hopkins (2017) have shown that smaller mammals such as rodents and lagomorphs correspond more closely with the timing of habitat changes than those studied here most likely because of their smaller ranges and shorter generation times. **Figure 6** shows comparative familial mesowear patterns over time. These patterns closely mirror hypsodonty trends (**Figure 1B**) in terms of synchrony in the timing of the acquisition of increased dietary abrasion, as evidenced by higher mesowear scores when hypsodonty increases. An interesting difference, however, is that while antilocaprids attain relatively high hypsodonty indices in the late Miocene, the spike in their mesowear scores is relatively lower comparatively than what is observed in equids or camelids. This most likely reflects more intermittent exposure to abrasive elements via seasonal or regional mixed feeding than the high level of dirty browsing (reflected by extreme pitting and coarser scratches) seen in the camelids and more grazing seen in the equids. Antilocaprids also show finer (though still relatively coarse) scratch textures than equids or camelids further explaining their somewhat lower mesowear scores in the late Miocene and presaging their further drop in abrasion as they moved into the Recent and adopted a browse-dominant diet.

We need to insert a word of caution when comparing hypsodonty levels in equids and other ungulates (principally ruminant artiodactyls). Equids experience a greater degree of dental wear for any given diet than other ungulates due to both their digestive physiology and their feeding behavior: thus, even if only considering the relative height of a single tooth, an equid will be more hypsodont than other ungulates consuming the same diet. The living species of equids (all grazers) are not only more hypsodont than other ungulates in terms of measures of individual molars, they also have a greater total postcanine tooth volume (due to their large and molarized premolars, which are as hypsodont as the molars, in contrast to the partially molarized premolars of ruminants, which may be reduced in both size and number, and are not as hypsodont as the molars) (see Janis, 1988). A further additional factor is that equid postcanine teeth do not form roots when they are first laid down; root formation is delayed until around 2 years of age, with additional crown growth during this time, so height of an unerupted molar does not measure the total (functional) height of the tooth as it cannot capture the length of crown added before tooth closure. This dental condition is rare in hypsodont artiodactyls, but it has been reported in a few, such as *Ovis*, *Capra*, and *Antilocapra* (Webb and Hulbert, 1986; Ackermans et al., 2019). We do not know of a comprehensive survey of extinct hypsodont equids that might determine whether the *Equus* condition is seen throughout the clade, but open-rooted molars have been reported in specimens of the hipparionine equid *Pseudhipparion simpsoni* (but not in other species of this genus) (Webb and Hulbert, 1986).

Equids (at least those in the hypsodont subfamily Equinae) also have a greater amount of enamel in their postcanine dentition than most ruminant artiodactyls, due to complication of the occlusal enamel surface. Famoso et al. (2016) attribute this occlusal enamel complexity (OEC) to dental durability, noting that it is more extensive in the tribe Hipparionini than in the tribe Equini (of which *Equus* is the surviving genus): because hipparionines are generally less hypsodont than equinines, they conclude that OEC is an alternative mode of resisting dental wear to hypsodonty. But the issue is more complex than this: for example, high levels of OEC are seen in Pleistocene species of *Equus* whose mesowear is indicative of browsing (Juha Saarinen, personal communication). Similar OEC is seen in specialized grazing bovids, such as *Bos* (Bovini), *Hippotragus* (Hippotragini), and *Connochaetes* (Alcelaphini). For mechanical reasons, OEC can only be a feature of teeth that have a flat occlusal surface, and Sanson (2016) considers that this dental pattern is related to food manipulation on this surface. A flat occlusal surface in bovids is seen only among grazers, while it is a characteristic feature of the Equinae, even though other dental parameters (microwear, mesowear, hypsodonty index) indicate that many of these species were not grazers (especially among the Hipparionini). This is an interesting issue that requires further investigation; but the data suggest that OEC relates to other issues besides resisting rates of tooth wear.

The reason why equids require a greater tooth volume (i.e., greater resistance to tooth wear) than other ungulates on similar diets relates both to differences in digestive physiology and to food intake behavior. As originally noted by Janis (1988), the less efficient hindgut fermentation of perissodactyls means that they must consume more food per day than a similarly-sized ruminant artiodactyl eating a diet of similar fiber content, and hence equids encounter more total tooth wear per lifetime. Additionally, in contrast to both ruminant artiodactyls, and other perissodactyls such as rhinos, horses grind their food to a fine particle size on its initial ingestion, a behavior which must take a toll on their dentition (Clauss et al., 2015). Although fecal particle size is slightly smaller in ruminants than in horses, attesting to a greater total amount of oral preparation, the majority of this processing takes place during rumination when the food has been softened by the effects of fermentation. In addition, the rechewed food has the benefit of being "washed" in the rumen: abrasive particles such as sand sink to the bottom of the rumen and are not included in the regurgitated bolus (Dittman et al., 2017).

Figures 9–13 show comparative dietary assignments of fossil families in each time period based on average scratch and pit results and reveal some very interesting differences between these North American families. The Camelidae and Merycoidodontidae, though attaining hypsodonty in some forms, were committed browsers throughout most of their evolutionary history but with a type of browsing that incurred a large amount of abrasion (i.e., "dirty" browsing) right from the beginning. Solounias and Semprebon (2002) and Semprebon and Rivals (2007, 2010) have demonstrated a similar pattern of microwear in extant taxa that occupy open and arid habitats such as camels and pronghorns. Thus, any hypsodonty attained by these forms, due most likely to continuous exposure to exogenous grit, would allow them to forage on grass periodically, thus providing a mechanism to broaden their niche. Antilocaprids appear to have shifted their dietary behavior between grass and browse through much of their evolutionary history but returned to mainly browsing in the Recent. Lastly, it is clear that the Equidae exhibited a wider array of dietary behaviors than the other families through most of their evolutionary history (except in the Recent). Even so, grass apparently was a much more common dietary item for equids than for the other families, and when combined with exogenous grit, which was more accelerated in the late Miocene onward (more pitting and coarser scratch textures), may explain the more extreme acquisition of hypsodonty in equids compared to camels and antilocaprids, and set the stage for the Equidae alone of the families studied here to become hypergrazers in the Recent. Our results are compatible with those of Hummel et al. (2011) by stressing that total exposure to abrasive elements (both phytoliths in plant material and exogenous abrasives) should be considered when interpreting factors relating to the acquisition of hypsodonty.

We would also like to caution that much remains to be learned regarding the effects of extrinsic abrasive particles of different sizes (i.e., dust vs. grit). It is obvious that small particles would inflict smaller enamel scars than larger particles and that smaller particles should be more quickly obliterated by wear than larger scars which should persist for a longer period of time. It is intuitive that very small particles such as dust could collectively remove large amounts of tissue without leaving many scars that would be simultaneously detectable by any of these dietary methods. Consequently, the wear rate in open habitats is accelerated despite the fact that large pits do not override the dietary signal, it should be considered that very small particles could be a major but unrecognized wear agent.

Winkler et al. (2019) have proposed that the state of hydration of plant tissue may also affect dental abrasion based on a controlled feeding experiment using guinea pigs fed with different types of forage (in both a fresh and dried state). They stress that water content as well as phytolith content may affect plant abrasiveness. This is very likely why browsers and browse-dominated mixed feeders in open habitats (e.g., camels, pronghorns) tend to have such a clear browser signal in their mesowear, from high attrition in combination with (moderately) high wear rates (Fortelius and Solounias, 2000). Further research should help to elucidate how surface texture wear patterns (as per Winkler et al.) translate into absolute wear rates.

CONCLUSIONS

Documenting changes in crown height (hypsodonty index), relative abrasion (mesowear) and diagnostic food and grit scar topography on dental enamel (microwear) allowed for the discernment of the relative contributions of grass vs. exogenous abrasives as potential driving forces in ungulate tooth evolutionary changes during the evolution of North American Equidae, Camelidae, Antilocapridae, Dromomerycidae, and Merycoidodontidae. The timing of hypsodonty acquisition is not consistent with grazing as the main driver for crown height changes in the equids or the artiodactyl families studied, as highly hypsodont ungulates post-date the appearance of widespread grasslands. Synchrony in the timing of the acquisition of hypsodonty and increased dietary abrasion incurred during feeding as measured via mesowear was seen in all five fossil families. High degrees of enamel pitting (particularly large pits) and unusually coarse scratch textures in all five fossil families as measured via microwear are consistent with exposure to exogenous grit or soil ingestion as the main driver of hypsodonty acquisition prior to the consumption of significant levels of grass and consistent with recent experimental controlled feeding studies in ungulates. Camelids, dromomerycids, and merycoidodontids, though attaining varying levels of hypsodonty in some forms, were committed browsers throughout most of their evolutionary history, but with a type of browsing that incurred a large amount of abrasion (i.e., "dirty" browsing). Antilocapridae browsed and grazed throughout most of their evolutionary history, but demonstrated unusual levels of large pitting and relatively coarser scratch textures consistent with exposure to exogenous grit. Equidae exhibited a wider array of dietary behavior than the other families through most of their evolutionary history (except the Recent). Even so, grass was a much more common dietary item for equids than for the other families. This combined with exposure to exogenous grit, which was more accelerated from the early Miocene onward based on more pitting and coarser scratch textures, may explain the more extreme acquisition of hypsodonty in equids compared to the artiodactyl families studied, setting the stage for the Equidae alone to become hypergrazers in the Recent.

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript, from indicated references and/or the supplementary files.

AUTHOR CONTRIBUTIONS

GS conceived of the idea, collected mesowear, and microwear data, FR and GS analyzed the data with advice from CJ. All authors contributed to the writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00065/full#supplementary-material

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REVIEW
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The Evolution of Equid Monodactyly: A Review Including a New Hypothesis

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The traditional story of horse evolution is well-known: over time, horses became larger, they attained higher-crowned teeth, and they changed from having three toes (tridactyly) to a single toe (monodactyly). Evolution is often perceived as a progression toward some optimum outcome, in this case the "Noble Steed." However, the evolutionary advantages of monodactyly are not entirely clear, other than the notion that it must somehow be "more efficient," especially at the larger body size of the genus *Equus*. It is not commonly appreciated that the reduction of the digits to the monodactyl condition was not the main anatomical foot transition in equid history. Rather, the most important change was the transformation of the original "pad foot" into the more derived "spring foot," with the acquisition of an unguligrade limb posture, characteristic of the family Equinae. Species within the Equinae tribes—Hipparionini, Protohippini, and Equini—evolved hypsodont teeth and diverged into both small and large body sizes, but monodactyly evolved only within the Equini. Despite the Plio-Pleistocene success of *Equus*, Hipparionini was by far the richest tribe for most of the Neogene, in terms of taxonomic diversity, numbers of individuals, and biogeographic distribution; but hipparionins remained persistently tridactyl over their duration (17–1 Ma). We propose that the adaptive reasons for monodactyly must be considered in the context of reasons why this morphology never evolved in the Hipparionini. Additionally, *Equus* inherited monodactyly from smaller species of Equini, and consideration of Miocene taxa such as *Pliohippus* is critical for any evolutionary hypothesis about the origins of monodactyly. We review the literature on equid locomotor biomechanics and evolution, and propose two novel hypotheses. (1) The foot morphology of derived Equini is primarily an adaptation for increasing locomotor efficiency via elastic energy storage, and the accompanying digit reduction may be circumstantial rather than adaptive. (2) Differences in foraging behavior and locomotor gait selection in Equini during late Miocene climatic change may have been a prime reason for the evolution of monodactyl horses from tridactyl ones.

Keywords: Equidae, Hipparionini, Equini, paleobiology, locomotion, evolution, monodactyly

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INTRODUCTION

The story of horse evolution is a familiar one, often used as the exemplar for evolutionary patterns (Osborn, 1918; Matthew, 1926; Simpson, 1951), and for this reason frequently maligned by creationists (see Janis, 2007). Although the originally-perceived linear pattern of horse evolution has been reinterpreted as a bushy, branching one (Simpson, 1951; MacFadden, 1992), nevertheless the story of horse evolution remains one of some degree of "progression": from small animals with many toes and simple, low-crowned teeth (brachydont), to large animals with a single toe and complex, high-crowned teeth (hypsodont). Branches of the family that were not in the direct line of ancestry to the modern *Equus* have been sidelined in the evolutionary narratives, including the two lineages that migrated from North America to the Old World before the Pleistocene migration of *Equus*: anchitheriines (large-bodied, specialized browsers) in the early Miocene, and hipparionins (more closely related to *Equus*, and resembling modern equids in many respects, but persistently tridactyl) in the early late Miocene.

Modern equids, and their more immediate relatives (derived members of the tribe Equini), differ from the great majority of fossil equids in the loss of the medial and lateral digits (digits two and four, the proximal ends of the metapodials are retained as "splint bones") and the retention of only a single (third) digit; i.e., the condition of monodactyly. Because *Equus* is the only surviving genus, and it had a great diversity and biogeographic spread of species in the Pleistocene (originating in North America, and reaching South America as well as the Old World, although now extinct in the New World), monodactyly has been perceived as some sort of pinnacle of equid evolution, the ultimate locomotor adaptation (although occasional individuals of modern *Equus* possess complete additional digits as an atavism, see **Figure 1**). In addition, because *Equus* is in general of large body size for the family (modern species ranging between ∼200 and 400 kg, some extinct species were as large as ∼600 kg), larger than its North American tridactyl relatives, monodactyly has been interpreted as being related to this increased body size. However, Hipparionini in both the New and Old Worlds were a successful and diverse radiation of persistently tridactyl forms, more taxonomically diverse in the late Miocene than the emerging monodactyl Equini lineage, and many Old World hipparionins were as large or larger than modern and fossil members of *Equus*. (Body mass [BM] estimates in this paper are derived from Shoemaker and Clauset, 2014 [anchitheriines], and Cantalapiedra et al., 2017 [equines]). Thus, body size alone cannot be the reason for the evolution of monodactyly.

Here we review the evolutionary history of equid locomotor morphology, and pose the following question: if monodactyly was such a prominent adaptive feature in the lineage leading to modern equids, then why did it evolve only in this lineage? Why did the equally successful (at least in the Miocene) tridactyl hipparionins not also exhibit any trends toward this "progressive" morphology, especially as some Old World species paralleled species of *Equus* in hypsodonty and large body size? We propose that monodactyly is not necessarily a "superior" equid adaptation, but that its origins were in changes in foraging behavior in one particular equid lineage in increasingly arid conditions in the late Miocene of North America. Monodactyly in the genus *Equus* was a fortuitous preadaptation to the greater extent of aridity that affected all higher latitudes in the Plio-Pleistocene. In contrast, Old World hipparionins were well-suited for more wooded conditions with relatively mild seasonality, and their diversity was severely reduced with dramatic climatic shifts at the Mio-Pliocene boundary. We support this hypothesis by weaving together information from equid evolutionary history, foot anatomy, and locomotion, which provide the essential background information that informs our novel proposition.

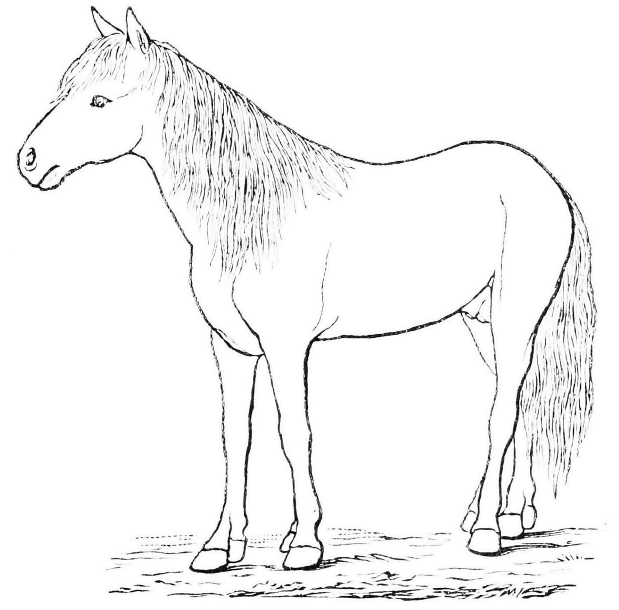


FIGURE 1 | A modern example of a polydactyl horse, showing additional digits (in this case, complete second digits) as an atavism. Image from Wikimedia, in the public domain. PSM_V16_D274_ "Outline_of_horse_with_extra_digit_on_each_foot," Popular Science Monthly vol 16 1879-1880.

A BRIEF HISTORY OF THE RADIATION OF THE EQUINAE (FAMILY EQUIDAE)

The Equidae consists of three subfamilies: a basal (Eocene) Hyracotheriinae, the late Eocene to latest Miocene Anchitheriinae, and the early Miocene to Recent Equinae. The first two subfamilies are paraphyletic, although the Miocene radiation of large-bodied anchitheres (Anchitheriini) is monophyletic. Equids likely originated in the Old World, and their sister taxon, Palaeotheriidae, was entirely European; but equid Paleogene evolutionary history was largely confined to North America. Both the Anchitheriinae and the Equinae originated in North America, and lineages from both subfamilies migrated to the Old World. The subfamily Equinae is diagnosed by a number of dental characters, including hypsodont cheek teeth with cementum, and a characteristic feature is the "spring foot" (although, as later discussed, this had its origin in derived anchitheriines) (see MacFadden, 1992, 1998). **Figure 2** shows a simplified phylogeny of the Equidae, with emphasis on the tribe Equini. **Figure 3** shows the distribution of Neogene equids in time and space.

The Equinae is subdivided into the tribes Hipparionini (late early Miocene to Pleistocene), Protohippini (middle Miocene to latest Miocene) and Equini (late early Miocene to Recent).

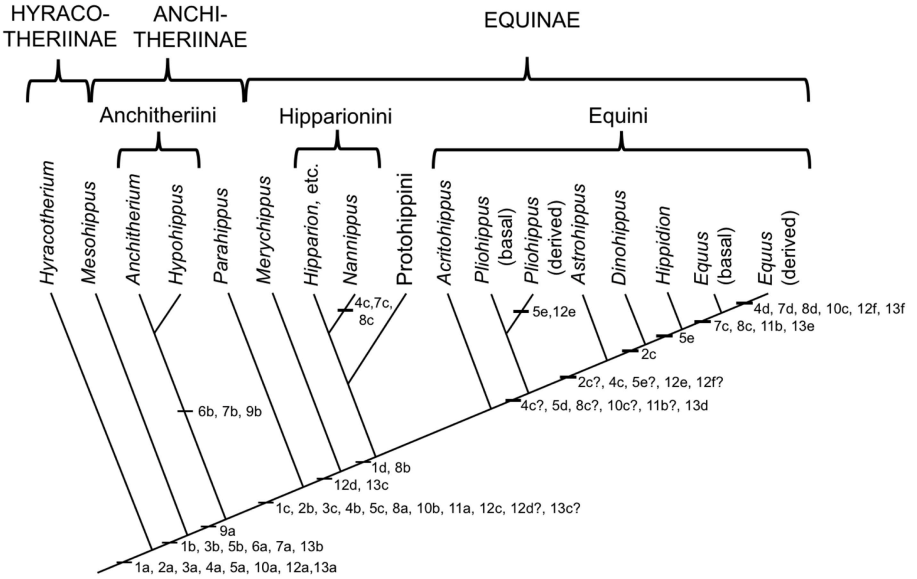
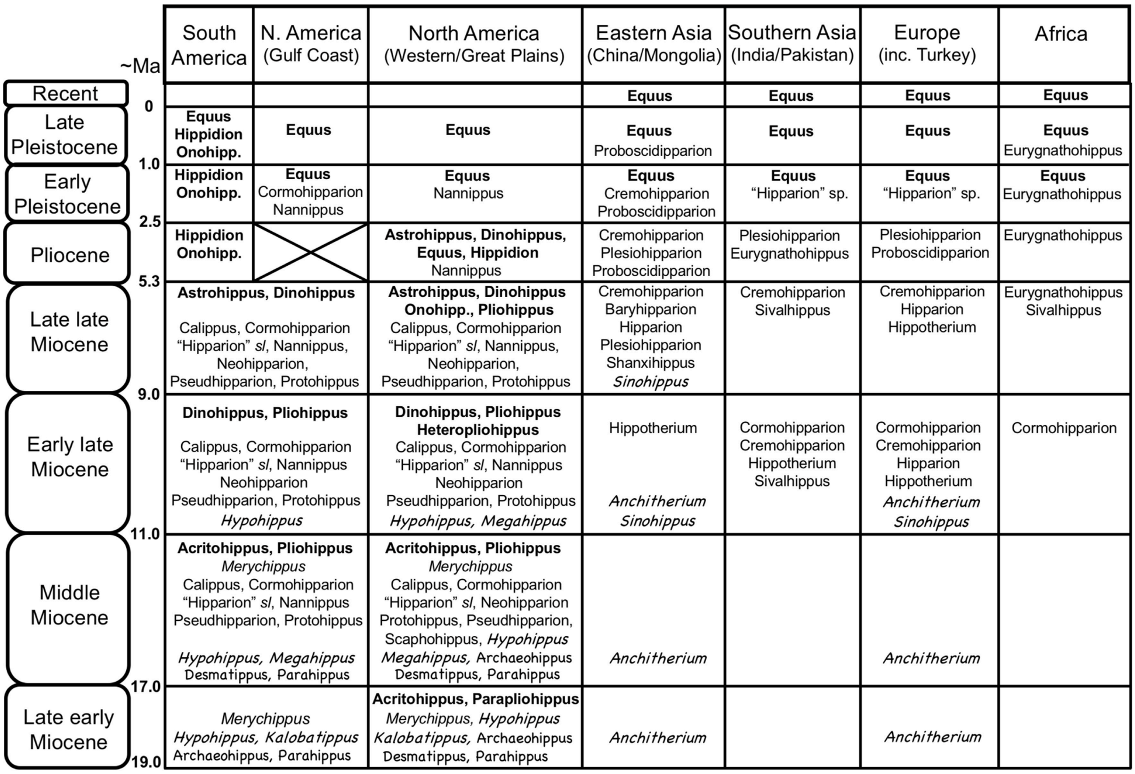


FIGURE 2 | Phylogeny of selected genera (discussed in this paper) within the Equidae based on the phylogeny in (Maguire and Stigall, 2009). Original drawing by CMJ, final figure rendered by James G. Napoli. The numbers on the phylogeny refer to the anatomical characters listed below: note that the "basal" characters are for reference for the generalized condition, and are not necessarily specific to the Equidae. *Miohippus* (not shown) is crownward of *Mesohippus* and basal to the Anchitheriini. Characters at the level of *Parahippus* probably also apply to the other stem equine anchitheres (i.e., crownward of the Anchitheriini) *Archaeohippus* and *Desmatippus* (both basal to *Parahippus*). *Anchitherium* is an Old World taxon, and North American early Miocene equids originally called *Anchitherium* should be referred to *Kalobatippus* (MacFadden, 1992, 1998). *Nannippus* is singled out because of its unique morphology, and is not the sister taxon to the other hipparionins. Within the Equini, *Parapliohippus, Heteropliohippus*, and *Onohippidium* (which may not be distinct from *Hippidion*) are not shown. 1. Foot posture and foot pad: (a) subunguligrade, foot pad extensive; (b) subunguligrade, foot pad slightly reduced; (c) unguligrade, foot pad converted to digital cushion (3rd phalanges contained within enlarged hoof); (d) Digital cushion reduced slightly. 2. Phalangeal proportions of third (central) digit: (a) 1st phalanx short (length $<$ 2X width), 3rd phalanx longer than 2nd, inclination to ground $<26^\circ$; (b) 1st phalanx elongated (length $>$ 2X width), 3rd phalanx shorter than second, inclination $>26^\circ$, $<35^\circ$; (c) inclination of third phalanx $> 40^\circ$ 3. Third (central) metapodial shaft: (a) similar size to second and fourth metapodials (slightly longer and broader), cross-sectional area oval or elliptical; (b) elongated relative to proximal limb bones, and proportionally longer and broader than second and fourth metapodials; (c) further increased in proportional size, cross-sectional area more circular. 4. Third (central) metapodial distal articulatory surface: (a) narrower in width than metapodial shaft above distal tubercules, sagittal ridge confined to volar surface; articulatory curvature $<180^\circ$, flexor (volar) surface with greater curvature than extensor (dorsal) surface; (b) sagittal ridge more prominent, encroaches onto dorsal surface, received by groove in first phalanx; articulatory curvature at least 180°, extensor surface with greater curvature than flexor surface, transverse ridge at point of change of curvature (documented for "*Merychippus*," presumed to occur in *Parahippus*); (c) Broader in width than metapodial shaft above distal tubercules, sagittal ridge still more prominent, further encroaching onto dorsal surface; (d) sagittal ridge extremely prominent, fully extended onto dorsal surface. 5. Other metapodials and associated digits: (a) complete metapodial 5 and digit 5 retained in manus, metapodial 1 and digit 1 lost; metapodials 2 and 4 large, not bound to central metapodial, associated digits likely contacted ground during regular locomotion; (b) metapodial 5 and digit 5 greatly reduced or lost, metapodials 2 and 4 more tightly bound to central metapodial; (c) shafts of metapodials 2 and 4 reduced, tightly bound to central metapodial by ligaments, associated digits smaller, no longer contact the ground during regular locomotion, but may do so during more extreme performance; (d) sagittal ridge/groove for articulation of 1st phalanges on metapodials 2 and 4 now very faint or lost entirely; shafts of metapodials 2 and 4 further reduced in width, associated digits further reduced in size; (e) shafts of metapodial 2 and 4 confined to proximal two thirds of central metapodial (i.e., transformed to "splint" bones), associated digits lost. 6. Scars for cruciate sesamoid ligaments (proximal volar surface of 1st phalanx): (a) present; (b) enlarged. 7. Scar for central sesamoidean ligament (mid volar surface of 1st phalanx of 3rd digit): (a) present; (b) enlarged; (c) reduced; (d) lost/merged with V-scar for oblique ligaments. 8. Scars for oblique sesamoid ligaments (proximal to mid volar surface of 1st phalanx of 3rd digit): (a) present, small, round, extend no more than 30% down phalanx; (b) enlarged, forming incipient V-scar, extend further down phalanx ($<$50% of bone); (c) elongated, extend $>$50% down phalanx; (d) merge to form more distinct V-scar, extend 66% down phalanx. 9. Scars for straight sesamoid ligament (proximal volar surface of 2nd phalanx of 3rd digit): (a) present; (b) enlarged. 10. Suspensory ligament: (a) probably fully muscular (= interosseous muscle of 3rd metapodial and digit); (b) at least partially tendinous; (c) fully tendinous (evidenced by loss of volar gulley on third metapodials). 11. Size of proximal sesamoid bones of 3rd digit: (a) increase in size to support the suspensory apparatus; (b) further enlarged. 12. Tarsus: (a) astragalus articulates predominantly with navicular, distal articulation rounded, ridges of trochlea directed anteriolaterally (angle with sagittal plane 14–20°), considerable intertarsal movement possible, relatively long astragalar neck; (b) astragalar neck shorter; (c) more restrictive tibia–astragalar articulation, distal articulation of astragulus with navicular wider and flatter; (d) ridges of astragalar trochleae higher, restricting motion to parasagittal plane, intertarsal movement more restricted by ligaments; (e) width of astragalus greater than length; (f) ridges of astragalar trochlea narrower and directed more anteriorly (angle with sagittal plane 10–15°), reduced lateral swing of foot, little or no intratarsal movement possible. 13. Knee joint: (a) angle at knee joint $\sim 102^\circ$, large and rugose area on tibia for attachment of semitendinosus muscle for limb retraction–reflects more flexed knee joint and tibial rotation on limb retraction; (b) angle at knee joint $\sim 108^\circ$; (c) angle at knee joint $\sim 131^\circ$; (d) area of attachment of semitendinosus of moderate size; (e) angle at knee joint $\sim 140^\circ$; (f) Area of attachment of semitendinosus weak, angle at knee joint $\sim 150^\circ$.

Members of these tribes will be referred to as "hipparionins," "protohippins," and "equins," respectively, while "equines" refers to members of the subfamily Equinae.

The taxon *Merychippus* was originally considered the basal type of equine (e.g., Simpson, 1951), but species ascribed to this genus actually represent a paraphyletic grade of smaller,



	~Ma	South America	N. America (Gulf Coast)	North America (Western/Great Plains)	Eastern Asia (China/Mongolia)	Southern Asia (India/Pakistan)	Europe (inc. Turkey)	Africa
Recent	0				**Equus**	**Equus**	**Equus**	**Equus**
Late Pleistocene	1.0	**Equus** **Hippidion** **Onohipp.**	**Equus**	**Equus**	**Equus** Proboscidipparion	**Equus**	**Equus**	**Equus** Eurygnathohippus
Early Pleistocene	2.5	**Hippidion** **Onohipp.**	**Equus** Cormohipparion Nannippus	**Equus** Nannippus	**Equus** Cremohipparion Proboscidipparion	**Equus** “Hipparion” sp.	**Equus** “Hipparion” sp.	**Equus** Eurygnathohippus
Pliocene	5.3	**Hippidion** **Onohipp.**	☒	**Astrohippus, Dinohippus, Equus, Hippidion** Nannippus	Cremohipparion Plesiohipparion Proboscidipparion	Plesiohipparion Eurygnathohippus	Plesiohipparion Proboscidipparion	Eurygnathohippus
Late late Miocene	9.0	**Astrohippus, Dinohippus** Calippus, Cormohipparion “Hipparion” *sl*, Nannippus, Neohipparion, Pseudhipparion, Protohippus		**Astrohippus, Dinohippus** **Onohipp., Pliohippus** Calippus, Cormohipparion “Hipparion” *sl*, Nannippus, Neohipparion, Pseudhipparion, Protohippus	Cremohipparion Baryhipparion Hipparion Plesiohipparion Shanxihippus *Sinohippus*	Cremohipparion Sivalhippus	Cremohipparion Hipparion Hippotherium	Eurygnathohippus Sivalhippus
Early late Miocene	11.0	**Dinohippus, Pliohippus** Calippus, Cormohipparion “Hipparion” *sl*, Nannippus Neohipparion Pseudhipparion, Protohippus *Hypohippus*		**Dinohippus, Pliohippus** **Heteropliohippus** Calippus, Cormohipparion “Hipparion” *sl*, Nannippus Neohipparion Pseudhipparion, Protohippus *Hypohippus, Megahippus*	Hippotherium *Anchitherium* *Sinohippus*	Cormohipparion Cremohipparion Hippotherium Sivalhippus	Cormohipparion Cremohipparion Hipparion Hippotherium *Anchitherium* *Sinohippus*	Cormohipparion
Middle Miocene	17.0	**Acritohippus, Pliohippus** *Merychippus* Calippus, Cormohipparion “Hipparion” *sl*, Nannippus Pseudhipparion, Protohippus *Hypohippus, Megahippus* Desmatippus, Parahippus		**Acritohippus, Pliohippus** *Merychippus* Calippus, Cormohipparion “Hipparion” *sl*, Neohipparion Protohippus, Pseudhipparion, Scaphohippus, *Hypohippus* *Megahippus,* Archaeohippus Desmatippus, Parahippus	*Anchitherium*		*Anchitherium*	
Late early Miocene	19.0	*Merychippus* *Hypohippus, Kalobatippus* Archaeohippus, Parahippus		**Acritohippus, Parapliohippus** *Merychippus, Hypohippus* *Kalobatippus,* Archaeohippus Desmatippus, Parahippus	*Anchitherium*		*Anchitherium*	

FIGURE 3 | Global distribution of Neogene equid genera, showing the diversity of the different families/subfamilies. Original drawing by CMJ, final figure rendered by James G. Napoli. Key to equid taxonomy: Roman type = Equinae: bold face = Equini (Onohipp. = *Onohippidium*); regular type = Hipparionini (including Protohippini) (*sl* = *sensu lato*); italics = "*Merychippus*" *sensu stricto* (i.e., basal species, more derived species not shown, but none persist past the middle Miocene). Chalkboard type = Anchitheriinae: regular type = stem Equinae anchitheres; italics = Anchitheriini. Although anchitheriine equids are only considered briefly in this paper, their distribution in time and space is interesting, and their persistence alongside of the Miocene Equinae is often disregarded. Information from Janis et al. (2008), MacFadden (2013), Salesa et al. (2004), the NOW database, Fossilworks, and Bernor et al. (1996). Divisions within epochs are approximate to accommodate both North American Land Mammal Ages and Eurasian MN/MQ zones + Land Mammal Ages. Late Pleistocene = Rancholabrean/MQ2; early Pleistocene = Irvingtonian + late Blancan/MQ1; Pliocene = early Blancan (+ very latest Hemphillian)/MN14-16/Ruscinian (no faunas known from the North American Gulf Coast); late Miocene = Hemphillian/MN13-11/Turolian + late Vallesian; early late Miocene = Clarendonian/MN9-10/early Vallesian + late Astracean; middle Miocene = Barstovian/earliest Clarendonian/MN5-8/Astracean + late Orleanian; late early Miocene = Hemingfordian/MN3(later part)-4/middle Orleanian.

less hypsodont Equinae, and the taxon name is now usually placed in quotes. "*Merychippus*" *gunteri* is the most basal equine, "*Merychippus*" *primus* is the sister taxon to the grouping of the Equinae tribes, and other "*Merychippus*" species mostly belong to the Hipparionini (including the type species "*Merychippus*" *insignis*: Hulbert and MacFadden, 1991): note that "*Merychippus*" *insignis* is the sister taxon of *Cormohipparion goorisi*, which is at the base of the North American *Cormohipparion*/Old World hipparionin radiation (Woodburne, 2007). The Equinae tribes are mainly diagnosed by dental characters, but while most of the Equinae retained the tridactyly seen in basal "*Merychippus*" species, monodactyly evolved only within the Equini. Full monodactyly (complete loss of medial and lateral digits) was first apparent in the early late Miocene (Clarendonian) in derived species of *Pliohippus*. All Clarendonian and younger Equini species were likely monodactyl although, as detailed below, this is not a simple issue.

The North American hipparionins comprise the genera "*Hipparion*" (not the same taxon as the Old World genus of that name), *Neohipparion*, *Pseudhipparion*, *Nannippus,* and *Cormohipparion* (MacFadden, 1992, 1998). Old World hipparionins take their origin from North American *Cormohipparion,* with their oldest occurrence being in the Pannonian Basin Zone C between 11.4 and 11.0 Ma (Bernor et al., 2017). There was an extensive Old World radiation including the genera *Hipparion* sensu stricto, *Hippotherium, Cremohipparion, Sivalhippus, Eurygnathohippus, Plesiohipparion, Proboscidipparion* and *Shanxihippus* (Bernor et al., 1996, 2018; Bernor and Sun, 2015).

The "core" (i.e., the monodactyl genera) of the Equini comprises the Pliocene to Recent genus *Equus*; the Plio-Pleistocene predominantly South American genera *Hippidion* and *Onohippidium* (*Hippidion* is shown by mitochondrial DNA to be the likely sister taxon to *Equus*; Der Sarkission et al., 2015); and, as successive outgroups to this grouping, *Dinohippus* (paraphyletic with respect to *Equus*), *Astrohippus*, *Heteropliohippus*, and *Pliohippus*. The basal equins (all tridactyl) are now considered to be *Acritohippus* (= "*Merychippus*" *tertius*, "*M.*" *stylodontus*, and "*M.*" *isonesus*) and (crownward) *Parapliohippus* (= "*Merychippus*" *carrizoensis*) (see Kelly, 1995, 1998). With the exception of *Equus*, *Hippidion*, and *Onohippidium*, the Equini were all exclusively North American.

The North American genera *Protohippus*, *Calippus*, and *Scaphohippus* (= "*Merychippus*" *sumani* and "*M.*" *intermontanus*) were originally placed within the Equini, basal to the above-mentioned Equini taxa (see e.g., Hulbert and MacFadden, 1991; MacFadden, 1992, 1998). More recent analyses have assigned them to their own tribe, Protohippini, as the sister taxon to the Hipparionini (e.g., Kelly, 1995, 1998; Pagnac, 2006), and we include them with the hipparionins in our discussions here.

Hipparionins (including protohippinins) and equins differed in their craniodental morphology, and probably had different feeding ecologies. Hipparionins had molariform teeth that had more complex occlusal enamel morphology than those of the equins, often with densely plicated enamel, and the occlusal surface relief was usually higher [but note that the highly hypsodont *Eurygnathohippus woldegabrieli* (Bernor et al., 2013) had very low occlusal relief], and their teeth were usually less hypsodont than those of equins (Famoso et al., 2016). In addition, hipparionin mesowear tends to be indicative of browsing-to-mixed feeding while that of the equins is usually more indicative of grazing (Mihlbachler et al., 2011, but note that dental microwear studies do not support this conclusion; e.g., Bernor et al., 2013; Semprebon et al., 2016).

The radiation of the North American Equinae was explosive in the late early Miocene (late Hemingfordian, ca. 17.5 Ma), and reached a peak in diversity in the late middle Miocene (late Barstovian, ca. 14 Ma) through the early late Miocene (Clarendonian, ca. 11.5–8.5 Ma) (see **Figure 3**). During this time, individual localities could have as many as eight contemporaneous equid species [data from Janis et al. (2004a)], and the hipparionins were more diverse than the equins. By the latest Miocene (Hemphillian) the equid radiation was declining, reflected in the overall number of taxa, the abundance of individuals in the fossil record, and the number of sympatric species at fossil localities (three to four species, down to one to two species in the Pliocene; Janis et al., 2004a). The genus *Equus* is first known from the earliest Pliocene. Only a few of the Miocene taxa survived into the Pliocene: out of the Equini, *Dinohippus*, *Astrohippus*, *Onohippidium* and *Hippidion* and (the latter taxon surviving until the end of the Pleistocene in South America); out of the Hipparionini, *Cormohipparion* and *Nannippus* (the latter taxon possibly surviving into the early Pleistocene) (see Janis et al., 2008). The Pleistocene of North America was the time of extensive radiation of species of *Equus*, which migrated to the Old World at 2.6 Mya and is recognized initially by Eurasian and African "stenonine" horses (Azzaroli, 2000; Wang and Deng, 2011; Alberdi and Palombo, 2013; Bernor et al., 2018).

Cormohipparion was the founding genus for Old World hipparions, although it was not the earliest known form, which was *Hippotherium*, known from ca. 11.2 Ma in Europe and China (Bernor et al., 2017, 2018). *Cormohipparion* has been recorded from 10.8 Ma levels of Pakistan and Turkey (Bernor et al., 2003), and slightly younger (10.5 Ma) from Algeria. *Sivalhippus* likewise diverged in the Vallesian, ca. 10.5 Ma, in Indo-Pakistan (Wolf et al., 2013) and underwent a local radiation there, then extended its range into China and East Africa. *Eurygnathohippus* is known from late Miocene aged deposits of Kenya, Ethiopia, Libya and Morocco (Bernor et al., 2012). *Plesiohipparion* originated in China, and was later known from Turkey, India, and Spain. *Proboscidipparion* originated in the latest Miocene of China, and in the Plio-Pleistocene was known from China and Turkey (Bernor et al., 2018; Sun et al., 2018). In contrast to the North American Miocene, only two or three species of equids are known in any given faunal locality in the Old World Miocene.

Equus was first known in the Old World in Eurasia at 2.6 Ma (the *Equus* Datum, Lindsay et al., 1980; Azzaroli, 2000; Bernor et al., 2018), and diverged into a dozen or more species during the Pleistocene (not including the seven surviving species). The genus first appeared in Africa at around 2.3 Ma. Distribution of extant Old World clades of *Equus* has been reviewed by Bernor et al. (2010).

THE EVOLUTION OF UNGULIGRADY AND MONODACTYLY IN EQUIDS

Structure and Function of the Modern Equid Foot

Extant equids have a single main digit (the third) and retain only the proximal shafts of the medial (second) and lateral (fourth) metapodials (also known as the "splint bones"), which extend approximately halfway down the central metapodial. Although these structures are often described as "vestigial," their proximal ends clearly have an indispensable function in supporting the articulation of the manus and pes with the carpus and tarsus, respectively. The monodactyl litoptern (extinct South American ungulate) *Thoatherium* is often described as "more advanced" than equids, as it has apparently lost almost all of the shaft of the medial and lateral metapodials (MacFadden, 1992). But these conditions of monodactyly are convergent: there is no reason to think that the retention of the metapodial shafts in *Equus* represents some intermediate stage in the evolution of monodactyly. The anatomy of the equid foot, and the major tendons and ligaments is shown in **Figure 4**. Anatomical descriptions below are taken from Nickel et al. (1986), Stashak (2006).

The equid foot posture is unguligrade: unguligrady is seen elsewhere today only among ruminant artiodactyls, where the foot is formed of two separate digits in the "cloven-hoof" condition. In equids, weight is directed through the tip of the third (distal) phalanx, which is encased in a keratinous hoof and supported on the volar (= plantar or palmar) side by a fibrous digital cushion. The ventral surface of the foot is composed of keratinous epithelial structures; posteriorly by a thick V-shaped structure termed the "frog," which provides traction and aids the digital cushion in its shock-absorbing function, and anteriorly by a thinner sole.

The principal joint in the foot is the fetlock, between the metapodial and the first (proximal) phalanx (there is little motion at the interphalangeal joints). This joint is

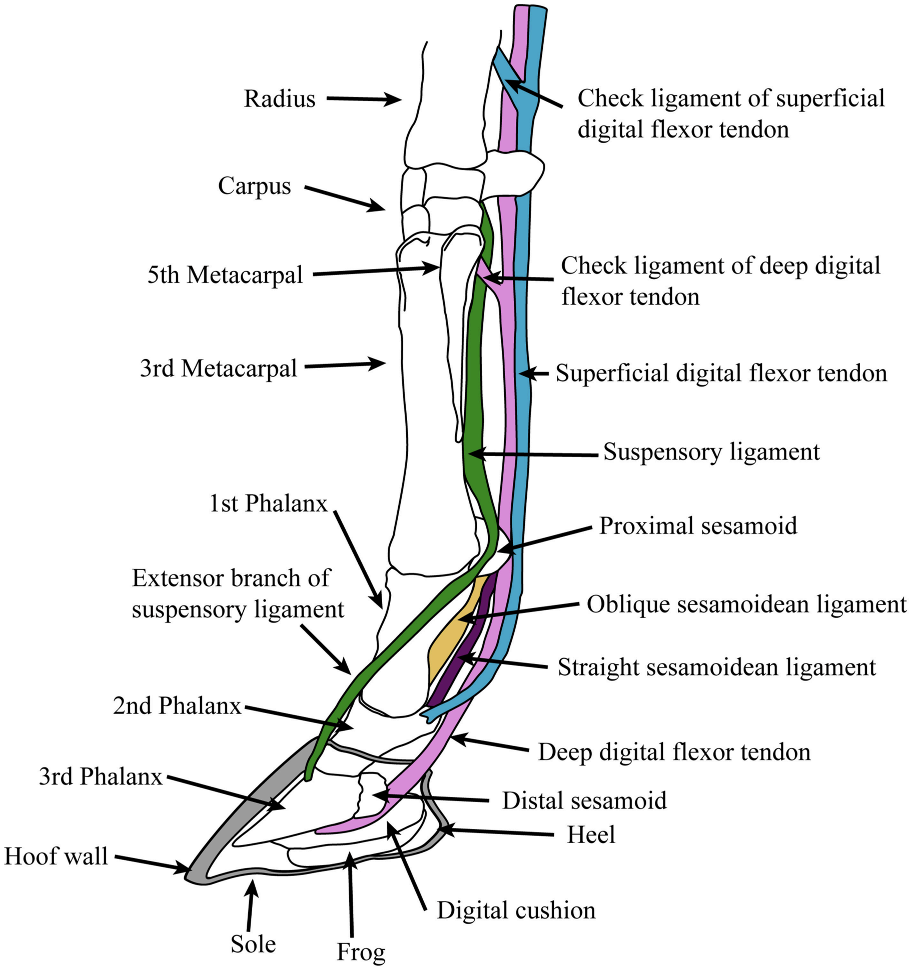


FIGURE 4 | Diagram of supportive tendons and ligaments of the equine foot (only selected ligaments, referred to in the text, are shown). The hoof (covering the third phalanx and the distal portion of the second phalanx) is shown in cross section. Original drawing by CMJ, final illustration rendered by James G. Napoli.

held at an angle of around 25° to the vertical at rest, but is capable of extending (= dorsi-flexion) to an angle of 90° during extreme performance (galloping or jumping: intermediate angles of 40°-60° are observed during more routine locomotion) (McGuigan and Wilson, 2003). This fetlock flexion is the basis of the equid "spring foot," which both reduces the impact of the forces acting on the foot during rapid locomotion and, by means of stretching the flexor tendons, acts to store elastic energy in these tendons, saving up to 40% of locomotor energy during foot recovery (Biewener, 1998). The elongation of the first phalanx is an important component of this mechanism, allowing for the fetlock to be held higher off the ground, resulting in greater stretch of the flexor tendons. However, this increase in distance between foot and fetlock magnifies the moment arm of the ground reaction force around the fetlock joint, necessitating a firm ligamentous apparatus supported by stout proximal sesamoid bones (Thomason, 1986). Note that this "spring foot" action is essentially passive: similar force vs. length curves are seen in feet of living horses and in applying force to the limbs of cadavers (McGuigan and Wilson, 2003).

The "spring foot" involves a complex series of supportive ligaments. The suspensory ligament, derived from the interosseous muscle of the third metapodial and digit, holds the fetlock in a sling, limiting both flexion and hyperextension. It originates from the proximal volar surface of the third metapodial and the distal carpal (or tarsal) bones, and runs along the volar surface of the central metapodial. Near the distal end of the metapodial it splits into two slips, inserting onto the proximal sesamoid bones on either side of the volar metapodial surface. Two extensor branches then extend forward to join with the common digital extensor tendon, which inserts on the extensor process on the proximal dorsal aspect of the third phalanx.

Sesamoidean ligaments bind the proximal sesamoids to each other and to the foot bones, and transmit forces experienced during locomotion to the suspensory ligament (Thomason, 1986). These include the cruciate ligaments, the lateral (oblique) ligaments and the straight (rectus) ligament. These ligaments leave scars on the volar surface of the phalanges, and so their history through equid evolution can be traced (see legend for **Figure 2**). Other supportive foot ligaments include various collateral ligaments that run laterally from one foot bone to the neighboring one, and three annular ligaments that encircle the volar side of the foot, superficial to all of the other ligaments and tendons; the most proximal of these, the palmar annular ligament, is of particular importance in binding the proximal sesamoid bones and associated ligaments to the rest of the foot.

The primary elastic energy storage is in the digital flexor tendons, both deep and superficial, which are stretched during locomotion with the extension of the fetlock. These structures are muscular only in their most proximal portions, small super-pinnate muscles that function as spring dampeners (Wilson et al., 2001). The flexor tendons course superficial to the suspensory and sesamoidean ligaments and have "check ligaments" that aid in the passive suspensory apparatus of the foot (see **Figure 4**); these prevent excessive stretch of the tendons, and may act as additional parallel elastic elements (Wilson et al., 2001). The superficial digital flexor tendon divides into two before inserting onto the second phalanx on either side of the straight sesamoidean ligament. The deep digital flexor tendon, which experiences the greatest locomotor strains and contributes the most to elastic energy savings (Biewener, 1998), passes over the distal sesamoid (articulating with the proximal third phalanx and distal second phalanx) and inserts onto the flexor cortex of the third phalanx.

Locomotion in Modern Horses

The familiar gaits of horses, from slow to fast, are the walk, trot, and gallop (a slow gallop is called a canter). In all tetrapods there is a fundamental difference between the walk gait and other, faster gaits (collectively termed "running"). In walking, the animal vaults over strut-like limbs, and the center of mass (COM) is at its highest during the foot supportive phase: the mechanics are basically those of an inverted pendulum, with exchange of potential and kinetic energy contributing to the recovery of up to 70% of mechanical energy. In running, the animal engages in spring-mass mechanics on compliant legs, and the COM is at its lowest during foot support. Up to 40% of mechanical energy can be recovered via storage and release of elastic energy in tendons and ligaments: this results in a greater efficiency of locomotion (less total energy expenditure per unit distance traveled).

Walking gaits do not usually involve a period of suspension (i.e., an aerial phase, when all four feet are off the ground), while running gaits usually do, but this is not invariant. With increasing speed within any one gait, the limbs are subjected to greater vertical forces (and hence to more bone stress) as the limbs move faster, and the amount of time each foot is on the ground decreases: these musculoskeletal stresses may be the trigger to switch gaits (see Biknevicius and Reilly, 2006; Biknevicius et al., 2006, for review). In horses, at least, while the walk involves pendular mechanics, and the trot spring-mass mechanics, the gallop is considered to involve some combination of the two. The energy savings from pendular mechanics in walking are 25–47%, while those in the gallop are 7–14%: in contrast, in trotting elastic energy recovery savings are 21–45% (greater in larger horses) (Reilly and Biknevicius, 2007). Horses are unusual among the mammals studied in that their running gaits are no cheaper than their walking gait, and running may be more expensive than walking in larger horses. This is likely due to extremely efficient walking in horses, rather than any deficiency with running, and horses may store some elastic energy during their walk gait (fetlock extension is observed in walking horses), thereby reducing locomotor costs (see Reilly and Biknevicius, 2007).

The walk and the trot are both symmetrical gaits. During walking, a four beat gait, each foot is moved in sequence (i.e., single-foot) in an ipsilateral pattern (i.e., the right hind is followed by the right fore, etc.) with no aerial phase in the stride cycle. During trotting, a two beat gait, contralateral pairs of legs are moved together, with two aerial phases in the stride cycle, the horse essentially bouncing from one diagonal pair of supportive legs to the other. The gallop is an asymmetrical, four beat gait, with the sequential support of the two hind limbs being followed by the two forelimbs; there is a "gathered" aerial phase before the hind limbs are again engaged in support (see Clayton, 2004, for a description of horse gaits). There is little contribution from spinal flexion to the stride in the gallop (except at the lumbo-sacral junction), although some elastic energy may be stored and recovered in vertebral column ligaments (Alexander, 1988). In contrast to the horse "stiff-back" mode of galloping, cursorial carnivorans such as the cheetah (and also some smaller artiodactyls) practice a "flexible-back" gallop, where there are two aerial phases and considerable spinal flexion, which potentially contributes to elastic energy storage as well as to stride length (the "transverse gallop" vs. "rotary gallop" of Bertram and Gutmann, 2009).

A few types of domestic horses practice a gait called the running-walk or amble, best known as the tölt of Icelandic horses. This gait is practiced at similar speeds to the trot (∼11–18 km/h), and is often used in place of a trot in the walk-trot-gallop sequence, although the running-walk may extend into the speeds where trotting horses will switch to a gallop (up to 30 km/h) (Clayton, 2004; Barrey, 2013). As many as 16 varieties of this gait and other "single-foot" gaits have been recorded among different horse breeds, collectively referred to as "gaited horses" (Nicodemus and Clayton, 2003), and the propensity for gaited locomotion has been traced to a single mutation in domestic horses (both the mutation and the gait are unknown in other equids) (Promerová et al., 2014). However, while the running-walk is rare in extant equids, trackways of the Pliocene hipparionin from Laetoli, Tanzania show that it was using this gait (Renders, 1984), a point to which we shall return.

The running-walk has the same lateral sequence single-foot pattern as the regular walk, usually lacking an aerial phase, but is speeded up so that up to three feet may be off the ground at any one time. Despite this similarity of footfall sequence to the walk, the tölt has the spring-mass mechanical properties of a running gait: the limb stiffness is comparable to that of trotting horses, but the vertical motion of the COM is much less. Icelandic horses employ the tölt over a similar range of speeds as the trot, and may extend this gait past the usual trot-to-gallop transition speed (Biknevicius et al., 2006).

Evolution of the Modern Equid Condition

Figure 2 shows the acquisition of the various derived features of the equid foot in the form of characters on a simplified phylogeny. This information is derived from Camp and Smith (1942) and Sondaar (1968), both writing about the forelimb, and Hussain (1975) on the hindlimb. Note that there are conflicts with some taxonomic nomenclature, as discussed in the previous section, especially with species of "*Merychippus*." Even though museum numbers are usually provided for the specimens examined, it would not be easy to determine their correct taxonomic affinities.

With these caveats in place, some obvious trends can be noted (the numbers refer to the numbers on the phylogeny). The largest cluster of changes is with the appearance of the "spring foot" anatomy (#1c), heralding the loss of the foot pad and the transition to an unguligrade foot posture. This involves changes in digit proportions (#2b,3c,5c), the medial and lateral digits no longer contacting the ground during regular locomotion; changes in the articulation at the fetlock joint that limit lateral motion but allow for greater parasagittal rotation (#4b); changes in phalangeal proportions, with an elongated first phalanx, and a more vertically-positioned third phalanx that is now shorter than the second phalanx (#2b); and associated postural changes in the hind limb (#12c,12d,13c). There is also evidence of the development of the ligamentous suspensory apparatus with the appearance of scars for the oblique sesamoidean ligaments (#8a), and the suspensory ligament was now probably at least mostly tendinous (#10b) (see **Figure 4**).

The "spring foot" is often thought to be a novel feature of the Equinae (e.g., Thomason, 1985, 1986), but its inception was actually at the level of the stem equine anchitheres (here represented by *Parahippus*) (see also O'Sullivan, 2008, on the lengthening of the first phalanx being the key indicator of this postural change). Although more basal anchitheres such as *Mesohippus* and *Miohippus* retained a pad foot, there were a number of changes between hyracotheres and *Mesohippus* that relate to a greater complexity of supportive ligaments as well as changes in the relative sizes of the pedal bones. Note that the acquisition of the straight sesamoidean ligament (#9a) in equids more derived than *Mesohippus* and *Miohippus* may be related to support of a greater body weight than in earlier equids (i.e., > ∼50 kg), and that the very large-bodied (>200 kg) anchitheres *Megahippus* and *Hypohippus* (Anchitheriini) possess a number of ligamentous features indicative of restricted motion at the fetlock (#6b,7b,8b). A number of other morphological changes are seen with the transition to the "spring foot" that also relate to classic anatomical "cursorial adaptations," such as the great reduction or loss of the distal ulna and fibula (MacFadden, 1992). The proximal sesamoid bones, involved in the support of the ligamentous suspensory apparatus, may also become larger at the transition to the "spring foot" (#11a; *Mesohippus* [F:AM 74048] has smaller proximal sesamoids than *Parahippus* [MCZ 17877]).

Following the acquisition of the "spring foot," there is little functional change observed in the pedal morphology of most tridactyl Equinae, although Camp and Smith (1942) proposed a reduction in the size of the digital cushion above the level of "*Merychippus*" (#1d), and the scars for the oblique sesamoidean ligaments now extend to around 50% of the volar surface of the first phalanx (#8b), forming the beginnings of the V-scar (see **Figure 5**) that is most prominent in modern species of *Equus*. There is little or no discussion in the literature of any instance of reduction of medial and lateral digits in North American hipparionins (except possibly for *Nannippus*, see below), although Deng et al. (2012) report a reduction in the size of these digits in the long-limbed *Hipparion* (=*Plesiohipparion*) *zandaense* from the Pliocene of Tibet. Deng et al. (2012) also report other morphological features that resemble those of monodactyl equids: a larger medial trochlear ridge on the distal femur, longer and more distinct V-scars on the first phalanx, a relatively reduced width across the distal metapodial tuberosities, and a better developed sagittal ridge on the distal articular surface of the third metapodial. Parker et al. (2018) employ a "toe reduction index" in their examination of equid morphological traits, and their Figure 3 suggests that there has been toe reduction in several hipparionin lineages, although not in any systematic phylogenetic fashion. We consider that the possibility of digit reduction in North American hipparionins requires a more systematic investigation. There is no report of medial and lateral digital reduction in Old World hipparionins other than that by Deng et al. (2012).

Camp and Smith (1942), Sondaar (1968), and Hussain (1975) all note that the small (dwarfed) hipparionin *Nannippus* (BM ∼50–100 kg) paralleled the monodactyl equins in aspects of the fetlock joint articulation and suspension (#4c,7c,8c). Sondaar (1968) claims that the medial and lateral digits were reduced in size, but Parker et al. (2018) report a toe reduction index less than most other North American hipparionins, and similar to *Parahippus*. Sondaar (1968) also notes a number of features of the articulation for carpal and tarsal bones on the central metapodials that show convergence with the condition in *Equus*. Additionally, *Nannippus* also appears to have had a stiffer lumbar region than other hipparionins, approaching the condition in *Equus* (Jones, 2016).

The evolution of monodactyly in the *Pliohippus*–*Equus* portion of the Equini phylogeny involves many other changes in locomotor anatomy. [Note that the species of *Pliohippus* considered by Camp and Smith (1942) and Sondaar (1968) have been reassigned to *Dinohippus*; some information on *Pliohippus* presented here is derived from personal observations of CMJ, but the precise morphology of species within this taxon needs further investigation, as noted by the question marks on the characters in **Figure 2**]. While a couple of features occurred convergently between derived (monodactyl) *Pliohippus* and the other monodactyl equids (not only the complete loss of digits two and four [#8a], but also the relative broadening of the astragalus [#12e]), there are a number of other features shared by this clade of Equini that indicate a strengthening of the ligamentous suspensory apparatus, increased rotation of the fetlock joint, and the greater restriction of hind limb motion to the parasagittal plane.

Anatomical changes shared by the clade of *Pliohippus*–*Equus* include the following (note that some of these are queried at this level and require further investigation): the increasing encroachment of the distal sagittal ridge on metapodials to

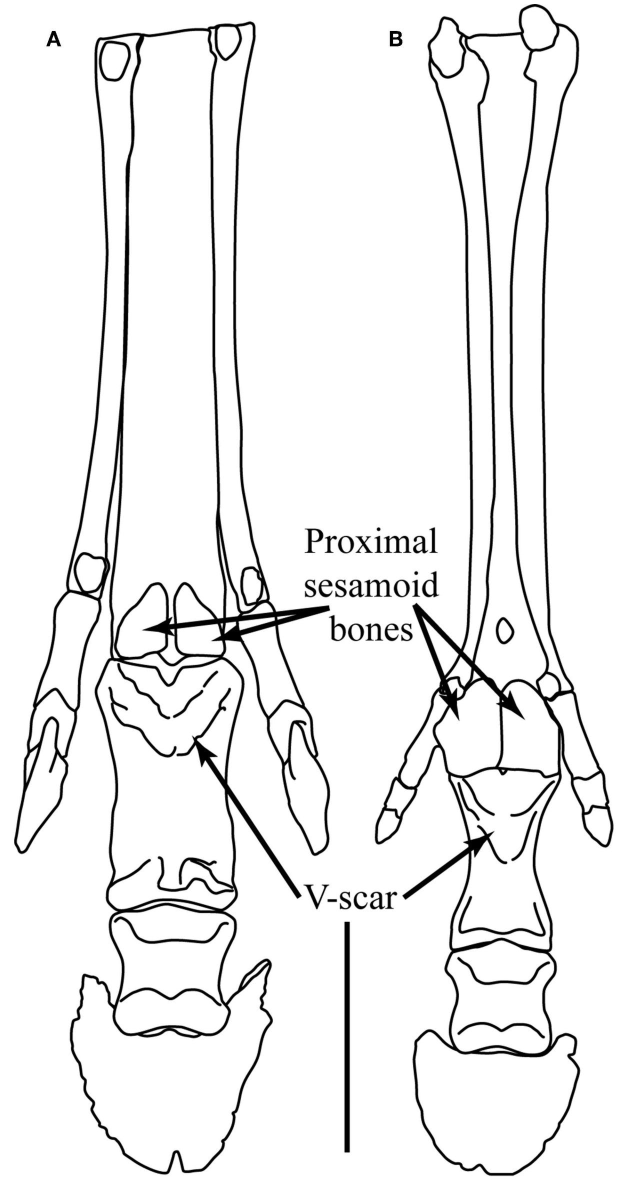


FIGURE 5 | Plantar view of the left foot of **(A)** *Hippotherium primigenium* and **(B)** *Pliohippus pernix*. *Hippotherium* is from the late Miocene of Höwenegg (Germany), and the illustration is modified from Figures 6.23.2 and 6.31.1 in Bernor et al. (1997). *Pliohippus* is based on F:AM 60803 from the early late Miocene (early Clarendonian) of Nebraska (June Quarry, Burge Member of the Valentine Formation) (photographs taken by CMJ, third phalanx mirror-imaged). Scale bar = 5 cm. Illustration by James G. Napoli.

the dorsal surface of the articulation (#4c,d); the loss of the metapodial volar gully indicating a completely tendinous suspensory ligament (#10c); enlarged proximal sesamoid bones indicative of an enhanced suspensory apparatus (#11b); the elongation and fusion of the oblique sesamoid ligaments to form a distinct V-scar (#8c); and a somewhat less-flexed knee joint (#13d). Changes occurring in more derived Equini (crownward of *Pliohippus*) include a more vertical position of the third phalanx within the hoof (#2c); a further less-flexed knee joint (#13,e,f); and an astragalus that limits the motion of the hind limb to the parasagittal plane to a greater extent (#12e,f). Note that a number of the features seen in extant *Equus* are present in a less derived state in more basal species of the genus, as well as in other monodactyl equids.

In summary: (1) The acquisition of the "spring foot" was a key feature for the evolution and radiation of the Equinae, allowing for increased efficiency of locomotion: but, as noted by Thomason (1986), it may also be a liability, as it magnifies the forces acting on the musculoskeletal system. (2) Monodactyl Equinae differ from tridactyl ones not only in the loss of the medial and lateral digits, but also in having an enhanced "spring foot," with evidence of greater extension at the fetlock joint (and stronger ligaments to support this motion), accompanied by limb movement more restricted to the parasagittal plane.

The Origin of Monodactyly

Monodactyly is known in derived species in the genus *Pliohippus* and all Equini genera crownward of *Pliohippus* (see **Figure 2**). *Pliohippus* is first known in the United States from the late Barstovian (late middle Miocene, 12.6–14.8 Ma, although it has been reported from the early Barstovian of Mexico; see Janis et al., 2008). *Pliohippus* survived until the end of the Miocene, but was only common in the mid-Miocene (Barstovian to early Clarendonian) (MacFadden, 1998). *Pliohippus* was originally considered to be directly ancestral to later monodactyl equids (e.g., Stirton, 1940), but this genus has a number of its own unique features, including complex facial fossae that are smaller or absent in crownward Equini (MacFadden, 1998), and so was excluded from ancestry of more derived equins. However, all recent equid phylogenies place *Pliohippus* as the sister taxon to the other monodactyl members of the Equini. There has been considerable confusion between species of *Pliohippus* and the more derived Equini genera *Astrohippus* and *Dinohippus* (see MacFadden, 1998). *Dinohippus* is an early late Miocene to Pliocene genus (Clarendonian to early Blancan), and *Astrohippus* is a latest Miocene to Pliocene genus (Hemphillian to early Blancan); both genera are distinct from *Pliohippus* in the reduction of the preorbital facial fossae (to a greater extent in *Dinohippus* than in *Astrohippus*). *Dinohippus* (BM ∼170–500 kg) also tends to be of larger body size than *Pliohippus* (BM ∼110–170 kg) or *Astrohippus* (BM ∼125–190 kg).

Pliohippus has also been noted to be variable in the incidence of monodactyly, with tridactyl individuals reported. The most well-known example is among individuals of a single death assemblage of *Pliohippus pernix* from the Ashfall Fossil Beds in Nebraska (early Clarendonian, Cl-2 ca. 11 Ma) (Voorhies, 1994; Tucker et al., 2014), although the limb morphology of these fossils has not been studied in a quantitative fashion. Hussain (1975) notes incidences of both monodactyly and tridactyly among the specimens of *Pliohippus* in the Frick collection at the American Museum of Natural History (New York) (AMNH). He claims that the first monodactyl *Pliohippus* is F:AM 60812, known from Bear Creek Quarry in the Cap Rock Member of the Ash Hollow Formation (the same member and formation as the Ashfall Fossil Beds). Based on information in MacFadden (1998) this is also likely to be *Pliohippus pernix*. Another specimen of *Pliohippus pernix* studied by Hussain (1975), F:AM 60803, is slightly older (from June Quarry, Burge Member of the Valentine Formation, earliest Clarendonian, Cl-1, ca. 13 Ma), and is quite definitely tridactyl, even though the medial and lateral digits are small (see **Figure 5**). We know of no systematic study of variability of digit number in species of *Pliohippus* in general. **Figure 5** compares the forefeet of the Old World hipparionin *Hippotherium primigenium*, and a tridactyl specimen of *Pliohippus pernix*. Note the smaller size of the medial and lateral digits in *Pliohippus*, and also the larger proximal sesamoid bones and the greater extent of the incipient V-scar.

Because *Pliohippus* includes tridactyl individuals it has been common to claim that monodactyly evolved convergently in *Pliohippus* and *Equus* (e.g., Azzaroli, 1992, who claimed that monodactyly evolved on four separate occasions, additionally in *Astrohippus*, and *Hippidion* + *Onohippidium*). However, as noted above, tridactyl individuals of *Pliohippus* have phalanges of the medial and lateral digits that are reduced in size in comparison to other tridactyl equines, and they have a number of other pedal features elsewhere seen only in monodactyl equids. We consider that functional monodactyly evolved only once within the Equidae, in the common ancestor of *Pliohippus* and the more derived members of the Equini. However, the complete loss of the medial and lateral digits (i.e., the transition to full monodactyly) evidently occurred convergently at least twice, as discussed below.

Although the phylogeny in **Figure 2** places monodactyly as a feature of all equids crownwards of *Pliohippus*, it is not known for certain whether or not any species or individuals of *Astrohippus* or *Dinohippus* retained medial and lateral digits. MacFadden (1998) claimed that both genera are monodactyl, as far as is known. Although MacFadden (1992, p. 255) originally noted that *Dinohippus* was variably tridactyl, this is actually a reference to the Ashfall specimens of *Pliohippus*, referred to as *Dinohippus* in Voorhies (1981). This is also the source of the claim in Parker et al. (2018) that *Dinohippus* was variably tridactyl (pers. comm. of CMJ with Abigail Parker). Azzaroli (1992) also appeared to have been under a similar misunderstanding in claiming for variability in digit reduction in *Protohippus*: again, he was referring to the Ashfall *Pliohippus*.

An examination by CMJ of a collection of metapodials of *Astrohippus* from Guymon area in Texas (late Hemphillian) in the AMNH revealed no evidence of scars for the medial and lateral metapodials extending further than around halfway down the bone. Hussain (1975, p. 218) claimed that *Dinohippus* "also became monodactyl at about the same time" (as *Pliohippus*), but he did not further elaborate on any incidence of tridactyly in *Dinohippus*. However, there is some evidence for the retention of side toes in *Dinohippus*. A UNSM specimen (27855) definitively referred to as *Dinohippus* evidences lateral and medial first phalanges. An AMNH specimen referred to as *Dinohippus* sp. (F:AM 116128), from the Burge Member of the Valentine Formation (the same member as *Pliohippus pernix*, which would make it younger than any other recorded member of the genus), evidences complete (but very slender) medial and lateral metapodials with articulatory facets on their distal ends. From its age, it seems more likely that this individual would represent a specimen of *Pliohippus*, but the well-preserved skull (of similar size to *P. pernix*) shows only a shallow dorsal preorbital facial fossa, and no evidence of a malar fossa, resembling the condition in *Dinohippus*.

Further research is clearly needed to clarify the issue of the exact pattern of the origin of monodactyly in the Equini: that is, to determine whether there were only two instances of convergence in the loss of the medial and lateral digits (in *Pliohippus* and in the common ancestor of the more derived Equini), or if there were one or more instances within genera in the Equini lineage crownward of *Pliohippus* (i.e., whether basal members of *Astrohippus* and/or *Dinohippus* were fully monodactyl).

Hypotheses for the Evolution of Monodactyly

Most hypotheses about equid monodactyly relate to the notion of some sort of "improved" form of locomotion, accompanying increasing body size. Almost all authors perceive the acquisition of the "spring foot" as some sort of "precursor" to monodactyly, which of course it is in absolute terms, but it is not irrevocably linked with this further change in locomotor anatomy. Nevertheless, the reasons for evolving the "spring foot" should first be considered.

The Evolution of the "Spring Foot"

Thomason (1986) considered increased body size (i.e., larger than *Mesohippus*) to be an important factor. *Mesohippus* species were 40–60 kg in body mass, and the "break point" between more basal anchitheriines and the stem-equine anchitheriines appears to be around 70 kg. Larger animals experience greater change in the rate of momentum during locomotor foot impact, and the shock-absorption capacity of the "spring foot" would compensate for this. Additionally, recovery of elastic energy is also relatively less in smaller animals. However, size alone cannot be the reason as the "spring foot" never evolved in the Anchitheriinae, some of which attained sizes as large as any extant *Equus* and, as noted earlier, acquired their own ways of stabilizing the fetlock joint. Thomason (1986) also cited the likely complicating factors of habitat choice and ground compliance, noting that "spring-footed" equids were open-habitat animals (and a harder ground surface would mean greater foot concussion on impact). This observation may be extended to the "spring-footed" stem equine anchitheriines, which commenced their radiation in the late Oligocene, before the spread of grasslands in the early Miocene of North America, but at a time when open habitats were likely prevalent (see Damuth and Janis, 2011). Open-habitat ungulates have larger home ranges and travel greater daily distances (Janis and Wilhelm, 1993), and the energy-saving potential of the "spring foot" may have become important at this time.

Although this change to an unguligrade posture is termed a "cursorial adaptation," and is usually assumed to be adaptive for fast running, Reilly and Biknevicius (2007) consider that it may have been more related to slow transportation (walking) over long distances, especially as in modern wild horses trotting and galloping only comprises around 2.5% of their locomotor repertoire (A similar point about cursorial anatomy and efficiency for walking was made by Janis et al., 2004b).

Reasons for Retaining the Medial and Lateral Digits

Thomason (1985, 1986) also considered the transition to monodactyly, noting that most authors are more concerned about the function of the medial and lateral digits in the tridactyl equines than the reason for their loss. The consensus appears to be that the side toes would not contact the ground during locomotion, but might prevent sprains due to hyperextension of the central digit (Simpson, 1951), and/or offer additional support during extreme fetlock extension, such as during slipping on soft ground (Renders, 1984). Sondaar (1968) considered the retention of the side toes to be adaptive for locomotion on soft or muddy ground. Thomason (1986) cited Gromova (1952) for the notion that the medial and lateral digits may have acted to prevent lateral dislocation of the central digit, a function assumed in *Equus* by the extension of the sagittal ridge onto the dorsal surface of the distal metapodial articulation. Note, however, that the prominence of this ridge is a feature of derived *Equus* species, and the extent to which the ridge extended onto the dorsal articular surface in *Pliohippus* is not well-established. If this ridge was performing an essential function that was lost along with the medial and lateral digits, it seems probable that a modern *Equus*-like condition would be acquired sooner in monodactyl equids.

Thomason (1986) also cited Zhegallo (1978), who considered that the medial and lateral digits could help absorb the forces of impact through the ligamentous connections to the central digit. However, while this may explain the reason for the retention of medial and lateral metapodials, it does not address the reason for retention of the medial and lateral digits. This hypothesis may, in fact, explain the retention of much of the shaft of the medial and lateral metapodials in monodactyl equids.

Shotwell (1961) presented evidence to show that, during the early late Miocene (Clarendonian) of North America, hipparionin horses were found in more mesic, woodland-savanna-like environments, many of which (for example, those in the Northern Great Basin) did not contain monodactyl equines or their ancestors. But in the latest Miocene North American (Hemphillian) hipparionins declined and species of monodactyl equins spread in association with an encroachment of more arid, steppe-like habitats. Old World hipparionins also underwent a precipitous decline in diversity at the end of the Miocene, but were not replaced by equins; rather, a reduced number of hipparionin genera persisted between 5.3 and 2.6 Ma; *Equus first* occurred in the Old World 2.6 Ma. Shotwell (1961) considered that the retention of the side toes would have rendered tridactyl equines more agile, providing better ground traction, and made them better at dodging predators in the woodland-savanna environments, while in the more open grassland habitats preferred by *Pliohippus*, where high speed locomotion would have been required for predator escape. Shotwell (1961) does not speculate as to why a monodactyl foot would be better for high speed, except to say that in open environments "agility was then a burden." Bernor et al. (1997), in their description of the Höwenegg *Hippotherium primigenium* assemblage, argued that the slender bauplan, flexible spine and tridactyl foot were adapted to leaping and springing in their woodland setting.

Researchers have reexamined the issue of habitat differences between tridactyl and monodactyl horses in the past decade, availing themselves of modeling techniques and large databases on fossil occurrences unavailable to Shotwell. Maguire and Stigall (2008) employed a phylogenetic biogeographic analysis of the Equinae, and showed some regional differences between the tribes, both in the areas of their original diversification and in their subsequent dispersal. In terms of differences between tridactyl and monodactyl equines, they note that protohippins largely diversified in the Gulf Coast areas, while hipparionins and equins initially inhabited the same northern and western biogeographic regions. But with increasing late Neogene aridity and the spread of more open grasslands, by the Pliocene the hipparionins became restricted to the more mesic Gulf Coast region, while equins (primarily the genus *Equus*) diversified elsewhere. Maguire and Stigall (2008) followed Shotwell (1961) in suggesting that this difference was related to foot anatomy, tridactyl equids faring better in "muddy substrates."

Maguire and Stigall (2009) used niche modeling techniques, determining different habitat types within the Great Plains biogeographic region to examine the distribution of species occurrences. They concluded that a major difference between the mid Miocene interval (Barstovian and Clarendonian) and the later Miocene and Pliocene interval (Hemphillian and Blancan) was for habitats to become less fragmented, with a more homogenous type of grassland habitat predominating. Species ranges became broader, possibly resulting in reduced rates of speciation that contributed to the late Neogene overall taxonomic decline of equids in general. However, Parker et al. (2018), also used niche modeling techniques (employing ecomorphological traits such as body size, hypsodonty and toe number), and showed no evidence of differences in habitat occupancy between monodactyl and tridactyl equids, and no specific correlation of any of these traits with grassland habitats. They attributed the evolution of monodactyly to increasing body size and "other selective pressures" rather than to habitat choice, and they followed the general trend in considering tridactyly adaptive for "wet substrates." The latter hypothesis is rejected based on the Old World distribution of hipparionins and their ecological context (Bernor et al., 1996, 2010; Eronen et al., 2009; **Figure 3** herein).

In summary, it appears that, while hipparionins and equins may have occupied different biogeographic ranges to some extent, and that equins expanded in cooler and more arid regions in the late Neogene while hipparionins retreated from them, the fact that both types of equids had similar habitat occupancies for much of the later Miocene indicates that habitat preference *per se* cannot be the reason for the different locomotor morphologies. We propose later that, rather than different habitat occupancy, monodactyl and tridactyl horses had differences in their preferred gaits and economical travel speeds.

Reasons for Losing the Medial and Lateral Digits

There are two main hypotheses relating to digit loss: the notion of "inertial load," and the notion of "beam strength." Both were summarized by Thomason (1986). However, both hypotheses depend on the assumption that *Equus* has a larger body mass than all tridactyl equines, and that body size increase played an important role in this locomotor transition.

The "inertial load" hypothesis is perhaps the most common one, with the consideration that the additional toes add weight to the distal portion of the limb, and so would increase the metabolic cost of locomotion. This extra weight could be tolerated at smaller body sizes, especially if the medial and lateral digits retained some function; but with increasing body size the "inertial load" would become relatively greater, and there would be selection for digit reduction and loss. This hypothesis falters not only because many species of Old World hipparionins were within (or even exceeded) the size range of extant species of *Equus* (see e.g., Cantalapiedra et al., 2017), but also because the species of *Pliohippus* (whether monodactyl or tridactyl) were of similar body size to the contemporaneous (late Miocene) tridactyl equids, with body masses in the 100–200 kg range (excluding smaller "dwarfed" forms such as species of *Calippus* and *Nannippus*). A further consideration is that, because the central digit becomes enlarged in monodactyl forms (especially apparent in *Equus*; this would require investigation for the other monodactyl taxa), the larger central digit may equal the mass of the original three digits (in the derived tridactyl condition), and the overall inertia of the foot may not actually be reduced.

The "beam strength" hypothesis starts with the observation that a single beam is stronger in resistance to bending than two (or more) beams made of the same quantity of material and of similar cross-sectional shape (Alexander, 1980; Biewener, 1998). Thomason (1986) expanded on this idea, proposing a combination of single beam strength and reduction of inertia as the reason for the loss of the medial and lateral digits. However, it seems to us that while the "single beam" concept could explain a transition from a *Mesohippus*-like condition, with three digits of subequal size, to an *Equus*-like single digit condition, this transition was more-or-less accomplished with the enlargement of the central digit with the evolution of the "spring foot" in derived anchitheres. This notion of "beam strength" does not seem appropriate for a consideration of reasons for monodactyly in the Equinae, where all forms have a central digit that is much larger than the medial and lateral ones. Note that the cross-sectional diameter of the central metapodial scales with positive allometry in equids (Thomason, 1986), in part reflecting the "spring foot" transition when three subequal digits were essentially replaced by a single, larger one. Simple beam resistance does not explain the persistence of small medial and lateral digits in most tridactyl equines, nor their subsequent loss.

McHorse et al. (2017) undertook an elegant study on the beam strength and likelihood of fracture failure of equid metapodials, examining not only the strength of the central digit but also the contributions of the medial and lateral digits. They investigated how these biomechanical functions changed with increasing body size and digit reduction, quantifying the latter by employing a "toe reduction index" (TRI). They studied 11 different equid genera ranging from *Hyracotherium* to *Equus* (most represented by two specimens), and also included two specimens of tapir (*Tapirus bairdii*). *Pliohippus* was represented by a single specimen of *P. pernix* from Ashfall (University of Nebraska State Museum [UNSM] 52297), presumably one of the tridactyl individuals as its recorded TRI is barely less than the included hipparionins. The results they presented are for the metacarpals, but results for the metatarsals were similar.

The resistance of the central metacarpal to bending stress (i.e., beam strength) was much greater in *Equus* than in any tridactyl equine. *Tapirus* had similar resistance to the tridactyl equines, probably due to its large size, while the values were considerably less in the other equids (anchitheres and hyracotheres). The maximum stresses experienced by the central metacarpal during loadings for "normal locomotion" (trotting) were within the zone of bone safety factors for all taxa, but the results were different for "performance locomotion" (galloping or jumping). Here the stresses exceeded the safety factor range in most equids, the exception being *Equus* and three of the tridactyl equines (including *Pliohippus*); for most equids (and the tapirs), stresses in the central metacarpal were only kept below dangerous levels (approaching or exceeding fracture stresses) if contribution from the medial and lateral digits was taken into account.

McHorse et al. (2017) summarized their results by noting that both metacarpal cross-sectional area and second moment of area (=resistance to bending) increase with positive allometry in equids, a trend unusual among mammals, but most of the tridactyl equids (all considerably smaller than extant *Equus*) would have experienced unsafe levels of stress in performance locomotion without contributions from the medial and lateral digits. They noted that the increasing size of the central digit compensates for the increasing body mass throughout equid evolution, and the medial and lateral digits may have been lost simply because of relaxed selection once the central digit was strong enough to counter all locomotor forces (as apparent in most of the tridactyl Equinae); but the "inertial load" of the retained side toes may have reduced speed or increased locomotor costs, and so they would ultimately be selected against.

The research of McHorse et al. (2017) greatly increases our knowledge about the evolutionary biomechanics of the equid limbs, but their final conclusion is that their results support the hypothesis that "body mass was a potential driver of digit reduction." However, they did not consider data from *Equus*-size Old World hipparionins: for example, *Eurygnathohippus hasumensis* (BM ∼500 kg; see Bernor et al., 2010) and *Proboscidipparion sinense* (BM ∼465; see Sefve, 1927; Qiu et al., 1987; Bernor and Sun, 2015; Bernor and Sen, 2017) are both fully tridactyl, and thus body size increase cannot be the major driver of monodactyly. We again note that digit reduction begins at the level of *Pliohippus*, equins no larger than the contemporaneous hipparionins.

AN ALTERNATIVE HYPOTHESIS FOR THE EVOLUTION OF MONODACTYLY

Anatomical Features That Accompany Monodactyly

Monodactyly is accompanied by a suite of anatomical features related to the foot suspensory apparatus, many of which are apparent even in tridactyl individuals of *Pliohippus*. While it might be assumed that these pedal modifications compensate for the lack of the supportive function of the medial and lateral digits, it seems to us more likely that this notion should be reversed: that is, that the enhanced suspensory apparatus rendered the medial and lateral digits redundant. With this perspective, reasons for an enhanced suspensory apparatus should be the primary consideration.

The equid suspensory apparatus limits over-extension of the fetlock and helps to "spring" the foot back from an extended position. The amount of extension possible at the fetlock joint relates to the degree of curvature of the distal articular surface of the metapodials, as also reflected by the dorsal extent of the sagittal ridge around that surface. This anatomy (highly curved articular surface with dorsally-extended sagittal ridge) distinguishes *Equus* from "*Merychippus*," indicating a greater extent of fetlock extension (dorsi-flexion) in *Equus* (Thomason, 1985, 1986). Thomason (1986) estimates a maximum extension angle of around 65° (to the vertical) in "*Merychippus*," in contrast to 90° in *Equus*. Although this anatomy has not been systematically examined in other members of the Equinae, it appears that a trend toward the *Equus* condition (not even fully realized in early species of the genus) accompanies the trend toward monodactyly (see **Figure 2**). A more developed suspensory apparatus allows for a greater extension at the fetlock, and hence for a greater degree of stretching of the flexor tendons. This in turn allows for greater amount of elastic energy recovery during locomotion, and hence a greater efficiency of locomotion. Thus, we propose that the transition to monodactyly is correlated with selection for greater efficiency of locomotion, irrespective of any considerations of the loss of the "inertial load" of the side toes.

Another anatomical feature apparently correlated with monodactyly is the change from a more flexible back to a stiffer one, with restriction of sagittal movements of the lumbar region. Jones (2016) examined the lumbar region of a series of North American fossil horses and concluded that anterior and middle lumbar flexibility decreases throughout equid evolution (although posterior lumbar flexibility remains approximately the same). She showed shifts of decreasing flexibility to occur at the transition between hyracotheriines and basal anchitheriines (e.g., *Mesohippus*), between basal anchitheriines and stem equine anchitheriines (e.g., *Parahippus*: i.e., at the level of the acquisition of the "spring foot"), and then to an *Equus*-like condition at the level of *Hippidion* (BM ≥250 kg). She proposed that hyracotheres may have practiced a "flexible-back" type of gallop, but that more recent equids were more restricted. As previously mentioned, *Nannippus* (the only hipparionin included) shows more restricted lumbar flexibility, converging on the condition seen in *Equus*.

Jones (2016) concluded that increasing body size was the main driver in the evolution of equid lumbar stability. But, again, size cannot be the only factor: not only did the Old World hipparionins remain persistently tridactyl, they also had a lumbar region that evidences a much greater degree of mobility than *Equus*. *Hippotherium primigenium*, a basal Old World hipparionin from Höwenegg (late Miocene of Germany), was of a similar size (BM ∼295 kg) to a common zebra (*Equus quagga burchelli*), but also evidenced a capacity for greater medio-lateral lumbar rotation (Bernor et al., 1997). *Hippotherium* had comparably weakly-developed zygapophyses and expansion of the articular surfaces of the transverse processes; thoracic and lumbar vertebrae with long spinous processes indicative of well-developed epaxial musculature; and a sacrum that was long and narrow in comparison with *Equus*, with a more narrow flare of the ala ossis sacri that form the sacroiliac joint, and longer spinous processes with expanded distal tubercles (see **Figure 6**). Bernor et al. (1997) interpreted this spinal anatomy as enabling *Hippotherium* to leap and spring and to make sharp turns while running, advantageous in its original woodland habitat.

Although Jones (2016) interpreted the lumbar flexion of *Pliohippus pernix* (BM ∼175 kg) to be similar to that of the tridactyl equids *Parahippus* and "*Merychippus*," its sacrum is more like that of *Equus*. While the sacrum of the contemporaneous (and similarly-sized) hipparionin *Neohipparion* resembles that of *Hippotherium*, the one of *Pliohippus* is both shorter and broader, with spinous processes that are shorter, more posteriorly inclined, and more appressed to each other, approaching the *Equus* condition (see **Figure 6**). The hipparionin *Pseudhipparion* (UNSM 27837) has a sacrum of similar anatomy to *Neohipparion*. The hipparionin sacral anatomy appears to be the more basal condition: similarly long sacra can be seen on mounted skeletons in the Fossil Mammal Gallery at the American Museum of Natural History, including the anchitheriines *Parahippus* and *Hypohippus*, and the basal equin *Acritohippus* (= "*Merychippus*") *quinni*, while *Dinohippus* has a shorter, more *Equus*-like sacrum. We interpret this morphology as further indication of a more flexible back in hipparionins than in the monodactyl equins, with a stiffer back and shorter sacrum being a derived condition in the equins.

A Hypothesis of a Change in Preferred Gaits

We have shown that monodactyl equines combine a more extensive suspensory apparatus in the foot with a less flexible back than hipparioninins, and propose that this combination of anatomical features is indicative not only of selection for increased locomotor efficiency (via elastic return of some proportion of the energy lost over a stride cycle) but also of a difference in the preferred gait for travel at speeds faster than a walk. The trackways of a hipparionin from the Pliocene age locality of Laetoli, Tanzania show it to have been performing a running-walk (Renders, 1984). Of course, a single trackway is insufficient to determine that all tridactyl horses habitually used this gait: but we discuss below why the anatomy of monodactyl equines might be specifically adapted to the use of a trot for economical locomotion over distances, and why a running-walk may have been the preferred intermediate-speed gait for tridactyl equines. This proposal of differences in gait selection depends, in part, on the hypothesis (discussed in the following section) that, during their initial appearance in the late Neogene of North America, monodactyl equines adopted a diet that required a greater extent of daily or seasonal roaming behavior than that of the contemporaneous tridactyl forms.

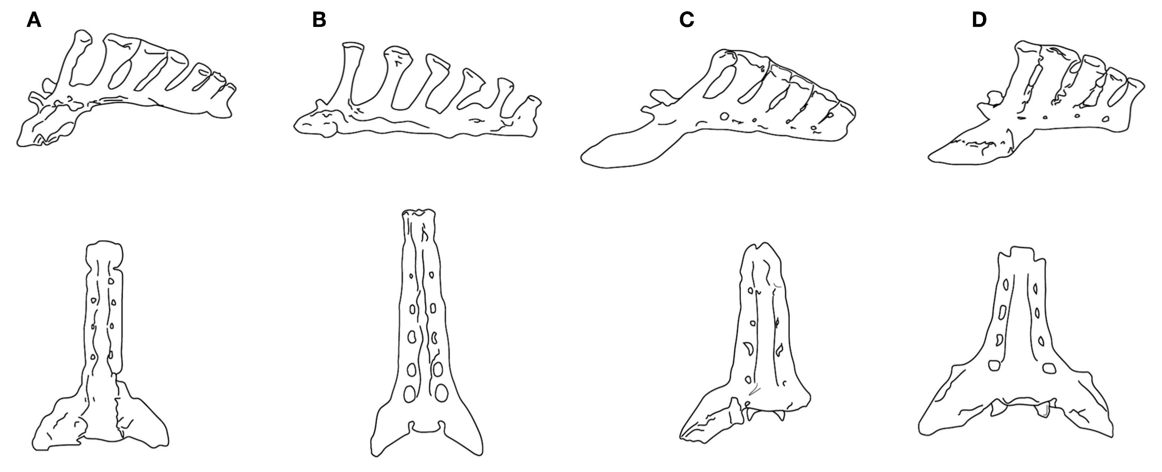


FIGURE 6 | Sacra in left lateral view (upper) and ventral view (lower). **(A)** *Neohipparion coloradense* (F:AM 69511); **(B)** *Hippotherium primigenium*, modified from Figure 5.4.2 in Bernor et al. (1997); **(C)** *Pliohippus pernix* (F:AM 60872); **(D)** *Equus grevyi* (AMNH 82036). (F:AM = Frick Collection, American Museum of Natural History). All specimens drawn to the same size, not to scale. Photographs taken by CMJ. Illustration by James G. Napoli.

Although, as previously discussed, the mechanical properties of the trot and running-walk gaits are similar, the trot is likely to be a more efficient gait for distance travel, while the running-walk might have advantages if economy over distance was not an issue. Biknevicius et al. (2006) note that peak ground reaction forces of individual limbs are smaller in tölting horses than in trotting horses (see also Waldern et al., 2015), which may mean that a running-walk could be comfortably sustained at speeds at which a trotting horse would have transitioned to a gallop. They also speculate that, with at least one foot being on the ground at all stages of the stride cycle, the running-walk might provide a both a better base of support and enhanced proprioception, and hence afford superior performance over uneven surfaces. The notion of enhanced proprioception is especially interesting, as this may have been a functional reason for retaining non-weight-bearing medial and lateral digits.

However, a disadvantage of the running-walk is that it may be metabolically more expensive than trotting. In a comparison of the two gaits practiced by the same Icelandic horses, Waldern et al. (2015) noted that these horses had a shorter stride and a higher stride frequency when tölting than during trotting, and that they also experienced less limb compression. As the metabolic energy expended per stride is a constant (Taylor et al., 1982), this implies that a running-walk is more expensive than trotting, and Waldern et al. (2015) noted that the metabolic power required was around 5% greater. They also noted (citing Ingolfsdottir, 2013) that riders observe that Icelandic horses prefer the trot to the tölt when fatigued. In horses, metabolic costs increase less steeply with increasing speed in trotting than in either walking or galloping (Minetti et al., 1999), which contributes to it being an efficient gait, but it seems unlikely that this would be true for the running-walk.

As previously noted, monodactyl horses have anatomical evidence of a greater maximum extent of fetlock extension (dorsi-flexion) than tridactyl ones. Waldern et al. (2015) note a lesser degree of limb compression in tölting vs. trotting horses: this implies that the running-walk relies less on elastic energy return than the trot, as limb compression occurs primarily via hyperextension of the fetlock joint (especially in the forelimb). The corollary of this is that the trotting gait in horses is more reliant on fetlock hyperextension and elastic energy recovery than the running-walk. Interestingly, Biewener (1998) noted that the maximum energy storage (40%) occurred during the transition from walk to trot, and that energy storage in the trot is greater than in the gallop. Biewener (1998) also noted that it is the deep digital flexor tendons that experience the greatest strains and contribute most to elastic energy savings.

How might the relative stiffness of the back (including the shorter and broader sacrum) in monodactyl horses be correlated with the above observations? The trot gait in extant equids is a stiff-backed gait compared with the gallop, which entails a greater extent of lumbar flexion (Harris, 2016). However, perhaps it is not that the stiffer back aids a trotting gait, but more that it is a consequence of having more "springy" legs. More competent leg springs might reduce the need for the demands for elastic function in the back during the gallop: stiffening the back might then be advantageous in reducing epaxial muscle activation required for stiffening the torso during locomotion (we thank Jim Usherwood for this proposition). This hypothesis could be explored by comparing the size of the vertebral spinous processes (supporting the epaxial musculature) in hipparionins and equins: note that these are large in *Hippotherium* (Bernor et al., 1997), and that the sacral spinous processes are larger in the hipparionins depicted in **Figure 6**. It is also interesting in this regard that among gaited domestic horse breeds, those practicing a running-walk are favored by longer backs and hips (i.e., the sacral area).

In summary, it appears that the running-walk might have certain locomotor advantages, especially on uneven surfaces or mixed terrestrial substrates such as found in wooded and forested settings, but a trot gait would be more metabolically efficient for distance travel at a medium-speed sustained gait. A tridactyl horse employing a trot would benefit from increased elastic energy storage (more so than when doing a running-walk), and so there would be selection for an increased extent of fetlock hyperextension and concomitant increased support for this motion from the ligamentous suspensory apparatus. Thus, we propose that an initial change in behavior (change in preferred gait, due to a greater extent of daily roaming) would result in selection for change in morphology (e.g., Lister, 2014); even small changes would incrementally reduce locomotor costs.

It is evident from the morphology that monodactyl horses are maximizing their capacity for elastic energy recovery, but why would this also be associated with the loss of the medial and lateral digits? It is conceivable that there was no active selection for the loss of the medial and lateral digits, but rather that this was a corollary of enlarging the central digit. In equid ontogeny, the foot originally develops with five digits and all but the central one are reduced by means of cell death (Cooper et al., 2014). In tridactyl equids there must have been a lesser extent of apoptotic digit reduction; but could it be possible that selection for a more predominant third digit might have the side effect of a greater reduction of the second and fourth ones during ontogeny? In particular, given the importance of the digital flexor tendon in elastic energy storage, perhaps an initial part of this selection was for a larger distal sesamoid bone for its support and insertion. This notion is admittedly speculative; but our point is that the essence of pedal anatomy in monodactyl equids may primarily be a large central digit in a foot with greater ligamentous support and an enhanced suspensory apparatus. The loss of the medial and lateral digits may not necessarily be adaptive *per se,* but, rather, may merely represent an ontological consequence.

SUMMARY AND CONCLUSIONS

Monodactyly is often perceived as an evolutionary "improvement" in equid locomotion. But this notion of "improvement" does not explain the persistence of tridactyl horses for millions of years after monodactyly first appeared, nor why only a single equid lineage made the transition to (greater) reduction and/or loss of the medial and lateral digits. The Old World hipparionins were highly diverse, and paralleled the New World equins in changes in body size (both increases and decreases) and hypsodonty (Cantalapiedra et al., 2017), yet they showed no trend toward monodactyly. MacFadden (1992) notes that, in the overall scenario of late Neogene equid evolution, it was the tridactyl horses that were the most successful radiation.

Monodactyly (or incipient monodactyly) was first apparent in North America, with the genus *Pliohippus* in the middle Miocene around 15 Ma (definitively monodactyl forms apparent by ca. 10 Ma). At this time tridactyl equines were the predominant forms (∼10 genera, see **Figure 3**). Tridactyl equines did not decrease in diversity until around 5 Ma (by which time they had become increasingly restricted to more southern regions). Tridactyl equines became extinct in North America at ca. 2 Ma, and at <1 Ma in southern Asia and Africa, by which time the only remaining monodactyl equin was the genus *Equus* (see MacFadden, 1992, 1998; Janis et al., 2008). Considering the early evolution of monodactyly, rather than the eventual success of *Equus*, monodactyl horses must initially have been doing something different in a world where tridactyl horses were predominant.

We propose that the divergence of the lineage of equines that became monodactyl from their tridactyl relatives had its origins in a difference in diet and foraging behavior. Although niche modeling has demonstrated that North American Miocene monodactyl and tridactyl horses did not live in completely different habitats (Parker et al., 2018), nevertheless there must have been differential selection on the locomotor morphologies of tridactyl and monodactyl lineages. We propose that North American Miocene monodactyl horses adopted a feeding regime that entailed a greater extent of roaming behavior, on a daily and/or seasonal basis. African zebras evolved as part of a migratory ungulate community that was dependent on long-distance roaming. This original (Miocene) diet may have comprised a greater percentage of grass than in the tridactyl equines, as implied by some (but not all) studies of dental morphology and wear; but our hypothesis does not depend on the actual composition of the diet, only of the foraging behavior necessary to subsist on it.

A greater extent of roaming behavior would have led to selection for limb morphology that supported more efficient distance transport. This might simply have been for more efficient walking, as proposed by Reilly and Biknevicius (2007). Zebras usually walk while migrating (Pennycuick, 1975), but the locomotory issue for the members of the equin lineage may have been for a combination of speed and efficiency for daily travel between patchy resources of food. Wild horses are known to trot for daily distance travel; the trot was used for efficient transport by the US cavalry, and endurance equestrians habitually select the trot gait (Harris, 2016; Egenes, 2017). The trot gait involves a much greater degree of storage of elastic energy in the flexor tendons than the walk: as we propose that it is this aspect of locomotor performance (i.e., greater efficiency resulting from enhanced elastic energy storage) that drove the evolution of monodactyly, it is a plausible proposition that a preference for a trot gait at speeds between walk and gallop was the selective factor for anatomical change. The adoption of the trot as the preferred medium-speed gait may have been a key difference between equins and hipparionins, given that trackways evidence a running-walk in a hipparionin (Renders, 1984). This proposed locomotor difference may also explain the difference in the lumbar and sacral regions of hipparionins (longer and more flexible) and equins (shorter and stiffer), and also the less-flexed knee joint of equins (Hussain, 1975). In modern horses, as previously noted, the running-walk gait may have advantages for stability and proprioception over uneven surfaces, but it is metabolically more demanding than a trot.

Although both running-walk and trot gaits in modern horses rely on spring-mass mechanics with compliant legs, there is a greater extent of limb compression in trotting horses, and thus likely a greater amount of return of stored elastic energy in the foot tendons and ligaments. Both monodactyl and tridactyl equines had a "spring foot" that would have promoted storage and recovery of elastic energy during locomotion; but monodactyl equines show osteological evidence for greater amount of hyperextension of the fetlock (morphology of the distal metapodial articular surface) and a more extensive suspensory apparatus to support the distal foot during this hyperextension (larger proximal sesamoid bones). The foot anatomy of monodactyl equines primarily reflects a greater extent of energy storage and recovery during locomotion, and hence more economical transport: the loss of the medial and lateral digits may not be adaptive *per se*, but may simply be a consequence for selection for a foot that is superior in economy for distance transport.

If monodactyl horses were initially in the minority, how did monodactyly, the distinguishing feature of the genus *Equus*, come to predominate and eventually be the only form of equid foot anatomy? Monodactyly in North American equids first appears in the later Miocene, when higher latitude cooling and aridification was starting to dominate Cenozoic climatic regimes (Zachos et al., 2001). However, aridification had an earlier onset in North America than in the Old World (late Miocene vs. Plio-Pleistocene); this may explain the success of many mammals migrating to the Old World in the Plio-Pleistocene (*Equus* among them), as they would have been preadapted to the emerging Old World arid conditions (Eronen et al., 2012). Thus, the late Miocene North American equids would have been experiencing increasingly arid conditions, while the Old World ones were still inhabiting a more mesic world. This may explain why no Old World tridactyl lineage adopted the type of roaming behavior that we hypothesize characterized the emerging New World monodactyl lineage.

Note that with further increasing aridity in North America in the earliest Pliocene, the remaining tridactyl equines became more or less restricted to more southern regions, while the monodactyl equines diversified in the more northern grasslands. Maguire and Stigall (2008) attributed this biogeographic divergence to substrate differences, but we consider it more likely that the different equine lineages were following divergent dietary preferences and, hence, divergent foraging behaviors. It is also of interest that the one hipparionin that did adopt some *Equus*-like locomotor morphology of the feet and back, *Nannippus*, was the only hipparionin to survive into the Pliocene in the more northern regions of North America (see **Figure 3**). Note also that this was a dwarfed form (estimated BM of Pliocene *N. peninsulatus* = 75 kg), which contrasts with the hypotheses for the evolution of *Equus* pedal morphology being related to an increase in body size (and also note that the monodactyl litoptern, *Thoatherium*, was even smaller, ∼25 kg.).

When the genus *Equus* migrated to the Old World at the start of the Pleistocene (2.6 Ma) the hipparionins were still present, although of reduced diversity; but hipparionins persisted alongside of *Equus* until sometime later than 1.0 Ma in China and Africa. *Equus* may have had the advantage in the Old World Pleistocene, as with the encroaching aridity and cooling it would have been preadapted for more efficient distance transport. Would Old World hipparionins have evolved monodactyly if not for the presence of *Equus*? The question is unanswerable, but it is worth noting that the lineage leading to *Equus* had at least 10 million prior years of evolutionary history leading to the foot anatomy seen in modern species of the genus. As previously noted, although monodactyly was established somewhere around the *Astrohippus/Dinohippus* stage in the latest Miocene, even early species of *Equus* lacked the full suite of derived anatomical features seen in extant equids (see **Figure 2**). It may well be that the Old World hipparionins would never have "progressed" to monodactyly, as was the fate of their New World relatives and, moreover, they never showed this tendency in their 10 Ma (or more) of evolution in Eurasia and Africa.

We conclude that the monodactyly of *Equus* represents an exaptation for the cooler and more arid world of the Plio-Pleistocene and the present day. We propose that the origins of monodactyly were in the divergent foraging behaviors of late Miocene North American hipparionin and equin lineages, leading to selection in the latter lineage for a greater efficiency of locomotion. This novel locomotor adaptation, manifested in the monodactyl condition, set the stage for the genus *Equus* to survive and flourish globally in the Plio-Pleistocene, while the tridactyl horses that had dominated the late Miocene were not so fortunate. In terms of monodactyly, at least, *Equu*s was fundamentally a lucky genus in the grand scheme of equid evolution.

AUTHOR CONTRIBUTIONS

CJ conceived of the idea, and provided the information on North American equids. RB provided the information on Old World equids. Both authors contributed to the writing of the paper.

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Hypsodont Crowns as Additional Roots: A New Explanation for Hypsodonty

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The hypsodont crown of *Equus* and of other hypsodont ungulates has two functions: It has an extra crown in the alveolus which erupts and becomes a functional crown that enables the horse to live longer and feed on abrasive foods and grit. The second functional aspect is that the crown, while it is in the alveolus, acts as a root to support high stress during mastication. In general, roots do not increase in size during evolution when the tooth crown increases. Delayed development of the true root is a heterochrony phenomenon and is possibly dynamically interactive with the forces applied on the crown. Thus, when the crown becomes worn, as in old age, the mastication forces acting on it are very strong. This is an interesting phenomenon and reinforces our hypothesis of the second functional difference that the young tooth's crown embedded in the alveolus acts as a supporting root. The *Equus* hypsodont tooth has been represented by a class I lever. That is, the fulcrum is in the middle: the effort is applied on one side of the fulcrum and the resistance (or load) on the other side, for example, as in a crowbar. As an individual *Equus* ages, the alveolar tooth height decreases. Data display an exponential increase in force generated as tooth height decreases. The elongation and closure of the root is delayed until the crown is almost entirely worn. When the crown becomes worn, the mastication forces acting on it are very strong. This is an interesting phenomenon and reinforces our hypothesis that the young tooth's crown, embedded in the alveolus, acts as a supporting root. This discovery is based on the observation that fossil ungulates *most commonly die at an early age, leaving a substantial amount of crown unused*. The unused crown is not likely a reserve tooth crown for a season of hardship because it is rare to find examples of such hardships in the fossil record.

Keywords: *Equus*, hypsodont, roots, evolution of hypsodonty, crowns as roots

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INTRODUCTION

Ungulate (hoofed) mammals have often evolved tall tooth crowns. The tall-crowned teeth have been termed hypsodont teeth (hypso; meaning tall) (Van Valen, 1960). Hypsodonty is a common specialization in many herbivorous mammals and it is found in artiodactyls, perissodactyls, suids, proboscideans, rodents, South American ungulates, and other groups (Janis, 1988; Williams and Kay, 2001; Mihlbachler and Solounias, 2006; Damuth and Janis, 2011). It has evolved independently from a low crowned tooth termed brachydont (brachy; meaning short). Among these, *Equus* is one of the most hypsodont ungulates known (Stirton, 1947; Simpson, 1951). In *Equus* and in all other species with hypsodont teeth, a major part of the crown is embedded in the alveoli which erupts slowly to replace the active crown that has become worn. Hypsodonty has been studied extensively (see Damuth and Janis, 2011; Madden, 2015 for reviews). Our study is not meant to be a review of hypsodonty. The equid hypsodonty is commonly envisioned as an adaptation for grazing. Grasses are abrasive to teeth as they contain more phytoliths than other plants. Phytoliths are intracellular silica inorganic particles, which are thought to abrade teeth. Hence, equids and other ungulates that feed on grass and other abrasive vegetation wear down their enamel crowns more and faster (Strömberg, 2006; Janis, 2008). Mihlbachler et al. (2011) have shown that in the evolution of Equidae, hypsodonty correlates with the onset and further adaptation to grazing. Semprebon et al. (2016) show that Pleistocene grazing in *Equus* is not the only factor but grit plays a role as well (Sneva et al., 1983; Madden, 2015). Equid grazers need an extra crown, which is exactly what a hypsodont tooth can provide. That extra crown is situated in the alveoli. In contrast, browsers feed on softer vegetation than grazers and the entire tooth is exposed in the oral cavity. Only the roots are positioned in the alveoli. Browsers wear down about 0.9 microns of enamel per day. Grazers wear about 8.1 microns of enamel per day and hence possess more crown than browsers (Solounias et al., 1994; from Table 1). Recently, many researchers tend to think that it is grit that is the main cause of tooth wear (see Damuth and Janis, 2011 and Madden, 2015 for reviews). What is interesting, however, is that grit should wear down the teeth of browsers as well; a topic avoided. Pronghorns, goats and camels are hypsodont browsers, but the majority of browsers are brachydont. Many problems on how teeth actually become worn down remain to be solved.

Numerous articles and books have been written specifically about the evolution of equids (e.g., Matthew, 1926; Stirton, 1947; Simpson, 1951; Rensberger et al., 1984; MacFadden, 1994; Strömberg, 2006; Mihlbachler et al., 2011; Evans and Janis, 2008). If one considers broader studies on ungulates, including equids, an additional 20 pivotal studies could be included. The evolution of horses over the past 55 million years is clearly reflected in the changes of their teeth and diet (Mihlbachler et al., 2011; Semprebon et al., 2016). The present study does not question that hypsodonty relates to the abrasive grass diet or exposure to exogenous grit. It certainly does. An additional function, however, is put forward for the unerupted tooth crown. As vegetation contacts the tooth crown in the oral cavity, major stress is generated on that crown. It is proposed that *Equus* requires additional roots to take on excessive masticatory stress. The hypothesis is that the active exposed crown cannot be supported by the regular roots alone. Genetically, roots in mammals have a conservative morphology and apparently cannot increase in number or size. The new hypothesis is that the unerupted crown of *Equus* functions as a root. We propose that two functional regimes are present: (1) an extra crown for an abrasive diet (2) a root to support the stress. Our new hypothesis is similar to the alveolar hypothesis discussing eruption (Fortelius, 1985). The proposed term for this type of root is a plioroot. Plio means more in Greek; more root-additional root. It is also a pun as many of the hypsodonts evolve during the Pliocene which is a time of notable increase of grasslands and of hypsodont ungulates. In our study we treat the forces of mastication, tall teeth and the alveolus, and exposed functioning enamel as a first-class lever system. Archimedes, the ancient Greek polymath, referred to a first-class lever in his famous quote "Give me one firm spot on which to rest (a fulcrum) and I will move the Earth."

This study was inspired by the observation that in most species, death occurs well before the entire tooth is used (by NS). So why make so much more enamel if the species in question is not going to need it for mastication? The plioroot hypothesis explains these observations.

Recent studies have addressed hypsodonty and emphasized how it would form as a response to stress from feeding affecting the growth zone. Renvoisé and Michon (2014) explained in a different way that a hypsodont tooth is merely an expansion of the same framework of a brachydont tooth, by prolonging the growth zone between the root and enamel. It is an acceleration of that boundary which results in a heterochrony of the enamel. That extra growth will result in a wall (the tall crown). This wall of enamel-band was one of the types of hypsodonty in von Koeningswald's categories (von Koeningswald, 2011). Heterochrony results in that acceleration while the size and shape remain in their ancestral relationship (Gould, 1977). Renvoisé and Michon (2014) also thought of the stress during mastication which would create a feedback loop affecting heterochronic growth at the boundary of the enamel with the root. Witzel et al. (2018) pointed out that the formation of enamel occurs after the tooth has erupted and, hence its function. Thus, function relates and can affect growth. Growth of enamel may relate to longevity.

MATERIALS AND METHODS

Specimens of *Equus* were examined in the mammalogy and the paleontology collections of the American Museum of Natural History (AMNH), the University of Colorado Museum in Boulder (UCM), and the Natural History Museum of Basel (NHMBa). Specimens of *Equus* sp. from Alaska, *Hyracotherium* spp., *Mesohippus bairdii*, *Merychippus insignis* and *Protohippus primus,* and *Equus* sp. were examined to estimate root sizes. We had access to four domesticated *Equus caballus* specimens of a known age in the laboratory of NS.

A small number of specimens were used to support the development of this new theory, at this initial qualitative stage. For these, root, crown height, as well as occlusal lengths and widths were measured with digital calipers (**Figure 1**). **Figure 1** shows the excavated maxilla and mandible of *Equus*.

By examination of the dentition, the specimens we scored either as a younger adult or as very old. NS asked the question: was the crown completely exposed in the oral cavity or was there more enamel deep in the alveoli? If the crown is completely exposed, the roots should be visible where they contact the enamel. Visual comparison between younger and older teeth of the same species facilitated the scoring and the data collection. In

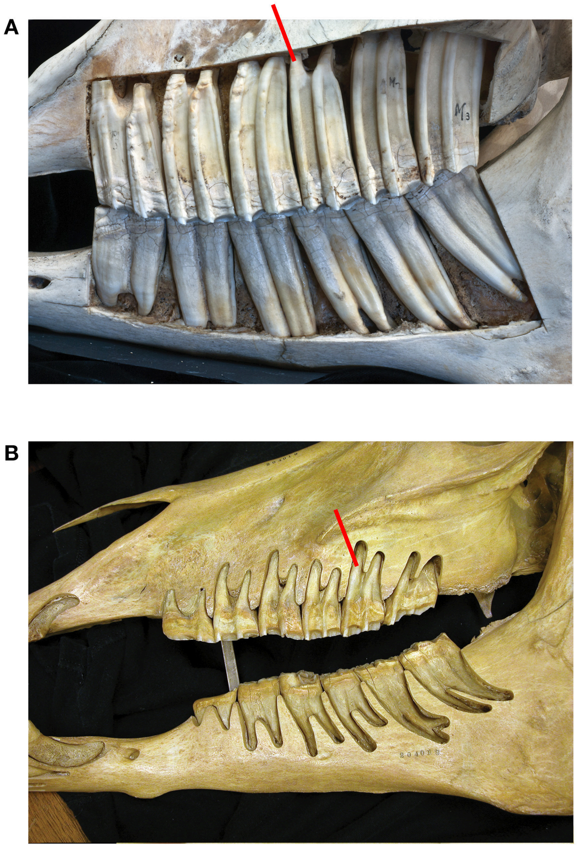

FIGURE 1 | (A) In *Equus caballus* NHMBa 28, extreme hypsodonty is observed; all six teeth (three premolars and three molars) are approximately equally hypsodont. The maxilla and mandible have been cut open to show the crown contained in the alveoli. The active crown is the exposed part. Red square shows the roots which are short and open-ended. **(B)** An old *Equus* individual AMNH 204019. The enamel crowns have been almost totally worn out. In this specimen, the roots are longer than in younger horses and closed. Root increase is most likely an epigenetic response to the reduction of the height of the crown which transmits increased forces. The pressures of mastication change and that induces the roots to grow longer.

TABLE 1 | Measurements of roots and crowns in mm.

Root	Crown	Length	Width
HYRACOTHERIUM			
x	4.21	7.88	9.28
8.33	4.19	7.82	9.19
8.96	4.61	8.68	10.81
6.89	4.12	8.15	9.7
6.12	3.73	7.2	9.44
7.67	4.26	8.45	9.71
5.77	4.01	8.12	10.1
7.2	3.94	8.82	10.43
Average root	Average crown	Average length	Average width
7.277142857	4.13375	8.14	9.8325
MESOHIPPUS			
10.37	7.7	12.46	13.86
11.92	10.73	14.06	15.19
9.59	6.49	12.54	15.72
11.09	x	12.59	15.78
11.03	x	12.05	15.28
Average root	Average crown	Average length	Average width
10.8	8.30666667	12.74	15.166
MERYCHIPPUS			
16.04	23.55	19.3	22.45
13.88	26.04	20.05	20.87
15.82	x	19.64	22.64
16.4	x	19.69	22.7
Average root	Average crown	Average length	Average width
15.535	24.795	19.67	22.165
PROTOHIPPUS			
6.15	18.16	18.2	18.85
13.32	22.19	16.62	16.82
12.01	25.32	18	20.48
Average root	Average crown	Average length	Average width
10.4933333	21.89	17.6066667	18.7166667
Equus			
5.21	80.09	27	28.31
4.41	83.58	30.45	29.24
5.26	84.38	28.51	29
8.29	x	27.9	27.22
8.73	73.75	31.66	25
Average root	Average crown	Average length	Average width
6.38	80.45	29.104	27.754
OLD *Equus* INDIVIDUALS			
24.62	19.52	28.18	25
33.43	15	26.83	27
Average root	Average crown	Average length	Average width
29.025	17.26	27.505	26

hypsodont species, when the roots were visible, the individuals were older, as most of the crown was worn down. When scoring the age of individuals it is critical to observe the base of the crown and the roots. Using this methodology, we counted the number of young ungulate adults and very old individuals from 16 localities at the AMNH and UCM (**Table 2**). The exploratory sample of taxa were: dromomerycids, bovids, equids, and camelids.

A few root lengths and crown dimensions of some species were recorded (**Table 1**) at the AMNH. To measure root lengths dentitions were used where the roots were exposed due to the brakeage of the fossil.

Four domesticated *Equus caballus* skulls and teeth were sectioned with a carpenter's band saw in the lab (young samples included: a 7 year old male NS 10, 5 year old NS 295; old samples included: an 16 year old male NS 102, and an 18 year old whose sex could not be identified as the canines had been removed NS 104). These specimens were donated from the Bolton Equine Center. Open maxillae and mandibles exposed horse dentitions and the internal anatomy of the alveoli (**Table 1**).

The longitudinally sectioned molar was hand painted with physical paints to help isolate it in Image J for quantification

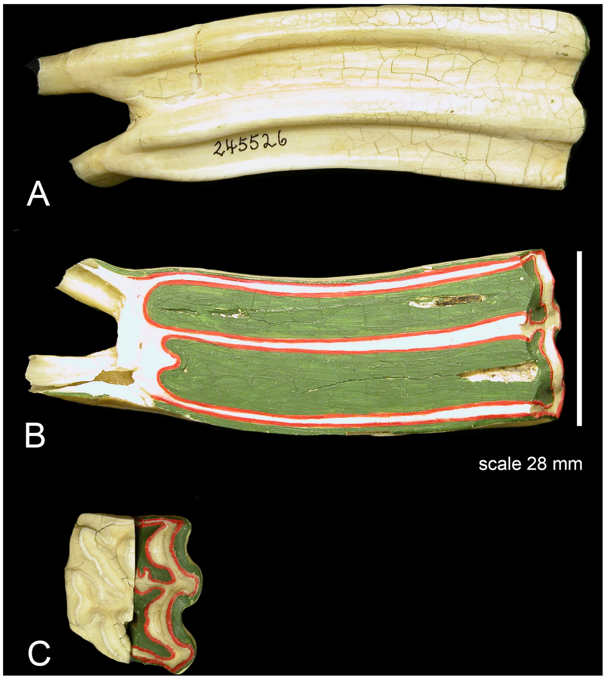

FIGURE 2 | An upper second molar of *Equus caballus* AMNH 245526 sectioned longitudinally and hand-painted. Colors: red is enamel, green cementum, white is dentine. The section is through the central cavities which are filled with cementum. The cementum is notably thick, and it surrounds the entire tooth. The enamel is thin. **(A)** The external aspect there the tooth is covered by cementum including the roots where it is thinner coating and hard to observe. **(B)** The inner aspect; note that the majority of the section is composed of cementum. The enamel is thin. **(C)** Occlusal view; half of the tooth is painted, and the other half is natural.

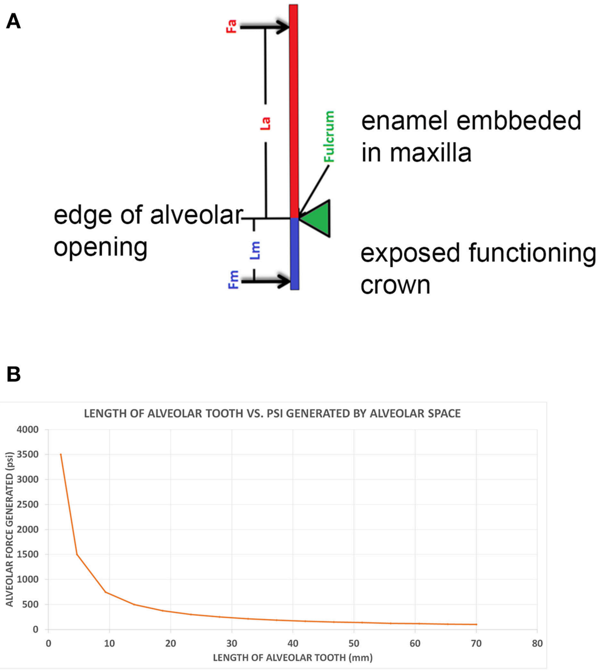

FIGURE 3 | (A) A class I lever representation of a hypsodont tooth. The black bar is the exposed functioning enamel crown. The black arrow is the transverse force not a vertical force. The green shows the fulcrum point as the opening of the alveolar space (again transverse) and the red line is the plioroot deep into the maxilla. In developing this model, the tooth is tilted horizontally. F_m is the force of mastication (estimated). L_m is the length of the exposed tooth to mastication (measured) in the oral cavity. L_a is the length of the crown embedded in the alveolus (measured). F_a is the force of the alveolar tooth needed to stabilize the tooth during mastication (calculated). The fulcrum represents the interface between the exposed tooth and alveolar tooth and is the oral opening of the alveolus. Blue indicates the exposed tooth and red indicates the hidden alveolar portion of the tooth. **(B)** Applying Equation 3 with constant values $L_m = 14$, $F_m = 500lbsF_m = 500lbs$, and knowing that the alveolar length of the tooth (L_α) for a horse at age three is 70 mm and age 18 is 2 mm, we can plot the alveolar force F_α vs. the alveolar length L_α, shown in **Figure 2**.

(**Figure 2**). In order to calculate enamel thickness and cementum we used Image J (Fiji) that quantified the tissues in photographs as pixels and calculated the square mm (specimen of **Figure 2**).

Mechanics

The study shows that hypsodonty reduces the force required for mastication. The mechanical interpretation of a tall crown can be studied for upper molar two as a two-dimensional structure; a simplified model. Therefore, the following findings apply to all hypsodont teeth, including the molars and premolars of *Equus*. The results are shown in the following two **Figures 3**, **4**.

The *Equus* hypsodont tooth is represented by a class I lever. That is, the fulcrum is in the middle: the effort is applied on one side of the fulcrum and the resistance (or load) on the other side, for example, as in a seesaw, a crowbar or a pair of scissors. The effort is in the oral cavity and the resistance is in the crown situated in the alveolus. The tall tooth is embedded in the alveolus and the force of chewing is on one side; in the oral cavity. This tooth leans on the side of the alveolus which acts like a supporting fulcrum. The force of mastication, F_m, was estimated while the length of exposed tooth to mastication, L_m, and the length of the crown, L_a, were measured. F_a is the force of the alveolar tooth needed to stabilize the tooth during mastication (calculated). The fulcrum helps demonstrate the transition between the exposed and alveolar tooth crown as well as the part of the crown embedded in the alveolus. Mastication occurs at the exposed portion of the tooth. The alveolar portion of the tooth stabilizes the exposed portion of the tooth during mastication. This static system assumes no movement of the tooth during mastication therefore indicating all forces will equate to zero in equilibrium. The fulcrum placement is at the location where the exposed tooth meets the alveolar tooth (gum line). The model in **Figure 3A** is based on the measured values for *Equus* which are shown in **Table 1**.

In **Figure 3A** the black bar is the exposed functioning enamel crown. The black arrow is the transverse force not a vertical force. The green shows the fulcrum point as the opening of the alveolar space (again transverse) and the red line is the plioroot deep into the maxilla. We rotated the model to make it as in an upper molar. Now all of our calculations are based on a horizontal

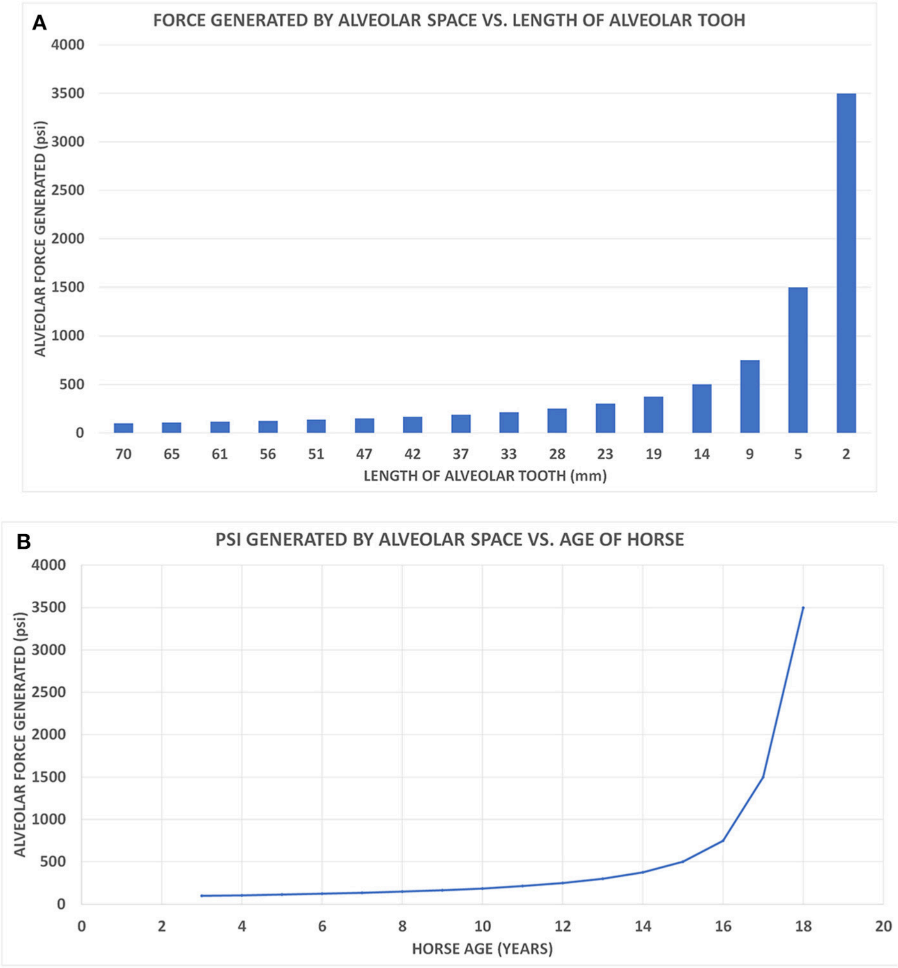

FIGURE 4 | (A) The alveolar force F_α vs. the alveolar length L_α shown on a bar chart to correspond with the age of the horse when read from left to right. **(B)** The graph displays the force generated by the alveolar space (F_α) vs. the age of the horse.

movement. This is a simplified version as there is a vertical force applied as well. However, this is a simple introductory model. A more complex model needs to be developed where both vertical, transverse, and torque forces are explored.

The transverse vector of mastication is estimated and applied as a perpendicular force to the tooth (F_m). Applying class I lever mechanics to **Figure 3A**, Equation 1 is applied to the system. Two instances of torque results in this condition: Torque due to mastication which equals the product of the mastication force and the length of the tooth ($F_m \times L_m$) in a counterclockwise direction. The second torque vector is the product of the force of the alveolar space force and the length of the alveolar tooth ($F_\alpha \times L_\alpha$) in a clockwise direction. Due to the hypsodont tooth not moving during mastication (static system), these opposite torque values are therefore equal, creating Equation 2 below. Solving for F_α (the only unknown value) in Equations (2, 3) is generated.

$$Torque = Force \times Distance \tag{1}$$

$$F_m \times L_m = F_\alpha \times L_\alpha \tag{2}$$

$$F_\alpha = \frac{F_m \times L_m}{L_a} \tag{3}$$

The change in forces is exponential. The dramatic increase in force generated is observed especially when the length of the alveolar tooth crown decreases.

BRIEF ANATOMY OF THE *EQUUS* MOLARS

In *Equus*, the enamel crowns are embedded in the maxilla and the mandible (**Figure 1A**). All six teeth (three premolars and three molars) are approximately equally hypsodont. The *Equus* M2 selected for this study is representative of the other molars and premolars (**Figure 2**). The outer walls of the enamel are relatively vertical and almost parallel to one another. This gives the tooth a uniform thickness and a columnar shape.

A substantial part of the crown in the *Equus* M2 is enclosed in the alveolar bone of the mandible and the maxilla (**Figure 1A**). Only a small part of the crown is exposed in the oral cavity: the active tooth crown. As the animal feeds, the active crown is worn-down by the ingested vegetation and or exogenous grit. An additional crown slowly emerges from the alveolar space to replace the worn crown. In older individuals, albeit rare in the wild and prior to death, very little if any crown remains in the alveoli (**Figure 1B**).

The tooth root of any mammal is encased externally in a thin coating of cementum. In *Equus* this coating also extends outside the enamel surface where it is thick (**Figure 2**). The cementum is a distinct tissue but histologically similar to the dentine (White, 1959; Peyer, 1968). The periodontal ligaments cannot attach to enamel directly. Thus, the cementum adheres to the enamel and provides a surface for the periodontal ligaments. Each alveolar space is lined internally by a thin layer of bone (the lamina dura) (Peyer, 1968; Fortelius, 1985; Williams, 1995 Gray's Anatomy; text figure 12.50). The periodontal ligaments bind the cementum to the lamina dura. The crowns of brachydont teeth are not in the alveoli and hence they have a thin layer of cementum only around the true roots.

The crown of the alveolus constantly erupts and progressively becomes the new active crown while the tooth wears with age. As the tooth emerges from the alveolar space, the empty alveolar space is gradually filled with spongy trabecular bone. The various structures of the hypsodont crown such as styles, ribs, and the vertical wall of the cementum/enamel are also inside the alveolar bone and contact the lamina dura. The lamina dura follows the shape of the three buccal styles of *Equus* teeth. These structures prevent rotation of the tooth and are clearly used in support during mastication. In older teeth where the very base of the crown does not have these styles, the tooth often rotates and is out of alignment. Worn down teeth create problems in horses (Kirkland et al., 1996; Dacre et al., 2008; Kopke et al., 2012).

RESULTS

This study uses a qualitative approach to develop a new theory. Hence, we have not used a statistical analysis to quantify our results. *Hyracotherium* and *Mesohippus* are brachydont taxa. *Protohippus* and *Merychippus* are mesodont while *Equus* is hypsodont. The geological age of the taxa is as follows: *Hyracotherium* (55–50 Ma); *Mesohippus* (40–30 Ma); *Protohippus* (15–7 Ma); *Merychippus* (23–14 Ma); *Equus* 1-present).

Size of Roots

Table 1 shows five representative species of equids. In *Equus* where the teeth are hypsodont, the roots similar in length to the roots of brachydont teeth. The number of specimens examined is small and the calculations are an approximation. Thus, the roots of *Hyracotherium* are even longer than those of *Equus* (**Table 1**). These preliminary results show the roots in evolution do not increase in size as hypsodonty increases; the roots rather decrease. The roots decrease when compared to the crown. Examination of a few roots provided the following findings: The *Hyracotherium leporinum* have a ratio of (crown height over root length) 1.77, crown/root. In *Mesohippus bairdi* the ratio is slightly decreased (1.30). That is, the crowns are more hypsodont than in *Hyracotherium*. In *Merychippus insignis,* the hypsodonty is evident as the ratio drops to 0.62. *Protohippus primus* has long roots and the ratio is 0.47. In the Pleistocene *Equus* sp. from Alaska, the height of the crown height is as much as 80 mm (**Table 1**) and the ratio to root is only 0.06.

Open Roots vs. Closed Roots

The adult *Equus* teeth display short roots that are open-ended implying potential for growth of these roots (**Table 1**; **Figures 2A,B**). The roots of old individuals are longer and closed. In domesticated cases, it is more common to find old individuals. In our collection, there are two old *Equus caballus* specimens where the crowns are almost completely worn off (**Table 1**). The same is true in AMNH 204019, which is an old specimen of *Equus caballus* (**Figure 1B**). In these three, the roots are elongated and not open-ended. This implies the elongated roots have completed their growth. The ratio of these old specimens of *Equus caballus* for crown height to root length is 0.79 and 0.44, respectively. These ratios are different from those of younger adult individuals where that ratio is 0.06 (**Table 1**).

It Is Rare to Find Wild Older Individuals in Fossils in Museums

It was possible to evaluate roughly the age of individuals and separate the adults from the old based on the stage of tooth eruption and tooth wear. In brachydont teeth, the entire crown is exposed, and the base of the roots is also exposed. Thus, in brachydont teeth, the roots can be seen at the opening of the alveoli at the base of the crowns but the same is not true in young hypsodont teeth. In these, the roots are very deep in the alveoli and can be seen only when the crown is heavily worn. Using this evaluation procedure, we examined 15 localities with ungulates. The species were: dromomerycids, bovids, cemelids, and equids and reveal a clear pattern. Namely, the majority of the examined specimens are young adults. The very old individuals were few to none (**Table 2**).

The Longitudinal Section Through the Middle of a Second Upper Molar of *Equus*

The central cavities are the dominant feature in this longitudinal cut and are filled with cementum (green). The dentine (white) is developed by the roots and along the enamel walls. The enamel (red) is not a dominant feature is this view. Using the surface of this longitudinal cut and the colors the areas in square millimeters of each color and hence material is: cementum: 953.369, enamel: 205.668, and dentine: 389.783 mm^2.

Mechanics

Another way of evaluating the interaction between force and tooth height is seen in **Figure 4A**. This bar graph (**Figure 4A**) allows the changes in tooth height to also parallel the hypsodont's lifespan as traveling from left to right on the x-axis. As an *Equus* ages, the alveolar tooth length decreases, which is why the graph follows time. Observing the force of the alveolar space compared to the length of the tooth, at 9 mm of alveolar length, there is a drastic increase in the force generated. This exponential trend continues for the last two points of 5 and 2 mm, respectively. Essentially this model indicates that as the tooth

TABLE 2 | Brief survey of number of young adults vs. very old for selected taxa of Dromomerycidae, Bovidae, Equidae, and Camelidae from the AMNH.

	Young adults	Very old
Rakomeryx sinclairi Olcott Nebraska	34	0
Bouromeryx supernebrasensis Observation Quarry Nebraska	12	0
Bouromeryx pseudonebrasensis Observation Quarry Nebraska	21	0
Pachytragus crassiornis Samos Q5, Greece	34	0
Pachytragus laticeps Samos Q1, Greece	57	1
Gazella sp. Samos Q5, Greece	20	0
Gazella sp. Samos Q1, Greece	21	0
Pseudohipparion retrusum Devils Gultch Horse Qarry	48	0
Pseudohipparion retrusum Burge Member, Burge Quarry Valentine Formation Nebraska	56	0
Merychippus insignis Olcott Formation Echo Quarry Nebraska	259	7
Protohippus primus Thomson Quarry Sheep Creek Formation	710	5
Michenia sp. Dunlap Camp Quarry Dewes CO Nebraska	47	0
Stenomylus gracilis Marshland CO Harrison Fm Wyoming	26	0
Aepicamelus sp. Tesique Fm Skull Ridge Member New Mexico	15	1
Pachytragus solignaci Beglia Formation Tunisia	81	1
Equus sp. Alaska Pleistocene	120	5

length approaches zero millimeters in length, the force of the alveolar space will approach infinity. It can be mathematically understood by having L_a (alveolar length) in Equation (3) approach zero, therefore resulting in F_a having a limit of infinity.

This graph displays an exponential increase in force generated as tooth length decreases. This is similar to **Figure 3B**, where the force exponentially increased with decrease in alveolar tooth height. Using the same y-axis force values from **Figure 4A**, a plot shows the alveolar force vs. the age of the hypsodont tooth as seen in **Figure 4B**. It is observed that the alveolar tooth height and the horse's age are inversely related following the same exponential trends of force as seen in **Figures 3B**, **4A**. **Figure 4B** shows the dramatic change in the force as the embedded crown is worn off which occurs in our model of wear after age 16.

DISCUSSION

A significant aspect in evaluating the proposed plioroot theory is that we do not yet have the true phylogenetic lineage for the evolution of *Equus*. The taxa listed represent an approximation to the real evolution which is not studied here and is not known. The taxa are simply used to make the point.

Roots do not appear to increase in size during evolution when the tooth crown increases. In fact, the roots of *Equus* are smaller than those of *Hyracotherium* in actual size. The difference in size of the two genera is great (9 kg for *Hyracotherium* vs. 380–1,000 kg for *Equus* (Radinsky, 1978; Bongianni, 1987; Edwards, 1994). We found that during evolution, the roots decrease in size as the tooth crown and body size increases. This may be due to the plioroot hypothesis, in which the crown in the alveolus acts as a root. Hence, the true roots alone are incapable of supporting the tooth. We observed no evolutionary diversification or enlargement of the true roots to support the extra crowns as teeth become more hypsodont.

The true roots of *Equus* are small and open-ended and contain live tissues for the possibility of growth. When a horse is old there is no more crown in the alveolus (Gregory, 1957, text figure 21.45) (**Figure 1B**). The forces of mastication tremendously affect the small remaining old tooth in several ways. One way is the root response. That is, the true roots develop more and they elongate and close at the tips. These longer roots support better the remaining feeble crown. Thus, elongation and closure of the root is delayed until the crown is almost entirely worn. Delayed development of the true roots is a heterochrony phenomenon and it is possibly dynamically interactive with the forces applied on the crown. When the crown is worn, the mastication forces acting on it are very strong. This is interesting and reinforces our hypothesis that the young tooth's crown embedded in the alveolus acts as a supporting root.

As previously stated, in old individuals, prior to death, very little, if any crown remains in the alveoli (Gregory, 1957; Rooney et al., 1977; Loweder and Mueller, 1998; Pence, 2002). It is known that when an individual runs out of crown it will die from starvation. In wild *Equus,* individuals often die well-before their entire enamel crown is used up. This observation is true for *Equus* and for other ungulates. Many samples have shown the absence of numerous old individuals in the fossil record. There are clearly exceptions to this observation but in general, it is true. In the Alaska *Equus* sp. sample, we found 120 adults and five old individuals. In domesticated species of *Equus,* it is possible for an individual to live up to the point where little or no enamel remains (Loweder and Mueller, 1998; Pence, 2002). The data suggest that individuals die long before they become old. Hence, they die with a substantial amount of tooth crowns unused (**Table 2**). The excess crown in the alveoli of fossil populations can be explained with our theory of it acting as the plioroot. Naturally, there are other reasons for the early death of extinct individuals. Two of these are predation and catastrophic events. In general, however the plioroot hypothesis cannot be ruled out.

A longitudinal section of the upper M2 is revealing. The cementum dominates and the enamel is less than what would expect. The enamel unsupported by the cementum would fracture. The cementum functions to provide support, and as it wears differently it enhances the relief which is useful during mastication. Thus, in equid evolution it is not the enamel that becomes taller alone, but that along with a thick cementum layer. As it is, the enamel wears and forms cutting edges which are constantly supported by the cementum and the dentine (Rensberger et al., 1984; Fortelius, 1985).

The hypothesis that the excess crown in the alveoli can be explained as two functions: by acting as a reservoir for wear in the oral cavity and as a root. This observation applies to *Equus* and it can be extended to all other hypsodont ungulates. DeMiguel et al. (2015) discussed the interplay of increased tooth crown height and chewing efficiency in Cervidae. In their study, they showed how selenodont teeth respond to become more hypsodont with an increased force of stress. What these authors found is that stresses are more concentrated in small areas (where the mastication loading occurs) as the teeth are more hypsodont. Accordingly, hypsodonty is interesting as an adaptation because it enables selenodont teeth to adopt a mechanically improved design that increases the pressure whilst shearing foods, which is highly advantageous when feeding on mechanically resistant, tough, and fibrous foods.

From *Merychippus* to *Equus,* the primary dental change is an increased degree of hypsodonty which follows increasing grazing (Matthew, 1926; Simpson, 1951; Stebbins, 1981; MacFadden, 1994; Strömberg, 2002; Mihlbachler et al., 2011) and/or exposure to exogenous grit (Gregory, 1957; Rensberger et al., 1984; Semprebon et al., 2016). The hypsodont tooth is interesting as an adaptation and has been a leading force in the evolution of Equidae (Damuth and Janis, 2011; Mihlbachler et al., 2011; Strömberg, 2011; Semprebon et al., 2016).

The three buccal styles described earlier inhibit the rotation of the tooth during mastication. The mastication rotation would be strongest in the direction of the buccal side as the mastication is slightly oblique (Fortelius, 1985, Figure 25) and buccal. The styles of the upper molars play the role of anchors. The usefulness of these styles becomes evident in older individuals where teeth and the molars often rotate as the styles are not present to prevent this.

The results of modeling the fulcrum and the forces show that the crown in the alveolus acts to function as a root. Hence, enlargement of the true roots is not necessary.

During mastication, the two different stresses are exerted on the teeth in various combinations. One extreme is that of transverse forces; another is that of vertical forces. In general, the *Equus* true roots appear to be conservative in shape and size and are small. The various ribs and styles as well as the vertical walls of the enamel clearly act as anchors supporting the active crown, preventing it from rotating and mal-occluding. For more vertical mastication modes, the true roots probably can sufficiently support the crown. In transverse forces as in cutting vegetation and grazing, the true roots cannot be of much support. In these conditions, hypsodonty evolves roots out of the additional crowns; the plioroots. These are hypotheses that need further testing.

Applying the laws of mechanics and torque to a two-dimensional class I lever representation of a hypsodont tooth, there appears to be a direct correlation between the force generated by the alveolar space and the length of the alveolar crown. Seen in **Figures 3B**, **4**, as the alveolar part of the crown becomes shorter due to wear, there is a linear increase in the force needed to maintain the tooth's stability and hence effectiveness. During the final years of the crown's life there is an exponential increase in the alveolar force due to the diminishing alveolar tooth length. This relates to Equation (1) when applying to a class I lever model. Assuming mastication is a constant force, the torque needed to counterbalance the system is based on the force generated and distance (Equation 1). If the alveolar tooth is continuously decreasing in height, the force will increase due to the inverse relationship.

Representing a single hypsodont tooth as a two-dimensional class I lever it is determined that the force needed to maintain the tooth during mastication linearly increases for approximately the first 12 years of the hypsodont tooth's life before exponentially increasing for the remainder of its life (**Figures 3B**, **4**). The *Equus* tooth is much more stable when the alveolar crown is longer, and hence more hypsodont. This provides a longer moment arm allowing the alveolar force to be drastically less during mastication. The presence of the alveolar portion of the tooth crown not only delivers the tooth vital material throughout its life but also likely provides essential mechanical support as indicated from the proposed model. Therefore, the extra enamel is likely there for two reasons, support and availability for eruption and ultimate wear in the oral cavity. The former is new to science, while the latter has been known and studied (Fortelius and Solounias, 2000).

We believe the abrupt increase in force for each bite shown reflects in nature why there is no large gradation of brachydont to hypsodont teeth in various species. The three types of teeth that exist (brachydont, hypsodont, mesodont) do not exist in a continuum. Rather they can be sorted into limited, albeit three, distinct categories (e.g., Fortelius and Solounias, 2000; Solounias and Semprebon, 2002; Semprebon et al., 2016). This observation needs to be studied further.

Is the extra tooth of hypsodont animals a reserve for hardships? If that were so, there would be fossil localities where old individuals have been sampled due to hardships upon these populations. However, there are no such samples of ungulates known to us in the fossil record. Hardship cases are not cited by Damuth and Janis (2011) as they surveyed all the reasons of hypsodonty.

CONCLUDING REMARKS

The physical fact that the crowns of hypsodont ungulates are embedded in the jaws and maxillae makes the concept of the crown acting as a necessary reinforcement to the root highly probable. Mechanically, it would seem to be impossible for such crowns not to act as roots, and we have proven this to be true for *Equus*.

The high transverse forces encountered with grit, abrasive vegetation or with high attrition were probably the selection for *Equus* hypsodonty and for other ungulate hypsodonty in its dual function; an extra crown to wear and an extra root. *Equus* and other species needed extra crowns for grit, abrasive, and attractive properties of foods. Species also had to evolve a type of root to endure the strong stresses during mastication. The available true roots were not designed for this and apparently, as in so many other examples, nature used what was adjacent and available; namely the crown. Selection favored the increase of crown height. An enamel crown is a formidably strong and an important support structure as a root. Add to this embedded crown the styles and the ribs, and you make a strong peg which also resists rotation.

The evolution of cementum external to enamel was needed to enable the periodontal ligaments to bind with the lamina dura of the alveolus. The same part of the crown can be used as a root in the alveolus or for wear in the oral cavity.

AUTHOR CONTRIBUTIONS

NS conceived the idea for this original research paper and collected the data at the museums for **Tables 1**, **2** while putting together the figures and text. IB worked on the text and tables and plots. ZC developed the physics of the root hypothesis. MD worked at the museum collecting data and worked on the text.

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Dietary Adaptations of Early and Middle Pleistocene Equids From the Anagni Basin (Frosinone, Central Italy)

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The intermontane Anagni Basin (Frosinone, central Italy) is an important region for Italian biochronology and paleoecology due to the presence of two rich fossil assemblages dated to the Early (Coste San Giacomo) and Middle Pleistocene (Fontana Ranuccio). These sites have yielded a vast collection of large fossil mammals with a well-documented presence of fossil equids in both localities (represented mostly by isolated teeth). Coste San Giacomo is dated to around 2.1 Ma, thereby having recorded the effects of the onset of the Quaternary glacial cycles, which led to a gradual trend toward colder and more arid conditions in the Northern Hemisphere. The fossil equids of this site belong to the first group of grazing stenonid equids of the genus *Equus* that spread to the Italian Peninsula during the so called "Elephant- *Equus"* event, which marked the appearance of new large mammals living in herds in open and arid environments. The site of Fontana Ranuccio is dated to around 400 ka, close to the MIS 12–11 succession (the "Mid-Brunhes event"), which marked the end of the Middle Pleistocene Transition. The fossil horses from Fontana Ranuccio represent one of the oldest caballoid (or "true horses") populations of the Italian Peninsula. The Anagni Basin, thus, provides important data to investigate paleoecological adaptations of these groups of equids in response to two critical environmental and climatic shifts of the Pleistocene. We explore their niche occupation by examining long-term dental wear patterns and tooth enamel carbon and oxygen stable isotopic composition. Both taxa appear to have exhibited a narrow dietary niche, displaying a clear abrasive (highly specialized) grass-rich diet. In particular, caballoid equids from Fontana Ranuccio show a more abrasion-dominated mesowear signature. Stenonid equids from Coste San Giacomo exploited broader and more diverse landscapes during the Early Pleistocene, whereas caballoid horses from Fontana Ranuccio appeared to have limited their dietary adaptations to a stricter grazing behavior in more closed environments.

Keywords: mesowear, isotopes, equids, *Equus*, Pleistocene, paleoecology, paleoenvironment

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INTRODUCTION

The intermontane Anagni Basin, situated in the central part of the Italian Peninsula, developed between the Late Pliocene and the early Middle Pleistocene (Carrara et al., 1995; Galadini and Messina, 2004). Two rich vertebrate fossil sites, the Early Pleistocene locality of Coste San Giacomo (CSG) and the Middle Pleistocene site of Fontana Ranuccio (FR), were discovered in the 1970s, following different surveys carried out by the Italian Institute of Human Paleontology (IsIPU) (**Figure 1**). CSG has been dated to around 2.1 Ma based on magnetostratigraphy, pollen, and its record of micro mammals recovered from alluvial deposits (Bellucci et al., 2014). It is one of the few Italian localities that record the terrestrial habitat conditions after the onset of the Pleistocene glaciations that marked the Plio-Pleistocene transition at 2.6 Ma (Lisiecki and Raymo, 2005, 2007). FR fossiliferous layer located within a succession of pyroclastic deposits has been dated to around 0.4 Ma (Pereira et al., 2018), close to the climatic transition of the "Mid-Brunhes Event" (MIS 12–11) with the definitive association of the glacial cycles ruled by a 100 kyr periodicity and the consolidation of the Early-Middle Pleistocene Transition (Head and Gibbard, 2015).

Importantly, both localities have yielded abundant fossil mammal material, among which equid remains are well-represented (Segre and Ascenzi, 1984; Bellucci et al., 2012, 2014; Strani et al., 2018a). Fossil human teeth were also unearthed in FR (Rubini et al., 2014). The equid remains from CSG were attributed to *Equus stenonis* by Biddittu et al. (1979), but a recent study (Palombo et al., 2017) points to stronger affinities with the middle-size *Equus senezensis* and proposes a new provisional identification of the CSG material as *E. senezensis* aff. *E. sen. stehlini*. This taxon is among the first groups of stenonid equids (monodactyl horses with a "V" shaped linguaflexid between the metaconid and metasylid of the lower cheek teeth; Forsten, 1988) to reach the Italian Peninsula during the so-called "Elephant-*Equus*" event with the appearance of new large mammals living in herds in drier habitats (Azzaroli, 1977; Lindsay et al., 1980). Equids' remains from FR have been tentatively classified as *Equus* cf. *E. mosbachensis* (Segre and Ascenzi, 1984), belonging to one of the first caballoid (or "true horses," monodactyl equids with a "U" shaped linguaflexid; Forsten, 1988) populations recorded on the Italian Peninsula after the disappearance of the early Middle Pleistocene stenonid forms (Caloi, 1997; Alberdi and Palombo, 2013).

Both modern and fossil *Equus* taxa are usually considered highly specialized grazers that consistently occupied similar habitats through the Pleistocene and Holocene (i.e., open grasslands), despite it has been observed that extant species can also include a noticeable amount of browse in their diet (Roeder, 1999) and that some fossil *Equus* populations displayed less abrasive feeding behaviors (Kaiser and Franz-Odendaal, 2004). The material from the Anagni basin represents an exceptional case to investigate the habitat occupation and resource use of two groups of fossil equids and test the hypothesis that both stenonid and caballoid horses exploited exclusively open habitats and fed mostly on grasses in Central Italian Peninsula. In this study we compare dental remains of *E. senezensis* aff. *E. sen. stehlini* from CSG and *Equus* cf. *E. mosbachensis* from FR in occlusal surface mesowear, a proxy for dietary abrasiveness in herbivorous mammals (Fortelius and Solounias, 2000), and in stable carbon and oxygen isotope abundances, proxies for habitat openness (Van der Merwe and Medina, 1991) and temperature (Dansgaard, 1964), to shed light on the niche occupation and resource exploitation mechanisms of stenonid and caballoid equids on central Italian Peninsula.

Our data will allow us to obtain comprehensive information on the paleoecological adaptations of the *Equus* genus in the region following two major climatic events, and to understand if this group could be more flexible in terms of feeding behavior and habitat occupation during the Early and Middle Pleistocene.

DENTAL WEAR PATTERNS AND ISOTOPES IN PALEOECOLOGY

Dental Mesowear

Mesowear reflects the cumulative effects at a macroscopical level of the items ingested by herbivores (foods and exogenous particles such as grit or dust) on tooth morphology that are produced in a long period of time compared to the lifespan of the animal (Fortelius and Solounias, 2000). Dental mesowear is a direct signal of a species' diet that varies between browsers, which feed mostly on soft plant resources (e.g., leaves, twigs, green stems), and grazers that clip abrasive vegetation (e.g., grasses) at or near ground level.

Attrition (tooth-to-tooth contact) and abrasion (tooth-to-food contact) are the main factors that influence the occlusal morphology of the teeth, determining the cusps sharpness and the height of the occlusal relief. In browsing animals attrition mainly determines the tooth wear leading to sharper cusps and a higher occlusal relief. In species that feed on more abrasive plant resources the higher level of tooth-to-food contact produces blunter cusps and a lower occlusal relief (Fortelius and Solounias, 2000). Traditional mesowear is limited to upper second molars (M2), but it can be extended to other tooth positions (Kaiser and Solounias, 2003; DeMiguel et al., 2010, 2012; Strani et al., 2015, 2018a,b).

The method has been developed to examine the diet-related dental wear patterns in ungulates and has been successfully employed to investigate dietary adaptations of different groups of both modern and fossil artiodactyls and perissodactyls (Fortelius and Solounias, 2000; Schulz et al., 2007; DeMiguel et al., 2008, 2011, 2018; Bernor et al., 2014; DeMiguel, 2016; Marín-Leyva et al., 2016; Maniakas and Kostopoulos, 2017). Dental mesowear also proved to be an optimal tool to study equid paleoecological adaptations, allowing to obtain information about the dietary change and evolution of this group from the early forms of the Eocene to the horses of the Pleistocene (Kaiser and Franz-Odendaal, 2004; Mihlbachler et al., 2011; Bernor et al., 2017).

Carbon Stable Isotopes

Carbon isotopic ($\delta^{13}C$) abundance in herbivores reflects the presence of C3 and C4 vegetation in lower and mid-latitude habitats as well as a degree of canopy closure vs. openness in wooded high-latitude habitats. C3 plants, or woody vegetation

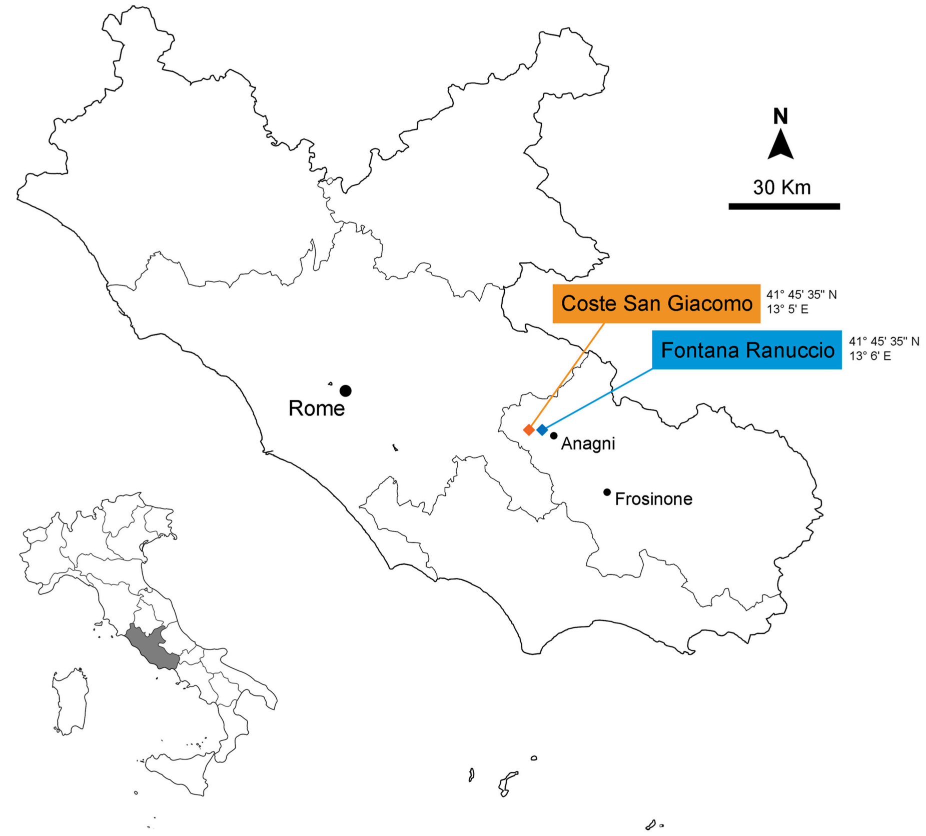

FIGURE 1 | Geographical location of the Coste San Giacomo and Fontana Ranuccio localities.

and grasses that have a cool growing season, have $\delta^{13}C$ values ranging between −34 and −23‰, with a suggested mean of −27‰ (Calvin and Benson, 1948; Hatch et al., 1967; Smith and Epstein, 1971; Koch, 1998). The canopy effect can result in up to 5‰ differences in $\delta^{13}C$ in the same species at one site in pure C3 forest environments between the herbivores feeding in a heavily enclosed wooded environment or on plants from different tree elevation, and the herbivores feeding in more open parkland or grassland environments with higher evapotranspiration (Van der Merwe and Medina, 1991; Bocherens et al., 1999; Feranec and MacFadden, 2006; Drucker et al., 2008; Hofman-Kaminska et al., 2018).

The $\delta^{13}C$ values of the carbonate fraction of bioapatite in large mammalian herbivores are higher than or enriched by 14‰ compared to their diet: $\delta^{13}C_{\text{bioapatite}} = \delta^{13}C_{\text{diet}} + 14‰$ (Cerling et al., 1999). In warm temperate and cold boreal environments $\delta^{13}C$ values higher than −13‰ in herbivore enamel indicates open landscapes, such as grasslands and steppes, in which the plants have $\delta^{13}C$ values higher than −27‰ in diet or ecosystem $\delta^{13}C$ values, whereas tooth enamel $\delta^{13}C$ values lower than −13‰ indicate woodlands and denser forests (Bocherens, 2014).

Oxygen Stable Isotopes

Oxygen isotopic ($\delta^{18}O$) abundance of the herbivores' enamel apatite reflects the source and amount of body-water ingested, either free drinking water or obtained from food and plants. The $\delta^{18}O$ in the enamel apatite is a proxy for $\delta^{18}O$ values of meteoric water, which varies due to the source of precipitation and effects of latitude, altitude, continentality, temperature, and evaporation (Dansgaard, 1964; Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995; Bryant et al., 1996; Kohn, 1996; Sponheimer and Lee-Thorp, 1999; Levin et al., 2006). Crudely, $\delta^{18}O$ values of meteoric water are higher in warmer or dryer environments (Dansgaard, 1964). Thus, as a general rule, herbivores feeding in open steppe habitat are expected to have more enriched $\delta^{18}O$ values than species from forested cooler and more humid habitat (Sponheimer and Lee-Thorp, 1999). Obligate or water-dependent drinkers usually have $\delta^{18}O$ values lower than non-obligate drinkers, being dependent on water availability and seasonality of rainfall. Seasonal variation in rainwater in mid- and high latitude environments and species migration can be significant, producing intra-tooth variations of 3–4‰, or more (e.g., in high-crowned ungulates, horses and bison, Hoppe et al., 2004; Feranec et al., 2009). Oxygen isotopic composition can be affected not only by daily ecology and migration but also by life history and physiology of mammals. Oxygen isotopic compositions are higher in nursing animals during lactation and weaning periods because of milk consumption, which is related to the body water in the mother, and more enriched in ^{18}O due to the preferential loss of ^{16}O through sweat, urine, and expired water vapor (Bryant and Froelich, 1995; Kohn, 1996).

MATERIALS AND METHODS

The material studied consists of upper cheek teeth belonging to *E. senezensis* aff. *E. sen. stehlini* from CSG and to *Equus* cf. *E. mosbachensis* from FR. All the examined fossil material is housed at the Italian Institute of Human Paleontology (IsIPU) (Anagni, Italy). The comparative material was obtained from literature (see in text).

Dental Mesowear

Past studies on the dental wear patterns of *E. senezensis* aff. *E. sen. stehlini* and *Equus* cf. *E. mosbachensis* from the Anagni Basin examined both upper and lower cheek teeth (Strani et al., 2015, 2018a,b). In this study we examined only upper teeth [P4-M3, following Kaiser and Solounias (2003)] in their occlusal relief (high or low) and cusp shape (sharp, rounded, or blunt) of the apex of the paracone or metacone and scored for a better comparison with available data of both modern and fossil equids because mesowear analysis is often restricted to the upper dentition. Occlusal relief and cusp shape scores were also converted to a single mesowear score (MWS) following the “mesowear ruler” developed for scoring dental mesowear on fossil equids by Mihlbachler et al. (2011). The method is based on seven cusp types (numbered from 0 to 6), ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6). Additionally, a “stage 7” is given to teeth with a convex cusp apex. A total of 30 specimens were scored using this method (*E. senezensis* aff. *E. sen. stehlini* $N = 20$; *Equus* cf. *E. mosbachensis* $N = 10$). Previously unavailable upper teeth of *E. senezensis* aff. *E. sen. stehlini* ($N = 9$) have been added to the original sample analyzed in Strani et al. (2015, 2018b).

Results were compared with mesowear data of four extant equids: plains zebras (*Equus quagga*) (data from Fortelius and Solounias, 2000 and Rivals and Semprebon, 2010), Grévy’s zebras (*Equus grevyi*) (data from Fortelius and Solounias, 2000), onagers (*Equus hemionus*), and African free ranging donkeys (*Equus asinus*) (data from Schulz et al., 2007). To distinguish fossil and modern equid taxa based on mesowear variables (percentages of high relief, rounded, and blunt cusps) a hierarchical cluster analysis was performed using the Ward’s method and the Euclidean distance. *E. senezensis* aff. *E. sen. stehlini* dental mesowear data were compared to those of *E. stenonis* from the Early Pleistocene locality of Olivola (∼1.8 Ma, north central Italy) (Strani et al., 2018c) and of the Britain sites of Mundesley and East Runton (∼1.8 Ma) (Rivals and Lister, 2016). *Equus* cf. *E. mosbachensis* dental wear patterns were also compared to those of the fossil Middle Pleistocene caballoid equid population from the central European localities (Steinheim and Heppenloch,MIS 11, Germany) (data from Rivals and Ziegler, 2018), from different Britain sites (Clacton, Hoxne and Swanscombe; MIS 11) (Rivals and Lister, 2016) and from Caune de l’Arago (438 ± 31 ka, France) (data from Rivals et al., 2015a).

Discriminant analysis was performed to examine the resolution of mesowear variables applied to the fossil. The percentages of high relief, rounded and blunt cusps were used as independent variables and two dietary (conservative and radical) classifications of modern ungulate taxa as grouping variables (Fortelius and Solounias, 2000). *Equus quagga* from Rumuruti (Rivals and Semprebon, 2010), *Equus hemionus* and *Equus asinus* (Schulz et al., 2007) were added to the modern taxa with known diets and treated as grazers in both conservative and radical classifications. All analyses were performed using IBM SPSS Statistics 24.

Stable Carbon and Oxygen Isotope Analyses and Preparation of Teeth Enamel Samples

We obtained stable carbon (δ^{13}C) and oxygen isotopic (δ^{18}O) abundances from the upper cheek teeth (upper first or second molars). In horses the isotopic composition in M1 or M2 would reflect nutrients from mother’s milk and should be slightly more depleted in ^{13}C and more enriched in ^{18}O compared to isotopic

TABLE 1 | Summary of dental mesowear analysis.

Taxa	Locality	Age	N	%High	%Low	%Sharp	%Round	%Blunt	MWS	References
Equus cf. *E. mosbachensis*	Fontana ranuccio	Middle pleistocene	10	0.0	100.0	30.0	50.0	20.0	4.8	This work; (Strani et al., 2018a)
Equus senezensis aff. *E. sen. stehlini*	Coste san giacomo	Early pleistocene	20	25.0	75.0	35.0	45.0	20.0	3.8	This work; (Strani et al., 2015, 2018c)
Equus quagga	Africa	Modern	121	0	100	27.0	39.3	33.6	5.0	Fortelius and Solounias, 2000
Equus quagga	Africa (Rumuruti, Mount Kenya)	Modern	28	0	100	28.6	64.3	7.1	4.3	Rivals and Semprebon, 2010
Equus grevyi	Africa	Modern	29	0	100	34.4	41.3	24.1	4.9	Fortelius and Solounias, 2000
Equus hemionus	Gobi desert	Modern	175	47.4	52.6	4	85.7	10.3	/	Schulz et al., 2007
Equus asinus	Emirate sharjah	Modern	184	55.4	44.6	43.5	39.1	17.4	/	Schulz et al., 2007

Number of specimens (N); percentage of specimens with high (%High) and low (%Low) occlusal relief; percentage of specimens with sharp (%Sharp); rounded (%Rounded), and blunt (%rBlunt); mesowear score (MWS).

composition of subsequently erupting P2, P3, M3, and P4 that would better reflect solid diet of an adult animal (Hoppe et al., 2004). Here we made comparisons with M1 or M2 from German sites and took into account this difference when comparing samples taken from premolars. We used 3 teeth samples of *Equus* cf. *E. mosbachensis* from FR and two *E. senezensis* aff. *E. sen. stehlini* from CSG. One FR horse sample was from PM4 and exhibited enrichment by 1‰ in ^{13}C and more enriched in ^{18}O compared to two FR M2. In German sites only *E. hydruntinus* had permanent teeth compared and the obtained values were within variation ranges of 1 and 2 ‰ in ^{13}C and ^{18}O, respectively.

Enamel samples were either mechanically separated and ground to a finer condition in an agate mortar or drilled with a diamond-impregnated rotary tool. The uppermost surface of the tooth was removed before sampling usually by drilling with a dremel© borer. Samples of approximately 20 mg were analyzed. Fossil enamel powders were pre-treated following the method described by Bocherens et al. (1996) but using the Continuous Flow (CF) for collecting carbon dioxide (Jacques et al., 2008; Bocherens et al., 2009). Our experience with fossil material from limestone cave has shown that the pre-treatment used here is strong enough to remove exogenous carbonates but we are aware of possible slight changes of the oxygen isotopic composition of tooth enamel carbonate.

Pretreated (Sample /Enamel) carbonate was reacted with 100% H_3PO_4 for 4 h at 70°C using a MultiFlow-Geo interfaced with the Elementar IsoPrime 100 IRMS. Final isotopic ratios are reported per mil (‰) calibrated with international standards (IAEA-603 δ^{13}C: 2.46/δ^{18}O: −2.37 and NBS-18 δ^{13}C: −5.014/δ^{18}O: −23.2), as well as three in-house standards. IonOS software (Version 3.2) by Elementar was used to carry out multi-point standard isotope calibration by generating a trend line (y = mx+c) that maps measured vs. expected isotopic results, which is then used to calibrate sample results. The measurement uncertainty was monitored using three in-house standards. The overall analytical precision is higher than 0.1‰ for carbon and better than 0.2‰ for oxygen isotopic values.

Stable isotopic results are expressed as the following standard δ-notation: X = [(Rsample/Rstandard)-1]*1,000, where X is referred to δ^{13}C and δ^{18}O values and R is equivalent to $^{13}C/^{12}C$ or $^{18}O/^{16}O$, respectively. The recorded delta values follow the international reference standards, a "Vienna PeeDee Belemnite" (VPDB) for the carbon and oxygen. Additionally, δ^{18}O values relative to "Vienna Standard Mean Ocean Water" (VSMOW) are given. In addition, the carbonate content ($CaCO_3$%) was determined using the ratio between amount of CO_2 released by the reaction, as detected from the peak intensity for mass 44 and the weight of pure carbonate used as a standard, with an analytical error of 0.3%, based on multiple analysis of reference enamel samples.

To calculate values for temperature and drinking water from oxygen isotope values, and convert oxygen carbonate and phosphate fractions, we used and equation from Lécuyer et al. (2010)

$$\delta^{18}O_c = 1.035\ \delta^{18}O_P + 8.33$$

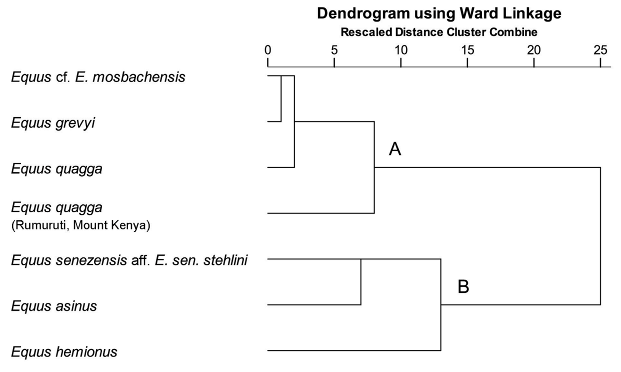

FIGURE 2 | Mesowear hierarchical cluster diagram based on the percentage of high occlusal relief, round and blunt cusps of fossil populations with extant equids. (Data for extant equids from Fortelius and Solounias, 2000; Schulz et al., 2007; Rivals and Semprebon, 2010).

The estimates of the δ^{18}O values of drinking water consumed by species were calculated, first, by converting the oxygen isotope composition of structural carbonate to its equivalent in phosphate, using equations that are robust for many different species: $\delta^{18}O_P = 0.71 \times \delta^{18}O_W + 22.60$ (Delgado Huertas et al., 1995).

Then the oxygen isotope composition of phosphate was converted to that of drinking water of different groups of species, according to formulas below and reformulated based on original data from Skrzypek et al. (2011) based on current relationship between air and water. We calculated temperature (°Celcius) using the formula for continental Europe:

$$T_{\text{air}} = 1.41 \times \delta^{18}O + 21.63$$

We used both parametric and non-parametric tests with $\alpha = 0.05$. To identify the sources of significant differences we used ANOVA and among unequal variances we used *post hoc* Tamhane tests.

The results were compared with the late middle and late Pleistocene horse data from Steinheim, Mauer, Bockstein and Vogelherd (Pushkina et al., 2014).

RESULTS

Dental Mesowear

E. senezensis aff. *E. sen. stehlini* upper teeth from CSG showed mostly low occlusal relief (75%) and a higher percentage of rounded cusps (45%) over sharp (35%) and blunt cusps (20%) (**Table 1**). Low occlusal relief and high occurrence of rounded cusps *E. senezensis* aff. *E. sen. stehlini* from CSG point to a generally abrasive diet. *Equus* cf. *E. mosbachensis* teeth also displayed low occlusal relief and mostly rounded cusps (50%) (**Table 1**), a pattern pointing to a dominance of abrasion over attrition.

E. senezensis aff. *E. sen. stehlini* was clustered with the onager and the free ranging donkeys (cluster B) both displaying a grazing signature but with *E. asinus* showing a less abrasion-dominated diet (Schulz et al., 2007) (**Figure 2**). *Equus* cf. *E. mosbachensis*

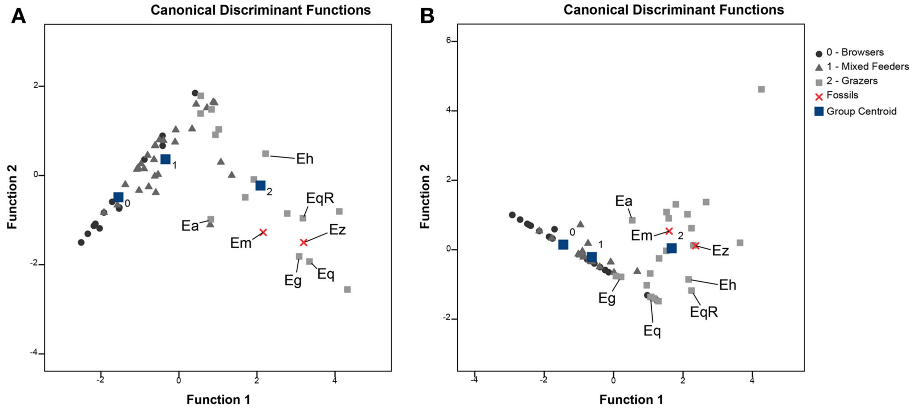

FIGURE 3 | Bivariate diagrams based on discriminant analysis: conservative classification **(A)** and radical classification **(B)**. Minute abraded brachydont species have been excluded. Fossil taxa Ez, *Equus senezensis* aff. *E. sen. stehlini*; Em, *Equus* cf. *E. mosbachensis*; Eq, *Equus quagga*; EqR, *Equus quagga* (Rumuruti population); Eg, *Equus grevyi*; Eh, *Equus hemionus*; Ea, *Equus asinus*. Group centroids: browsers (0); mixed feeders (1); grazers (2).

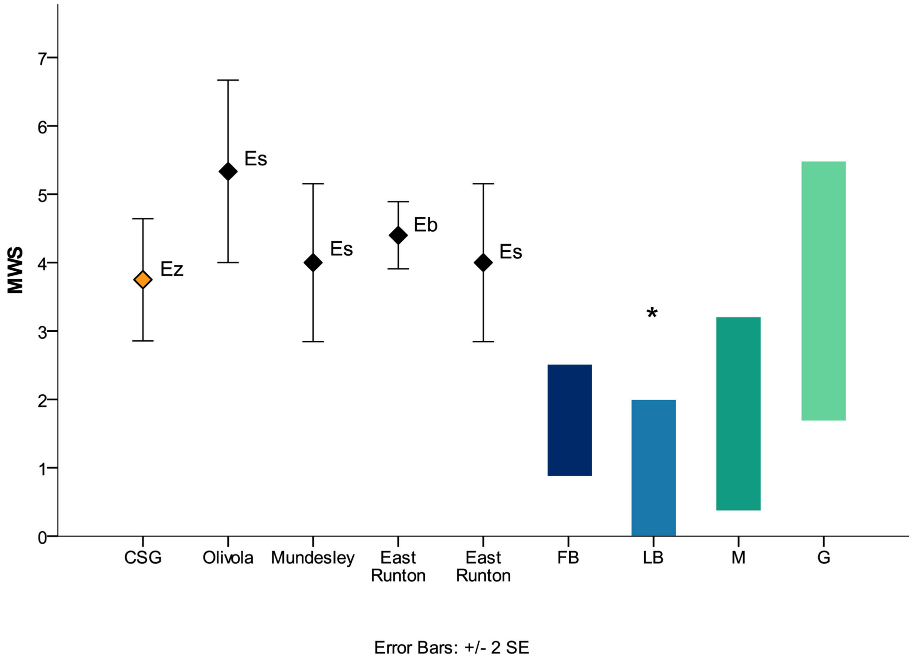

FIGURE 4 | Mesowear results of fossil stenonid equids and extant ungulates. Modern ungulates data from Fortelius and Solounias (2000) (diet information according to the radical classification; minute abraded brachydont species have been included), Rivals and Semprebon (2010). Mundesley and East Runton data from Rivals and Lister (2016). MWS, mesowear score; CSG, Coste San Giacomo; Ez, *Equus senezensis* aff. *E. sen. stehlini*; Es, *Equus stenonis*; Eb, *Equus bressanus*; FB, fruit browsers; LB, leaf browsers; M, mixed feeders; G, grazers; *, *Heterohyrax brucei*.

fell in cluster A with modern zebras (**Figure 2**), which are all characterized by strong abrasion-dominated mesowear patterns (**Table 1**) (Fortelius and Solounias, 2000; Rivals and Semprebon, 2010). Discriminant analysis performed with the mesowear variables provides a satisfactory dietary discrimination with 71.9% of extant taxa correctly classified according to the conservative classification and 75.4% according to the radical one (70.2 and 75.4%, respectively, in cross-validation). Both *E. senezensis* aff. *E. sen. stehlini* and *Equus* cf. *E. mosbachensis* are classified as grazers by both the conservative and radical classification (**Figures 3A,B**).

E. senezensis aff. *E. sen. stehlini* displayed an average MWS of 3.8, lower than the one recorded in the upper cheek teeth of *E. stenonis* from Olivola (5.3), from stenonid horses from East Runton (*E. bressanus,* 4.5; *E. stenonis,* 4.0) and from *E. stenonis* from Mundesley (**Figure 4**), pointing to a less strictly abrasion-dominated feeding behavior in the stenonid equid from Coste San Giacomo. *Equus* cf. *E. mosbachensis* from

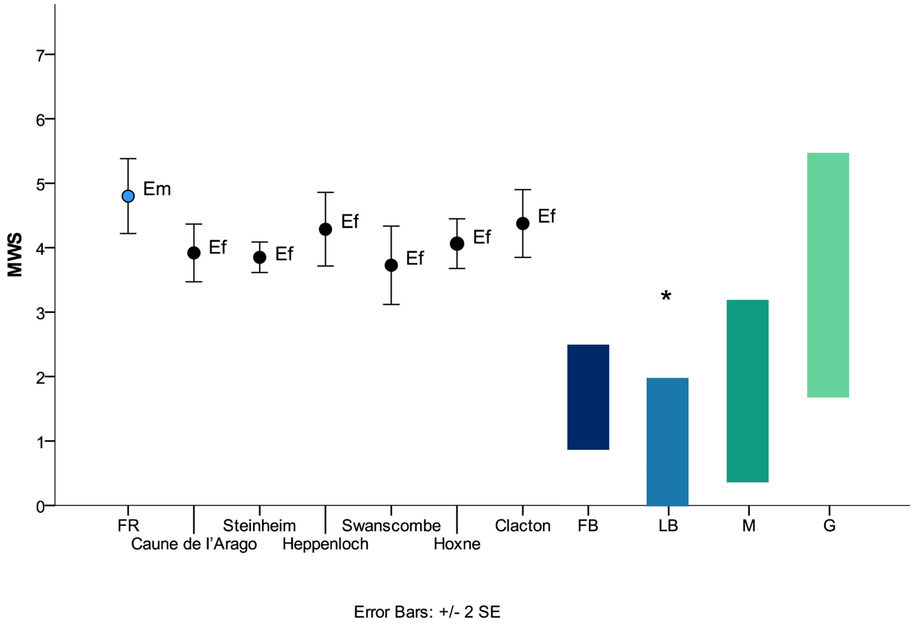

FIGURE 5 | Mesowear results of fossil stenonid equids and extant ungulates. Modern ungulates data from Fortelius and Solounias (2000) (diet information according to the radical classification; minute abraded brachydont species have been included), Rivals and Semprebon (2010). Caune de l'Arago, Steinheim, Heppenloch, Swanscombe, Hoxne and Clacton data from Rivals et al. (2015a), Rivals and Lister (2016) and Rivals and Ziegler (2018). MWS, mesowear score; CSG, Coste San Giacomo; Ez, *Equus senezensis* aff. *E. sen. stehlini*; Es, *Equus stenonis*; Eb, *Equus bressanus*; FB, fruit browsers; LB, leaf browsers; M, mixed feeders; G, grazers; *, *Heterohyrax brucei*.

Fontana Ranuccio, showed a mean MWS of 4.8 higher than the one recorded in all the other caballoid equids from Germany (Steinheim, 3.8; Heppenloch, 4.3), France (Caune de l'Arago, 3.9) and Britain (Swanscome, 3.7; Hoxne, 4.0; Clacton, 4.4) (**Figure 5**), suggesting an overall more abrasive diet for the Middle Pleistocene fossil caballoid equid of the Anagni Basin.

Stable Carbon and Oxygen Isotope Analyses

Compared equids *E. senezensis* aff. *E. sen. stehlini* from CSG, *Equus* cf. *E. mosbachensis* from FR and Mauer, *E. ferus/ E. hydruntinus/E. sp.* from Steinheim and *E. caballus* from Bockstein and Vogelherd varied significantly in δ^{13}C and δ^{18}O values (ANOVA [$F_{5,26} = 8.6$, $p < 0.001$, $r^2 = 0.55$] for δ^{13}C / ecosystem; [$F_{5,26} = 5.7$, $p < 0.001$, $r^2 = 0.43$] for δ^{18}O VPDB/VSMOW/temperature).

The δ^{13}C values of *E. senezensis* aff. *E. sen. stehlini* from the Early Pleistocene CSG were −12.49 and −11.94‰, falling within the values of the late Pleistocene horses from Bockstein and Vogelherd and middle late Pleistocene *E. hydruntinus* from Steinheim (**Table 2**) (**Figure 6A**). The δ^{18}O values of CSG *E. senezensis* aff. *E. sen. stehlini* were higher than in the compared German sites −4.02 and −6.19‰ (VPDB), −26.71 and −24.48‰ (CO_3 VSMOW) (**Table 2**) (**Figure 6B**), 17.76 and 15.6‰ (PO_4 VSMOW), respectively, suggesting that the horses used water sources with $\delta^{18}O_{water}$ −6.81 and −9.86‰.

The δ^{13}C values of *Equus* cf. *E. mosbachensis* from the Middle Pleistocene FR ranged from −13.93 to −12.63‰ (**Table 2**) (**Figure 6A**), which is similar to *E. mosbachensis* from Mauer and equids from Steinheim. *Equus* cf. *E. mosbachensis* differed from the late Pleistocene *Equus ferus* (*post hocs* Tamhane $p = 0.004$ δ^{13}C/ ecosystem).

The δ^{18}O values of FR *Equus* cf. *E. mosbachensis* varied between −6.96 and −4.24‰ (VPDB), −23.68 and −26.49‰ (CO_3 VSMOW) (**Table 2**) (**Figure 6B**), 14.83 and 17.54‰ (PO_4 VSMOW), respectively, indicating that water sources used had the $\delta^{18}O_{water}$ values of −10.94 and −7.12‰.

The only peculiar difference between the Italian and German sites is demonstrated in the temperature calculations, indicating much higher temperatures for both CSG and FR (6.2–12°C) than for the German sites (−0–6.8°C) (**Table 2**).

DISCUSSION

Mesowear and stable isotopic analyses suggest that horses in both sites inhabited rather open and dry environments with abrasive C_3 vegetation as a dietary source for the majority. As obligate drinkers, however, horses could have used different water sources in more humid and closed, or more open and arid environments, which could have been at slightly different elevation and subjected to seasonal variation in water availability. Both *E. senezensis* aff. *E. sen. stehlini* from CSG and *Equus* cf. *E. mosbachensis* from FR display dental mesowear patterns highly consistent with a grazing feeding behavior, according to the results reported in Strani et al. (2015, 2018a,b,c), where both upper and lower cheek teeth were analyzed. Differences, however, are observed in terms of niche occupation in the Early Pleistocene stenonid equid, displaying a less abrasion-dominated

TABLE 2 | Isotopic results for *Equus senezensis* aff. *E. sen. stehlini* from CSG, *Equus* cf. *E. mosbachensis* from FR, and for Pleistocene equids from German localities [data from Pushkina et al. (2014)].

Taxon	Site	d13C (‰ VPDB)	d18O (‰ VPDB)	d18O (‰ VSMOW)	Ecosystem	Temperature °C (central Europe)	References
Equus cf. *E. mosbachensis*	Fontana ranuccio	−13.87	−6.43	24.23	−27.87	7.7	This paper
Equus cf. *E. mosbachensis*	Fontana ranuccio	−12.63	−4.24	26.49	−26.63	13.2	This paper
Equus cf. *E. mosbachensis*	Fontana ranuccio	−13.93	−6.96	23.68	−27.93	6.33	This paper
Equus senezensis aff. *E. sen. stehlini*	Coste san giacomo	−12.49	−4.02	26.71	−26.49	13.75	This paper
Equus senezensis aff. *E. sen. stehlini*	Coste san giacomo	−11.94	−6.19	24.48	−25.94	8.28	This paper
Equus caballus	Bockstein	−11.94	−10.25	20.29	−24.44	−1.93	Pushkina et al., 2014
Equus caballus	Bockstein	−11.72	−8.66	21.93	−24.22	2.08	Pushkina et al., 2014
Equus caballus	Bockstein	−11.59	−8.99	21.6	−24.09	1.26	Pushkina et al., 2014
Equus caballus	Bockstein	−11.39	−9.39	21.18	−23.89	0.23	Pushkina et al., 2014
Equus mosbachensis	Mauer	−13.91	−7.73	22.89	−26.41	4.44	Pushkina et al., 2014
Equus mosbachensis	Mauer	−13.1	−9.05	21.53	−25.6	1.1	Pushkina et al., 2014
Equus mosbachensis	Mauer	−12.83	−6.67	23.98	−25.33	7.11	Pushkina et al., 2014
Equus mosbachensis	Mauer	−12.72	−9.37	21.2	−25.22	0.28	Pushkina et al., 2014
Equus ferus	Steinheim	−14.2	−8.9	21.7	−26.72	1.42	Pushkina et al., 2014
Equus ferus	Steinheim	−13.56	−7.91	22.71	−26.06	3.98	Pushkina et al., 2014
Equus ferus	Steinheim	−13.43	−6.91	23.74	−25.93	6.51	Pushkina et al., 2014
Equus ferus	Steinheim	−13.33	−9.39	21.18	−25.83	0.25	Pushkina et al., 2014
Equus ferus	Steinheim	−13.29	−8.94	24.64	−25.79	1.38	Pushkina et al., 2014
Equus ferus	Steinheim	−13.03	−9.31	21.26	−25.53	0.43	Pushkina et al., 2014
Equus ferus	Steinheim	−12.53	−8.97	21.62	−25.03	1.31	Pushkina et al., 2014
Equus ferus	Steinheim	−12.45	−7.97	22.64	−24.95	3.82	Pushkina et al., 2014
Equus ferus	Steinheim	−13.6	−7.6	23	−26.1	4.7	Pushkina et al., 2014
Equus ferus	Steinheim	−12.8	−8.3	22.3	−25.3	2.98	Pushkina et al., 2014
Equus hydruntinus	Steinheim	−12.7	−7.9	22.7	−25.16	3.98	Pushkina et al., 2014
Equus hydruntinus	Steinheim	−12.3	−7	23.7	−24.84	6.3	Pushkina et al., 2014
Equus hydruntinus	Steinheim	−12.2	−7.4	23.3	−24.7	5.35	Pushkina et al., 2014
Equus hydruntinus	Steinheim	−12	−9.1	21.5	−24.49	1	Pushkina et al., 2014
Equus sp. (ferus)	Steinheim	−13.8	−7.4	23.2	−26.3	5.16	Pushkina et al., 2014
Equus sp. (ferus)	Steinheim	−12.7	−7.2	23.4	−25.7	5.67	Pushkina et al., 2014
Equus sp. (ferus)	Steinheim	−12.5	−7.5	23.2	−25	5.12	Pushkina et al., 2014
Equus sp. (ferus) *germanicus*	Steinheim	−13.1	−7.3	23.3	−25.58	5.53	Pushkina et al. (2014)
Equus caballus	Vogelherd	−12.17	−9.49	21.08	−24.67	−0.01	Pushkina et al., 2014

diet in a more open landscape of steppe, shrubland, or light forest compared to the Middle Pleistocene caballoid species that fed strictly on abrasive sources in a more closed habitat of woodland or shrubland. Temperature-wise these localities did not appear to have differed. These findings allow us to provide information on the paleoecology of the two groups of fossil equids of the Anagni Basin, hereby shedding light on their ecological response to the major climatic events that marked the Early and Middle Pleistocene: the onset of the Pleistocene glaciation, which led to a gradual trend toward cooler climatic conditions and subsequent reduction of sub-tropical vegetation in Eurasia (Fortelius et al., 2006; Combourieu-Nebout et al., 2015), and strengthening of the Early-Middle Pleistocene Transition, which led to an increase of interglacial temperatures (Head and Gibbard, 2015). Isotopic results obtained for *E. senezensis* aff. *E. sen. stehlini* indicate that this equid occupied open and dry habitats similarly to the Late Pleistocene horses and middle Late Pleistocene *E. hydruntinus* from central Europe (Pushkina et al., 2014). Dental mesowear patterns are compatible with a grazing behavior similarly to *E. stenonis* populations, e.g., from Sésklo (MN17 biozone, Early Pleistocene, Greek Peninsula) (Rivals and Athanassiou, 2008) and from Olivola (∼1.8 Ma, Italian Peninsula) (Strani et al., 2018b).

E. stenonis is a common species of both Italian and Greek Peninsulas associated with fossil ungulates showing generally mixed or grazing dietary adaptations in open and dry environments (Rivals and Athanassiou, 2008; Strani et al., 2018b). In contrast, *E. senezensis* aff. *E. sen. stehlini* from CSG is associated with artiodactyls showing a wider range of feeding behaviors in a more heterogeneous landscape comprised of wetlands, forests and grasslands (Strani et al., 2015, 2018c), while displaying a less abrasion-dominated dental mesowear pattern than *E. stenonis* from Olivola (**Figure 4**). Similar conditions are observed in East Runton, where *E. bressanus* displayed

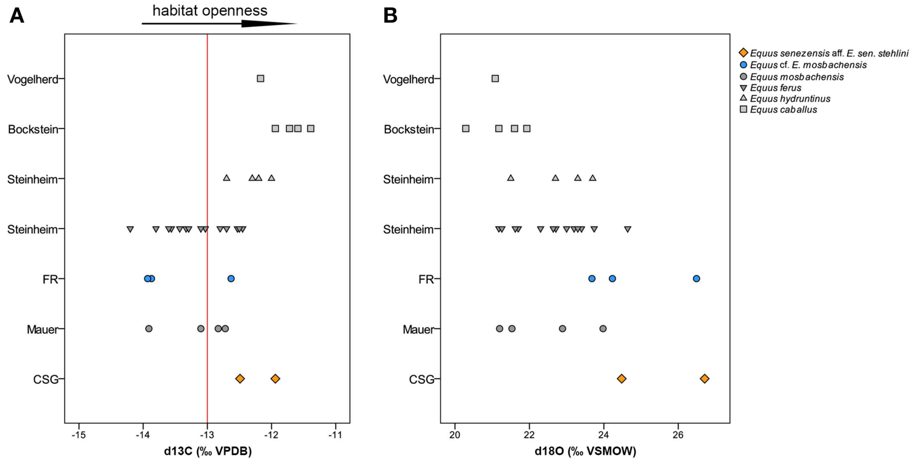

FIGURE 6 | $\delta^{13}C$ **(A)** and $\delta^{18}O$ **(B)** values of the studied taxa compared to fossil equids of central Europe (data from Pushkina et al., 2014). The red line represents the boundary between $\delta^{13}C$ values that indicate open ($\delta^{13}C > -13‰$) or closed landscapes ($\delta^{13}C < -13‰$) in warm temperate and cold boreal environments (Bocherens, 2014).

long-term grazing (according to molar mesowear) and short-term browsing diet (according to tooth microwear) and is grouped with other ungulates with a variety of feeding behaviors (Rivals and Lister, 2016).

The stenonid *Equus altidens* from the late Early Pleistocene Southern European site of Vallparadís Estació (layer EVT7) also displayed a certain dietary plasticity with a short-term mixed feeding behavior (Strani et al., 2019). *E. senezensis* aff. *E. sen. stehlini* is also one of the best represented ungulates from CSG, whereas fewer individuals have been recorded in Olivola (Strani et al., 2018b). This suggests that this equid, while feeding mostly on grasses, may have also accessed more diverse food items leading to a greater intake of softer plant resources compared to the similarly aged *E. stenonis* from Sésklo and to the later stenonid equids from Olivola. This scenario is consistent with the onset of a gradual trend toward cooler climatic conditions after the initiation at the Plio-Pleistocene boundary (2.6 Ma) of the Quaternary glaciations regulated by a 41 kyr periodicity (Lisiecki and Raymo, 2005), which led to the augmentation of open habitats and the disappearance of sub-tropical vegetation in the European continent (Bertini, 2003; Bertini, 2006, Fortelius et al., 2006; Bertini, 2010, 2013; Kahlke et al., 2011; Combourieu-Nebout et al., 2015). This process probably affected later Northern Europe as the paleoenvironmental conditions of East Runton appear to be more heterogeneous compared to the coeval locality of Olivola.

The more abrasion-dominated mesowear patterns of *Equus* cf. *E. mosbachensis* point to a stricter grazing diet, and are comparable to the ones observed in modern zebra populations, which feed almost exclusively on grasses (Bodenstein et al., 2000; Fortelius and Solounias, 2000; Rivals and Semprebon, 2010; Kartzinel et al., 2015). The same trend is observed also in the Middle Pleistocene caballoid equids from other European localities, which also display abrasion-dominated mesowear signatures (Rivals et al., 2008, 2015a; Rivals and Lister, 2016; Rivals and Ziegler, 2018). A similar trend from less abrasion-dominated to strictly grazing diet is observed even in Early and Middle Pleistocene equid populations of Britain (Rivals and Lister, 2016).

Isotope analysis points instead to a preference for slightly more closed environments in *Equus* cf. *E. mosbachensis* from FR similarly to *E. mosbachensis* from Mauer and Middle and Late Pleistocene equids from Steinheim (Pushkina et al., 2014) in comparison to *E. senezensis* aff. *E. sen. stehlini*. Long-term grazing behavior and short-term less abrasive diets are observed in *E. ferus* from the MIS 11 German localities of Hoppenloch and Steinheim (Rivals and Ziegler, 2018) and from the MIS 9 site Schöningen (Rivals et al., 2015b), suggesting that also in central Europe Middle Pleistocene horses appeared to have successfully exploited less open habitats.

FR *Equus* cf. *E. mosbachensis* is associated with ungulates displaying a wide range of feeding behavior with a noticeable abundance of browsing and mixed feedings cervids (Strani et al., 2018a,d). A similar condition is observed in Steinheim, where herbivores with diverse diets in humid and more closed habitats are recorded (Pushkina et al., 2014; Rivals and Ziegler, 2018). Isotopic analysis from the ungulates of Mauer also suggest warm and densely wooded landscape for this locality (Pushkina et al., 2014). On the contrary, fossil horses from the layer G (MIS 12) of Caune de l'Arago Cave (France) and from Hoppenloch are associated with a lower range of dietary traits pointing to drier environmental settings (Rivals et al., 2008; Rivals and Ziegler, 2018). This suggests that *Equus* cf. *E. mosbachensis* from the Anagni Basin occupied an ecological niche similar to the fossil horses from Steinheim in comparable environmental conditions, as grazers that feed also in more closed habitats. The higher MWS recorded in the FR population (4.8) compared to that of the Steinheim (3.8) (**Figure 5**), suggests that the fossil horses of central Italian Peninsula had a stricter grazing behavior compared to central European populations.

FR archeopaleontological layer with its fossil assemblage is dated to around "Mid-Brunhes event" (Biddittu et al., 1979; Muttoni et al., 2009; Pereira et al., 2018), which is associated with an increase in the amplitude of the interglacials and glacial cycles (Lang and Wolff, 2011; McClymont et al., 2013), and with one of the warmest and longest interglacial periods of the last 400 ka, registered during MIS 11 (Weirauch et al., 2008). According to palynological data from the MIS 11 Boiano Section (central Italian Peninsula) these warmer conditions led to the expansion of closed canopy forests with high summer precipitations (Combourieu-Nebout et al., 2015). The paleoecological information for the fossil horse of FR, suggests that in this scenario the Middle Pleistocene caballoid equids from central Italian Peninsula adapted to the reduction of open grasslands by exploiting also more closed habitats in heterogeneous landscapes. A possible competition with other large gregarious ungulates, such as *Bos primigenius* and *Stephanorhinus* sp., could have also played a key role in the niche occupation of this equid. The higher temperature gradient recorded by the isotopic analysis of the equid dental material compared to those observed in Steinheim, also can imply warmer conditions that characterized the Anagni Basin during this interval. This is concordant with the hypothesis of the Italian Peninsula acting as a southern refugium for mammal taxa and human populations during colder periods and extreme glacials of the Pleistocene (Manzi et al., 2011; Manzi, 2016).

CONCLUSIONS

This work offers important updated information on the paleoecological adaptations of Pleistocene equids of the Italian Peninsula. Overall Early Pleistocene stenonid horses grazed in open landscapes but demonstrated less abrasion-dominated diet compared to the later forms, suggesting the existence of more heterogeneous environmental conditions during the early Early Pleistocene before the Gelasian/Calabrian (middle/late Villafranchian) transition. In the same region, Middle Pleistocene caballoid populations displayed more abrasion-dominated long-term feeding behavior, having occupied less open habitats (at the edge between grasslands and woodlands) than stenonid forms of the Early Pleistocene, both in possibly warmer climatic conditions compared to French and German localities of the same age. Temperature calculations, however, should be considered with caution, since the sample size is quite small and based only on horses, and oxygen stable isotope variation apart from higher temperature can be associated with other factors, e.g., water sources from different elevation and subjected to seasonal variation in water availability.

Obtained data on the niche occupation of the stenonid *Equus* of the Anagni Basin support the spread of open landscapes in the Italian Peninsula following the initiation of the Pleistocene glacial cycles, suggesting, however, that these equids could have successfully adapted to exploit also more heterogeneous resources in the long-term timescale. Data from the caballoid *Equus* support the expansion of more closed environments in the region after the MIS 12–11 transition, though horses seemed to feed almost exclusively on abrasive vegetation possibly to avoid competition with other large ungulates that exploited softer food resources.

AUTHOR CONTRIBUTIONS

All authors have provided substantial contribution to the article. FS conceived the ideas and designed the approach. FS collected and elaborated the mesowear data. DP collected and performed the isotopic analysis with the help of HB, FS, and DP led the writing of the manuscript with the support of HB and DD. RS and LB provided helpful comments and inputs for the manuscript. All authors have approved the manuscript and agree with its submission to the journal.

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Dinohippus mexicanus (Early-Late, Late, and Latest Hemphillian) and the Transition to Genus *Equus*, in Central Mexico Faunas

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In the advances of the research of the sedimentary basins from central Mexico, it is significant the discovery of the first records of equids of Clarendonian and early Hemphillian age that are mentioned. The specimens were collected in southwest deposits of the San Miguel de Allende basin, the ages are verified by radiometric dates. The largest collection of *Dinohippus mexicanus* skulls jaws and isolated teeth recovered, have shown the wide geographical distribution in faunas of central Mexico. The study of these records from localities of Coecillos, Rinconada, Arroyo Emilio, and Rancho el Ocote faunas of the San Miguel Allende, Guanajuato state, Tecolotlán, Jalisco state and Juchipila basin Zacatecas state, have shown the variability and transitional features they have in the structures of the skull and upper and lower molars. The skull from Tecolotlán and Rancho El Ocote, of the late Hemphillian age present a well-defined dorsal fossa, in contrast the oldest skull from early-late Hemphillian of Juchipila, the fossa is just a depression in the Maxillary and nasal bone, however, the skull from Coecillos has structures that differentiate it from others. The most relevant records are the lower and upper molars collected at the top of the biostratigraphic sequence of Rancho El Ocote, in the sites named GTO 2 site D and F. These specimens present features that differentiate them from *Dinohippus* and suggest a primitive *Equus*. Upper teeth from the Blancan age of Tecolotlán basin, have a high crown but a pronounced curvature like the *Dinohippus mexicanus* collected in the late Hemphillian strata of this basin.

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INTRODUCTION

The research on paleontology of the sedimentary basins started at the Instituto de Geología has continued for more than 20 years at the Centro de Geociencias, Campus Juriquilla; both institutions belong to the Universidad Nacional Autónoma de México. The main objective of this project is to study the biostratigraphy of the Late Neogene sedimentary basins in the central region of Mexico.

These basins are in the Transmexican Volcanic Belt and north to it between the parallels 19° and 23°. The results obtained have demonstrated the importance of these sedimentary basins to complement the biostratigraphy of Mexico and North America.

The abundance and diversity of mammals that have been collected, with reliable stratigraphic and geographical information, have shown two faunal associations of different ages, Hemphillian and Blancan NALMA (North American Land Mammals Ages). These records allow us to understand important geological and biological events like the dispersal of mammals from the Temperate North America faunas to the central region of Mexico, the dispersal of the antilocaprids *Cosoryx* and *Plioceros* described in the Juchipila fauna in the early-late Hemphillian age, and the equids *Calippus martini* and the antilocaprid *Merycodus*, described from the la Nopalera locality in ages of 6.77 ± 0.21 My; these discoveries imply a reconsideration of the concepts of extinction, stratigraphic range and geographical distribution (Carranza-Castañeda et al., 2013; Robles-Rivera, 2015).

Another important result of the work in these basins refers to the most important biological event among the Americas, the Great American Biotic Interchange to (GABI). The recent discoveries of Neotropical immigrants in the Tecolotlán basin in deposits of 4.89 My confirm that there was more than one invasion of Neotropical faunas toward North America, prior to closing of the Panamanian land bridge (McDonald and Carranza-Castañeda, 2017). Additional contributions to these results refer to the exchange and displacement of mammals between the faunas of temperate North America toward the faunas of the central Mexico in both directions. Recent descriptions of neotropical mammals suggest that the western part of Mexico was an important migration route (Sussman et al., 2016; McDonald and Carranza-Castañeda, 2017; Carranza-Castañeda, 2018).

The above-mentioned information is based on an extensive collection of fossil mammals that has been integrated with the results of research in the sedimentary basins that have been studied, however, very little has been mentioned of the advances in the knowledge of the equids that have allowed to complement the biostratigraphic information of the strata that contain neotropical immigrants and mammals from the Great Plains of North America.

The objectives of this work are: to mention the first records of equids collected in the Clarendonian and early Hemphillian deposits, located south of the San Miguel de Allende basin, state of Guanajuato; to comment and describe the geographical distribution of *Dinohippus mexicanus* in the faunas of the central region of Mexico, defining the great variability that occurs in the facial region and the occlusal surface of upper and lower molars; to describe partially the stratigraphy of the most important faunas where diagnostic material of *D. mexicanus* was collected. In addition, the associated fauna in the stratigraphic levels where they were collected with the criterion that the age is determined by radiometric dates will be mentioned. The age of the records mentioned are determined to early-late Hemphillian, late Hemphillian (Hh3), and latest Hemphillian (Hh4). the analysis on interbedded volcanic ash and the associate fauna have determined the age of the fossils (Carranza-Castañeda et al., 2013; **Figure 1**).

MATERIALS AND METHODS

All the fossil materials mentioned in this paper are housed in the fossil collection of the Instituto de Geología, Ciudad Universitaria and the Centro de Geociencias, UNAM in Juriquilla. Querétaro.

To avoid the repetition of names, of the associated fauna with records of *D. mexicanus* is mentioned in **Supplementary Table 1**.

The terminology used in the description is from Lance (1950), MacFadden (1984, 2016).

The abbreviations used in the text and tables are: Ap, Anteroposterior, DPOF, Dorsal Preorbital fossa; Colo, Colotlán; HC, High crown; IGM, Instituto de Geología; Ii incisive; Jalp, Jalpan; Juch, Juchipila; JalTeco, JT Jalisco Tecolotlán; LACM, Natural History Los Angeles County Museum; L, Left; MPGJ, Museo de Paleontología Geociencias Juriquilla; Mm, molar; MSTHT, Mesostyle Crown Height; NMMNH, New Mexico Museum Natural History; Pp, Premolar; R, Right; Tab, Tabasco; Tr, transverse; Zac, Zacatecas; UNAM, Universidad Nacional Autónoma de México.

Recent Discoveries

The continuity of the investigations in southern San Miguel de Allende basin, have demonstrated new records of equids that correspond to Clarendonian and early Hemphillian ages, being the first time that in Mexico there are mentioned equids of unequivocal Clarendonian age, whose age is not inferred, but discovered a few meters below the andesites that have been dated.

Empalme Escobedo, Guanajuato

In the city of Comonfort, 25 km south of San Miguel de Allende, two new localities have been discovered, the locality with the older fauna is Locality GTO 92 Empalme Escobedo, located 5 km south of the town of the same name. The fossils were collected in a quarry of materials for road construction. The thickness of the sedimentary sequence is greater than 50 m and it is composed of different strata of igneous rocks and gravels at the base, covered by lacustrine sediments and layers of clay with sands. The fossils were collected in these layers. This sequence has a thickness of 5 m, is composed of clay and clays with gravel only 6 m above are the strata of andesites that cover the entire sequence.

The age of the sedimentary sequence is determined by the radiometric dates that were made in the andesites located 6 m above, by the method of $^{40}Ar/^{39}Ar$, which produced the result of 10.6 ± 0.3 My (Cerca-Martínez et al., 2000). These results confirm the Clarendonian age for this fauna. This is the only one known fauna of this age in central Mexico with well-determined ages.

The fossil material are two teeth, MPGJ 3031 assigned to *Protohippus* et al. sp., the other, MPGJ 3032, is referred to Hipparion (Robles-Rivera, 2015).

Order Perissodactyla Owen, 1848; Family Equidae Gray, 1821; *Protohippus* sp. Leidy, 1858

Description

The molar MPGJ 3031, M1, is hypsodont and curved, the protocone is small rounded with no heel, and is joined to the protoselene, by the isthmus that is constricted. The prefossette has multiple plications and a well-developed prefossette loop; the postfossette with the anterior border very simple and large plicaballin, with elongated hypocone.

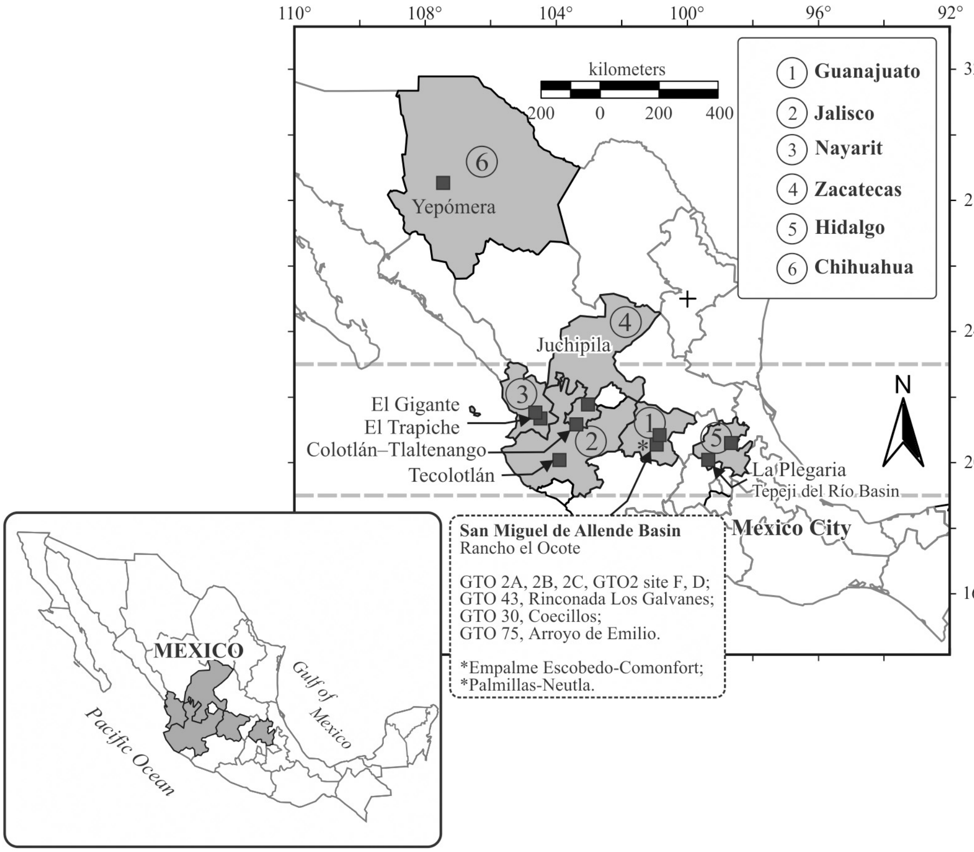

FIGURE 1 | On the map are the locations explained in the paper.

Hipparionine Christol, 1832

Description

MPGJ 3032 M1 fragment of upper molar, by the wear corresponds to an old adult, the main character for its assignment is the isolated and rounded protocone and simple fossettes without plications.

Area of Palmillas, Guanajuato

The second locality, GTO 91 Palmillas, is near the village of the same name. The area is very small; however, the fossils were collected in the deposits of the La Nopalera Formation (Ledezma, 1960). They consist of layers of clay with different concentrations of sand. These strata are covered by a layer of volcanic ash that was analyzed by the U/Pb method, produced a result of 6.77 ± 0.21 My, which refers them to the early Hemphillian.

The associated fauna includes remains of the antilocaprid *Merycodus* sp. and an incisor referred to *Megatylopus* (Robles-Rivera, 2015).

Family Equidae Gray, 1821; *Calippus Martini* Hesse, 1936

Material

Upper molars: MPGJ 1713 P2, MPGJ 1706 P34, MPGJ 1707 M2, MPGJ 1705 M3, MPGJ 712 M3, MPGJ 1708 M1, MPGJ 1709 M12, MPGJ 1711 M1, and MPGJ 1710 M3. Lower molar MPGJ 1824 m2. The main characters that justify the assignment to *C. martini*, refer to the protocone, arranged slightly diagonal, joined to the protoselene, and the shape change from oval to elongated; the curvature of the molars is moderate to pronounced, the fossettes with more plications in early stages of wear, hypocone open lobular to lenticular in old individuals.

The comparable *C. hondurensis* that has been described in faunas of central Mexico, differs considerably in size and the transverse and anteroposterior axes that are smaller compared with *C. martini.* The age for these deposits dated by U/Pb method is 6.77 ± 0.21 My, early Hemphillian (Robles-Rivera, 2015).

Dinohippus mexicanus IN FAUNAS OF THE CENTRAL REGION OF MEXICO

In all the Hemphillian faunas described in the sedimentary basins of central Mexico, there is a large diversity of mammals among which the equids are widely represented. However, *C. hondurensis* and *Astrohippus ansae* are present only in the early-late Hemphillian faunas. *Neohipparion eurystyle* and *D. mexicanus* are present in all sedimentary sequences, from the early-late and late Hemphillian, although in the deposits of the latest Hemphillian (Blanco Layer of Rancho El Ocote), only *D. mexicanus* survives until the unconformity of Blancan age (Carranza-Castañeda, 1989, 1992; Carranza-Castañeda et al., 2013).

STATE OF ZACATECAS

The Tlaltenango-Colotlán Basin

The lake sediments fill the basin and a few sites have fluvial deposits. The study began north of the city of Colotlán to its limit to the south in the village of Tepechitlán where some metapodial fragments were collected and that is at the end of the basin.

The most important is the locality Zac 9 Sanidad Animal (Carranza-Castañeda, 2006), where isolated teeth of *C. hondurensis* were recovered, besides *D. interpolatus*, however, by comparison with new material collected in Juchipila basin, they have been reassigned to *D. mexicanus*. The age was determined to the early-late Hemphillian by the presence of *Neohipparion* and *Calippus* (Carranza-Castañeda, 2006).

The Juchipila Basin

It is the most relevant area in the state of Zacatecas by the stratigraphy and the diversity and number of fossils collected with an extent of 165 and 15 km in width in the NNE direction. The first works on geology were made by students from the University of New Orleans, Lahiere (1982) and López (1991), who informally named the fluvial lacustrine deposits as Juchipila Formation. However, in their reports on the geology they only mention a molar of a peccary that they assigned to *Platygonus rex*. At the beginning of our investigations several important sites were discovered with different kinds of mammal fossils, as well as traces of birds, camelids, proboscideans, and equids in the lacustrine sediments. The relationships of the main localities were established (Aranda-Gómez et al., 2008).

The most important localities are in the central part of the basin, between the Tabasco city in the north and Moyahua in the south. The greatest extent is found in the middle part at the localities: El Mixtón and La Perdida, Cofradía and the Pitahaya area; and the Juchipila area with the localities El Resbalón, La Copa y El Epazote. In the northern part, the Tabasco area, the localities are La Escalera, Patos y Madera and the Wang locality. The associated fauna that has been described in previous works has been referred to the early-late Hemphillian age, was collected and supported by the radiometric date obtained in the analysis of volcanic ashes by the method of U/Pb which gave results of 6.95 ± 0.27 My in the lower and 5.59 ± 011 in the upper ash, ages that bracket the fauna in the early-late Hemphillian age (NALMA) (Aranda-Gómez et al., 2008; Carranza-Castañeda et al., 2013; Carranza-Castañeda, 2018).

The diversity of equids presented in these localities is remarkable. *C. hondurensis*, maxillaries, jaws and isolated upper and lower teeth, are widely distributed in all the localities of the basin; this is the largest representation of this equid in early-late Hemphillian faunas in the central region of Mexico, and so far, never is associated with *Nannippus* (Carranza-Castañeda and Espinosa-Arrubarena, 1996; Carranza-Castañeda et al., 2013).

The genus *N. eurystyle* in the Mixtón locality was collected in the same stratigraphic level; both parts of the maxillary of the same individual (catalog MPGJ 1870) and several isolated teeth have been collected.

The only jaw of *A. ansae* known in Mexican faunas was collected in the locality Zac Juch 48, La Copa. It consists of a complete left jaw with p2-m2. The main difference with *A. stockii* is the measurements of the Ap and Tr axis that are bigger and the paralophid is stouter, the protoconid and hypoconid are more rounded. The most important find was collected in the Mixtón sequence. It is a partial skull, MPGJ 1682, with the craniofacial region almost complete in both sides but better preserved in the right side where the dorsal fossa is more evident; the dentition includes part of the P2, and complete P3-M3, molars on the right side. The specimen has been referred to *D. mexicanus*; in addition, isolated upper molars collected in Zac Juch 47 El Resbalón, have a pronounced curvature, although are very short high crown (**Figures 2A,B**).

At the locality Zac Tab 34, Wang, located 45 km north of the Mixtón, a mandible referred to *D. mexicanus* was collected in a sequence of clays with different concentrations of fine sand. The jaw includes the complete right side with well-preserved p2-m3 and a whole symphysis including the incisors (**Figure 3**).

FIGURE 2 | MPGJ 1982 *Dinohippus mexicanus*, Zac Juch 30 Mixtón. **(A)** Right side of the skull, the nasal notch is on M2, the maxillary fossa is shallow, it is not pocketed posteriorly, the edges are poorly defined and the infraorbital foramen is included in the anterior part. **(B)** MPGJ 1683, ventral view of P3-M3, we observed the protocone with small anterior heel and P4-M1 the lingual edge is concave.

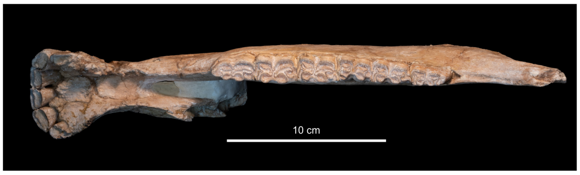

FIGURE 3 | MPGJ 1683 of Zac Tab 34 Wang Location, ventral view of the jaw, symphysis and incisors are complete, the incisors have wide infundibulum, the linguaflexid is wide, the metacónid and metastilid are lobular, the lingual edge of the protoconid and hypoconid is rounded.

Dinohippus mexicanus (Lance, 1950)

Referred specimen

Zac Juch 30 Mixtón. MPGJ 1982, partial cranium with right region facial well preserved and P3-M3 and fragment of P2. Zac Juch 47 El Resbalón MPGJ 4067 P4-M1, MPGJ 4095 M1, and MPGJ 4067 P4. Lower jaw, Zac Juch 34 Wang MPGJ 1683 belongs to young individual, with p2-m3 and i1-3, both sides and complete symphysis.

Locality and age

The specimen MPGJ 1682 partial skull collected in the locality Zac Juch 30 El Mixtón.

The jaw MPGJ 1683 from the locality Zac Tab 34 Wang, State of Zacatecas, México; early-late Hemphillian age. Collectors, Xiaoming Wang, Jorge Aranda-Gómez and the author.

Description

The skull (MPGJ 1682) on the left side is slightly squashed, the facial region on the right side is complete without deformation. The occipital region is also incomplete, although some of the structures are observed. The nasal notch is above the posterior part of P2, the row of P3-M3 has a length of 126 mm. The infraorbital foramen is located 68 mm above the alveolus of P4. The malar crest is remarkable and strong, it ends between P4 and the anterior part of M1. The malar fossa is absent. The nasomaxillary fossa (DPOF) is shallow, is 58 mm distant from the orbit, is a slight depression not pocketed posteriorly and the anterior end is above the M2. The fossa has poorly defined and rounded borders, the wider part is 38 mm and the infraorbital foramen is included. The distance from the orbit to the DPOF is 57 mm. The height from the alveolus of M2 to the orbit is 114 mm.

The premolar P2 is preserved. It has a prominent parastyle and mesostyle, the enamel is moderately thick and the fossettes are almost without plication by wear.

On the P3 (Ap 26.90 mm and Tr 27.18 mm), the prefossette is very worn and the postfossette is without plications. The hypocone is broad and the hypoconal groove is of moderate depth. They persist in the whole dentition but only reduce their size. The preprotoconal groove is constricted, the protocone is broad and moderately long, the anterior part forms a rounded heel, and the lingual border is flat and parallel to the lingual part of the alveoli. P4 (Ap 24.45 mm and Tr 25 mm), presents the parastyle and mesostyle that are of almost equal widths and flat. The protocone has a remarkable and blunt heel, the posterior part is long and rounded and the lingual border is concave in a "wooden shoe shape."

M1 (Ap 22.95 mm and Tr 25.44 mm), The fossettes are very worn, the protocone has the "wooden-shoe shape," posteriorly it is elongated and wide, the anterior with a notable heel, and the lingual border is concave. M2 (Ap 23.7 and Tr 23.06), it has a trapezoidal shape because the parastyle side is longer. The protocone is broad and elongated, with the posterior part triangular, and the anterior part forms an evident heel of rounded shape. On M3 (Ap 24.94 mm and Tr 20.46 mm) the most notable difference of the molar is reduction of the hypocone and hypoconal groove. The protocone in the anterior part forms a prominent heel, posteriorly is elongated and the lingual border is horizontal (**Figures 2A,B**).

Lower jaw. The specimen MPGJ 1683 preserves the right side, is broken on the horizontal edge, and only has part of the ascendant border of the coronoid process. The symphysis is complete with R and L i1-3, all have a wide infundibulum filled with cement. The canine is very small, which suggests a female. The pre-canine diastema is 8.13 mm, and the post-canine diastema is 74.45 mm. The maximum width between the L I3 and R 13 is 57.16 mm. The dentition p2-m3 is 147.5 length, the Ap of p3-p4 is 54.7 mm and Tr is 18.8; the Ap m1-m2 46.8 and Tr 16.3. The protoconid and hypoconid are rounded in molars and premolars. The metaconid and metastylid in the premolars are rounded almost with similar size and separated by a wide linguaflexid. In the molars, the metaconid is rounded, but the metastylid is smaller and slightly sharp posteriorly. The ectoflexid in the molars is deeper to almost touch the enamel-edge of the linguaflexid; in premolars, it does not penetrate the isthmus. The assigned age is determined associate fauna and analysis of the upper ash the result 5.9 My placed the jaw to early late Hemphillian.

According to the stratigraphic age the skull of Juchipila, early late Hemphillian, a protocone like *D. interpolatus* or *D. leidyanus* could be expected, without heel and inclined toward the lingual margin, however, the shape and disposition of the protocone, is like Dinohippus mexicanus of late Hemphillian (**Figure 3**).

STATE OF GUANAJUATO

San Miguel Allende Basin

The first reference to *D. mexicanus* is associated with the description of the equids from Rancho El Ocote fauna, however, it has had a complicated taxonomic history (Arellano, 1951; Mooser, 1958, 1960, 1965, 1973a,b; Carranza-Castañeda and Ferrusquía-Villafranca, 1978; Dalquest and Mooser, 1980; Carranza-Castañeda, 1992).

In the new investigations in Rancho El Ocote and other Hemphillian localities, the material of *A. stockii*, *N. eurystyle*, and *D. mexicanus* collected in different stratigraphic layers was compared with the Yepomera collection housed in the Museum of Los Angeles (LACM), arriving at the conclusion they are the same species, for which *N. floresi* and *N. arellanoi* are considered as junior synonym of *N. eurystyle* (Carranza-Castañeda and Ferrusquia-Villafranca, 1979; MacFadden, 1984), and *D. ocotensis* (Dalquest and Mooser, 1980; Dalquest, 1988), is a junior synonym of *D. mexicanus* from the faunas of central Mexico. All the records known in central Mexico are assigned to the same species as Yepómera (Carranza-Castañeda and Ferrusquia-Villafranca, 1979; MacFadden, 1984; Carranza-Castañeda, 1989, 1992, 2006).

Rancho El Ocote Local Fauna

The first mention of horses from Rancho El Ocote was made by Arellano (1951). Later several papers (Mooser, 1958, 1968, 1973b) describe different species, summarized in the last of these works like *D. ocotensis* (Dalquest and Mooser, 1980); they suggest that the locality represents only one age, late Hemphillian, and that was younger than the Yepomera fauna, however, they have never justified this comment. The Rancho el Ocote Local Fauna has been considered as the reference of the late Hemphillian faunas in central Mexico, by the diversity and abundance of the Hemphillian fossil indexes.

The results of new field work in this locality and studies of taphonomy have demonstrated two stratigraphic levels occur, each one with its own lithology and faunal content that corresponds to the late (Hh3) and latest (Hh4) Hemphillian; covered in erosional unconformity by deposits that contain a fauna of early Blancan age (Carranza-Castañeda, 1989, 2006; Carranza-Castañeda et al., 2013).

The lower layer is named the Rhino layer (GTO2B), because its contains: *Teleoceras*, *Machairodus*, *Borophagus secundus*, *Agriotherium*, *Pseudaelurus*, *Alforjas* and the equids *N. eurystyle* and *Nannippus aztecus*, which are the last records in all the central México Hemphillian faunas, *A. stockii* is recorder in the Rhino layer and in contact with the Blanco layer. These are the best representation of late Hemphillian fauna in central Mexico and have been referred to Hh3. *D. mexicanus* is well represented by skull, jaws, isolated upper, and lower molars, incisors and postcranial elements; the age of the fauna represents the late Hemphillian age. The result of the analysis of the ash by the methods of fission track in zircons gave the result of 4.8 ± 0.2 My that confirms the assigned age (Kowallis et al., 1999; Carranza-Castañeda et al., 2013).

The Rhino level is covered by the Blanco layer (GTO2 A), the lithology is a fine sand deposit and volcanic ash lenses, which contain a special distribution of fauna. The *A. stockii* material is recorder only at the base represented by a few teeth. *D. mexicanus* is found throughout the White layer, associated with *Stegomastodon*, *Megatylopus*, and *Hexobelomeryx* and some rodents and the oldest record of the South American immigrant *Paramylodon garbani* (Montellano-Ballesteros and Carranza-Castañeda, 1986; Carranza-Castañeda et al., 2013).

Above the Blanco layer, there are two-three meters of early Blancan sediments where *N. peninsulatus*, *Equus* teeth and a few osteoderms of the South American immigrant *Plaina* have been recovered. The age was obtained by the analysis of volcanic detritus by ^{40}Ar/^{39}Ar 4.7 ± 0.02 My; this result bracket the Hemphillian-Blancan boundary in Mexico in 4.74 ± 0.14 and 4.89 ± 0.16 (Kowallis et al., 1999; Flynn et al., 2005).

In the upper part of the Blanco level, there are small deposits of clay containing upper and lower molars that have the axes Ap and Tr larger than those collected in the Rhino level. The fossils from these sites have been cataloged as GTO 2 site D and GTO 2 site F (**Figure 4**).

Dinohippus mexicanus (Lance, 1950)

Referred material

Skull IGM 7596, skull with R I3, P2-M3, L I2-I3, P2-M3.

Lower Jaw. MPGJ 3739 P2-M3 GTO 2A, MPGJ 3872 L p2-p4 GTO 2b, Rhino layer, MPGJ 3946 R p2-m3, symphysis Ri 1-3 L 2-3, MPGJ 5125 GTO 2 A, Blanco layer, with p2-m1, canine and l 2-3 incisive the R I 2-3 broken, MPGJ 3018 R i1-3 Li 1-3.

Upper Molars, GT0 2A Blanco Layer: MPGJ 5131 M3, MPGJ 5151 M1, MPGJ 5132 P4, MPGJ 5153 P34. GTO 2B Rhino layer; MPGJ 510 M3, MPGJ 650 M1, MPGJ 2056 M1, MPGJ 2075 P4, MPGJ 2915 M1, MPGJ 3793 P4, MPGJ 3822 GTO M2, MPGJ 3841 P4, MPGJ 5128 P4, M3, MPGJ 5131M3, MPGJ 5135 M1, MPGJ 11500.

UPPER MOLARS GTO 2 site D, MPGJ 2825 p4, MPGJ 5111 P34, MPGJ 5113 P3, MPGJ 5126 P4, MPGJ 3947 M1.

UPPER MOLARS GTO 2 site F: MPGJ 4040 M1, MPGJ 5146 P4IGCU 5180 M2, IGCU 11503 P4, IGCU 11504 M1.

LOWER MOLARS GTO 2A; site D: MPGJ 5109 m3; MPGJ 2825 p4.

LOWER MOLARS GTO 2 SITE F, MPGJ 495 p3, MPGJ 2285 p34, MPGJ 2285 p43, MPGJ 3548 p3; IGCU 3858 p3; MPGJ 5116 p4, MPGJ 5117 p34, MPGJ 5118 p4, MPGJ 5119 m2, MPGJ 5120 p34, MPGJ 5129 p4, MPGJ 5130 p2, MPGJ 5134 p4, MPGJ 5144 p3, MPGJ 5145 p4; MPGJ 5147 p4, MPGJ 5149 m2, MPGJ 5150 m2.

Description

The skull has been described and discussed extensively by MacFadden and Carranza-Castañeda (2002). In this part only comparisons will be made with other skulls collected in the faunas mentioned in this paper.

Lower Jaw referred. The jaw MPGJ 3739 from GTO 2 A, collected from the upper part of Rhino layer, conserves the left side, the horizontal border is complete. The maximum depth is at the beginning of the angle of the mandible below the m3 with 114 mm. The Ap length of p2-m3 is 166 mm. To determine the relationship between jaw depth and the crown height at p4 and m2, an X-Ray of the jaw was made. It is remarkable that there is no relationship between jaw depth (m2) and the height of the crown, which justifies the larger size of the molars of the GTO 2 D and F sites.

The jaw MPGJ 3946 collected in GTO 2 B from the Rhino layer, preserves the symphysis, the canine is partially broken, the incisors form an almost curved row, R i1-3, and L i2-3. The i2, is wider. The infundibulum limited by enamel and filled with cement. The post-canine diastema is 89.74 mm, the pre-canine diastema is ∼7 mm. The length R i2- L i2 is 43.70 mm; the length Ap of p2-m3 is 156 mm, the premolars and molars are straight and hypsodont, p2 67 mm long, p4 is 76 mm high, m2 47.4 mm. The metaconid and metastylid are rounded almost the same size. All the teeth with a remarkable cover of cement, protoconid and hypoconid roughly flat.

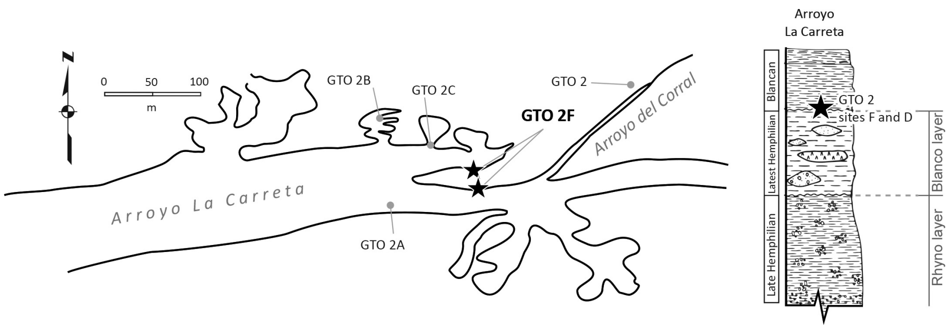

FIGURE 4 | Map of Arroyo La Carreta, where the fossil localities of Rancho El Ocote are located. Note that the GTO 2 site D and F are on top of Blanco layer, the stratigraphic column show the sites in the Blanco layer (Latest Hemphillian).

MPGJ 5125 is a fragment of left jaw collected in the GTO 2 A White layer, retains a robust symphysis with strong canines that are broken and the incisors with small infundibula without enamel. The jaw has its maximum depth of 101.3 mm, from the linguaflexid of p4 to the horizontal edge. The metaconid is lobular, and metastylid slightly pointed toward the lingual margin, V-shaped linguaflexid in molars, the ectoflexid is deep into the isthmus, the protoconid and hypoconid with well-defined flat edge in the labial border.

MPGJ 3872, is a fragment of left jaw with p2-p4. The most significant features are the metastylid pointed and the slightly rounded protoconid and hypoconid.

Discussion

The jaw MPGJ 3946 from GTO 2B is very deep, the maximum depth is in p4 and m1. To determine the length of these molars *in situ*, a complete X-Ray was made, in which the length (HC) of the teeth was measured, and compared with the length of the mandible MPGJ 3739 from GTO 2 A. The size is like isolated molars collected in the same localities. The measurement of the molars included in the alveolus of the mandible is smaller compared with the specimens of the GTO 2 sites D and F (**Figure 5**).

In the same stratigraphic sequence, at the Rhino and Blanco layers, numerous isolated molars have been collected. The analysis show similarities with the description mentions in lower molars that have been described in the jaws. However, at the top of the stratigraphic sequence, in clay deposits named GTO 2 site D and GTO 2 site F, lower and upper molars have been collected. The preservation is deficient, especially in length of the molars, however, the differences in size of the anteroposterior and transverse axis on the occlusal surface is remarkable.

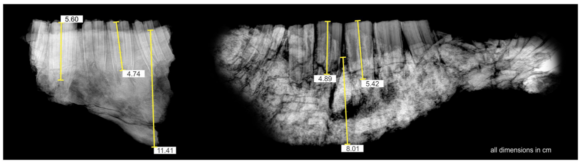

FIGURE 5 | MPGJ 3739 Jaw fragment from GTO 2A collected in the Blanco layer. The jaw is very deep with full dentition. The X-Ray was taken to know the HC of p4-m1 and to determine its real size in the alveolus, to compare with the height of the crown of the molars of the F site of GTO2.

The metaconid and metastylid are rounded and almost of the same size, the entoconid is round, the linguaflexid is open in V shape and wider in molars. Specimen MPGJ 5134 presents a pli caballinid, the protoconid and hypoconid large and flat in the lingual edge. The upper molars also differ from those collected from the Rhino layer: the crown is higher and straight, and the protocone developed. The Ap and Tr measurements of the p3-m2 of the mentioned jaws from GTO 2A and B have been plotted versus the molars of GTO 2 site D-F. It is remarkable the separation they have with the specimens collected in the sites GTO 2 D-F.

The MPGJ 5145 p4 from GTO 2 site F, was compared with MPGJ 5136 p4 of *Equus simplicidens* from GTO 6 Arrastracaballos locality early Blancan. The measurements are not very different, GTO 2 F Ap 29.87 Tr 17.46, the same measurements in MPGJ 5136 p4 Ap 32.53 Tr 20.23, which suggests that GTO 2 F specimens are a transitional group between the late Hemphillian *Dinohippus* and early Blancan *Equus* (**Figures 6A,B**).

Coecillos Area

The locality is situated 12 km southeast of Rancho El Ocote. The basal layer GTO 30, is a clay layer covered by ashy material, dated 5.32 ± 0.34 My. Above there is a sequence of clays of yellow color that contain *Dinohippus* material, besides abundant *A. stockii* and a few *N. aztecus* teeth. The upper part of the sedimentary sequence, located GTO 75, is covered by layers of compacted clay with abundant concretions. In these deposits, a fragment of skull and several jaws and isolated molars was collected isolated of *D. mexicanus*. It is the same stratigraphic sequence where the skunk *Conepatus sanmiguelensis* was recovered, which participated in previous GABI events. These sediments are covered by late Blancan-Irvingtonian deposits where *Glyptotherium texanum* was collected (Wang and Carranza-Castañeda, 2008; Gillette et al., 2016).

At the top of these deposits, the ash layer that covers the sequence was dated by the U/Pb method; the result is 4.54 ± 1.5 My. This means that the records of *Dinohippus* are

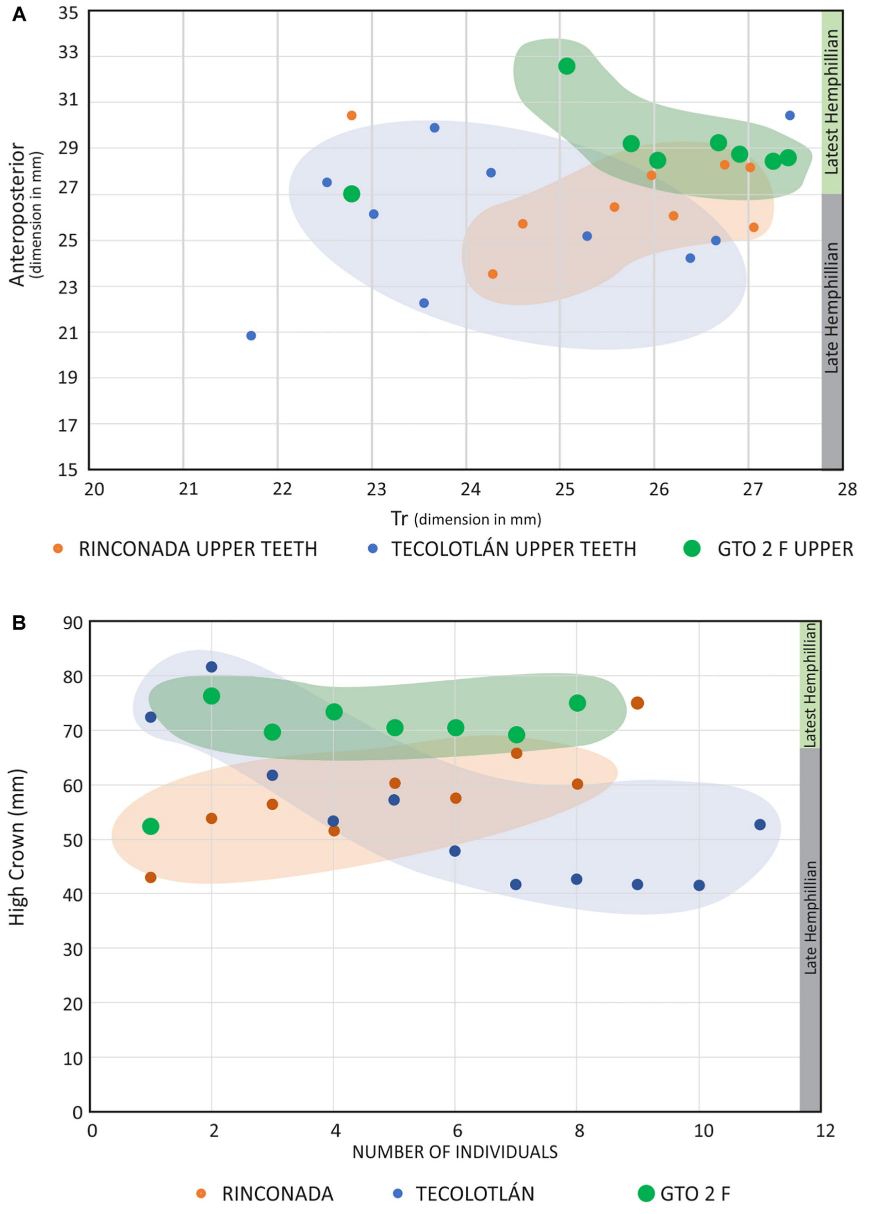

FIGURE 6 | (A) All measurements of the Ap and Tr of M1 in upper molars including those of GTO 2 site F, have been plotted. **(B)** The measurements of the HC of P4-M1 were also graphed. The separation of GTO 2 F in the two graphs is remarkable, which suggests a different population.

bracketed with the lower age dated by 5.32 ± 0.34 My, results that gave the importance to these records.

Dinohippus mexicanus (Lance, 1950)

Referred specimen

GTO 75 Arroyo de Emilio MPGJ 103, skull fragment with palate and pat of the facial area. MPGJ 131 R P4-M3 and L P4-M1 from GTO 75 Same individual. MPGJ 857 R jaw p2-m3, L i1-3, Ri, 2-3. MPGJ 729 M1, MPGJ 1559 P4, MPGJ 5439. P4.

Lower teeth. GTO 30: MPGJ 310 L p2-m3, IGCU 5201 p2-m1 -m3, c, L i1-3, R i2-3. Isolated lower teeth, GTO 30 5306 p4, IGCU 5308 m2, IGCU 5593 m1, GTO 30. Upper teeth: IGCU 5437 P4, IGCU 5593 M1MPGJ 5438 P3, MPGJ 5578 M1, IGCU 5580 P4.

Locality and age

In deposits of the Coecillos area. GTO 30 Coecillos and GTO 75, Arroyo de Emilio localities, late Hemphillian age.

Description

The skull MPGJ 103 from GTO 75 Arroyo de Emilio of the Coecillos area, consists of a fragment that preserves the complete palate and molars of both sides, the maximum length P3-M3 is 121 mm. The maxillary in the right side is the best preserved part including the wall of the orbit; however, there is no evidences of DPOF. The malar crest is well developed and ends in the anterior part of M1; there is no evidence of a malar fossa. The palate is well preserved in the ventral part, the posterior nasal orifices, the palatine bones, vomer, the anterior palatine holes and the palatal grooves. The maximum length Ap of the choana is 108 mm, the maximum transverse on the back of M3 is 49 mm. The maximum width of the palate between the lingual edge of M3 is 72 mm, maximum width between lingual edge of the protocone of P4 is 62 mm.

This skull MPGJ 103, is an old individual that does not present evidence of DPOF. According to the stratigraphic position almost at the top of the Coecillos sequence, the deposits where it was collected are only one meter below the ash that was analyzed and gave the result of 4.5 ± 1.5 My. It is possible to argue that corresponds to a primitive *Equus* with the support of the character of the teeth, however, the mandible MPGJ 857 that was collected at the same stratigraphic level presents characters in the dentition that are within the variability of *D. mexicanus*, although the protoconid and hypoconid are flat in the premolars and a little less in molars (**Figures 7A,B**).

Los Galvanes Area

Rinconada Local Fauna

Located almost in middle of the San Miguel Allende basin, limited by the Rancho Viejo hills in the east and the Tequisquiapan in the west. The fossiliferous deposits are 7 m thick.

The basal layer is unconsolidated sandy clay, covered by a lacustrine deposit about 1–2 m thick. This layer represents the bottom of the ancient lake, around 25 km long. The lithology is a sandy clay layer cemented by calcite and silica with a lens of volcanic ash and paleochannels of fine sand and gravel. All the fossils have been collected in this layer. A sandy clay layer covers the lake, and the top of the sequence is overlain by the unconformity of Hemphillian-Blancan age with a thickness of 1–2 m.

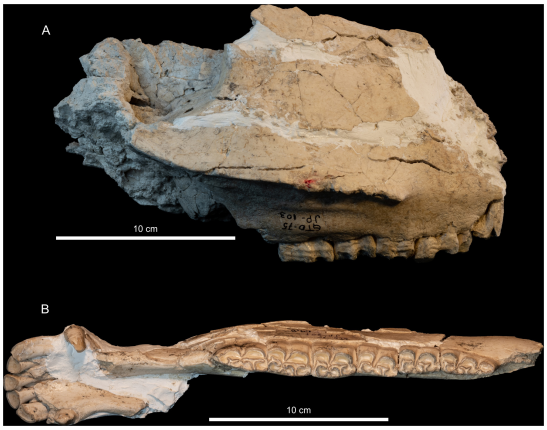

FIGURE 7 | (A) MPGJ 103, locality GTO 75 Arroyo de Emilio, we observe the facial region on the right side, part of the orbit, the nasal and maxillary bone without evidence of DPOF. The molar crest is strong and ends in P4.
(B) MPGJ 857 from the Coecillos area, right jaw with p2-m3, c and R and L i1-3. The symphysis is complete, it is observed that the incisors do not have a defined infundibulum, the hypoconid is slightly flatted in premolars and the protoconid is more rounded.

The equids collected in these sediments, *N. eurystyle*, *A. stockii*, and *D. mexicanus,* are associated with the best collection of carnivore that have been collected in the Hemphillian localities.

The faunal association is a typical of the late Hemphillian fauna Hh3. The result of radiometric analysis of the volcanic ash by the method of fission track of zircons is 4.4 ± 0.3 confirming this age (Carranza-Castañeda, 1992; Kowallis et al., 1999; Carranza-Castañeda et al., 2013).

Dinohippus mexicanus (Lance) 1950

Referred specimen

GTO 56 MPGJ 856 of skull fragment with two Maxillaries with P2-M3, corresponds to an old adult individual by the wear of the molars. Preorbital dorsal fossa (DPOF), is in the nasal and maxillary bones.

Locality and age

The locality GTO 56, late Hemphillian age, is located about 700 m south of the Rinconada Locality.

Locality GTO 43 Rinconada upper teeth: MPGJ 5137 M1, MPGJ 5138 P4, MPGJ 5139 P4, MPGJ 5140 P4, MPGJ 5141 P4, MPGJ 5142 M1, IGCU 8180 m2. IGCU 8879 P3, IGCU 9590 P4, MPGJ 5143 P4-M1, MPGJ 3764 flat Incisor row i1-3 R and L.

Description

MPGJ 856, two maxillaries with P2-M3, and fragment of nasal-maxillary bones with a dorsal fossa (DPOF), not pocketed posteriorly, like a shallow wide groove, the edges are smooth and poorly defined, with a maximum length of 60 mm.

The right maxillary is the most complete. The crest of the malar bone ends 25 mm above the anterior part of M1. The dentition is complete with P1-M3, (P2-M3, 159 mm, P1 is not included). The teeth are simple without folding in the fossettes, the hypocone and the groove are not present, the protocone is round and small in the premolars and slightly longer in M2-M3. On M1 it is worn away (**Figure 8**).

Lower Dentition. GTO 43 Rinconada locality, MPGJ 5132 jaw fragment Rp3-m2, MPGJ 5133 Rp2-m2 jaw fragment, 5136 p2-m3, MPGJ 10071 p4-m3. Isolated molars, GTO 43 Rinconada locality IGCU 8180 m2.

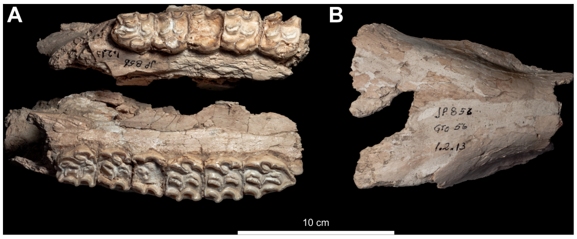

FIGURE 8 | (A) Left and right maxillaries, notice the teeth without hypocone. **(B)** Nasal bone with shallow DPOF, and smooth borders. The three bones belongs to the same individual.

Discussion

The jaws of this locality present some characters that differentiate them from the jaws collected in Rancho El Ocote. Among the important differences is the depth of the mandibular ramus. The specimen MPGJ 5136 of GTO 43, the maximum depth between p4-m1 is 72.43 mm, and on MPGJ 5132 with only p2-m2, the depth between p4-m1 is 75.56. In contrast, the mandible MPGJ 3749, of GTO 2A, the depth is 11.41 cm, and in MPGJ 3946 it is ~101.48 cm. Besides the linguaflexid in the jaws, MPGJ 5132, IGCU 5133 and MPGJ 5136 is wide and shallow. The metaconid is lobular and the metastylid is rounded with on acute and small lingual border. The entoconid is lobular with an open hypoconulid. In IGCU 6963, p3 and p4, have a small pli caballinid. The ectoflexid is deeper in m1 and m2. The protoconid and hypoconid are flat in premolars and relatively rounded in molars. On MPGJ 5136, MPGJ 5132, and MPGJ 5133, lower jaws, the protoconid and hypoconid are variable from flat to slightly rounded, and the linguaflexid is shallow and open (**Figures 9A–C**).

The upper and lower molars were widely discussed and compared between the localities of San Miguel de Allende and the material of the Yepomera fauna that is housed in LACM, reaching the conclusion that they correspond to the same species. However, in this work it has been observed that in the lower molars, the linguaflexid, protoconid and hypoconid are different and that separates them from the specimens collected in the Rhino level of Rancho el Ocote and from the specimens at the base of the sequence of Coecillos (Carranza-Castañeda, 1992).

STATE OF JALISCO

The Tecolotlán Basin

This basin is 90 km from the city of Guadalajara and is filled with fluviolacustrine deposits contain abundant North American Mammalian faunas, which represent the late Hemphillian age. The stratigraphic sequence has a thickness of 60 m and several sites have been mentioned where the late Hemphillian material has been collected. However, the stratigraphic sequence has been identified in two areas of main importance: Santa María sequence at the base and San José deposits that cover them. Resting in erosional unconformity are found the San Buenaventura deposits, thought to be of Blancan age (Carranza-Castañeda, 2016; Kowallis et al., 2017; McDonald and Carranza-Castañeda, 2017).

The mammalian fauna between the two areas, Santa María and San José, is almost the same. *D. mexicanus* and *N. eurystyle* remains are common in all the localities. The major difference is related to the presence of *N. aztecus* and *A. stockii* that so far never have been collected in the San José sequence. In these deposits are the last records of *Machairodus*, *B. secundus*, *Teleoceras*, *Neohipparion*, and *Nannippus*, that are well represented in the late Hemphillian fauna in central Mexico; among which has been described one of the first records of South American immigrants *Zacatzontli tecolotlanensis* that document the initial events of the GABI (McDonald and Carranza-Castañeda, 2017).

The age of the fauna has been determined by radiometric dating of the ashes that are interbedded with the fossiliferous strata. The ash found in the upper part of the San José area, was dated by the method of ^{40}Ar/^{39}Ar, and gave an age of 4.95 ± 0.02 My and (Kowallis et al., 2017). In recent works, a new date was made by the Laboratorio de Estudios Isotopicos, Centro de Geociencias, UNAM (LA-ICPMS), from a different site, by the method of U/Pb using zircons, which produced a date of 4.85 ± 0.1 My for the ash (McDonald and Carranza-Castañeda, 2017).

In erosional discordance are the deposits of the San Buenaventura sequence which has a thickness of ~30 m of gravels and paleochannels of sand and clays. The contact with the deposits of San Jose is not exposed. The age of the sequence of San Buenaventura has been referred to the Blancan (Kowallis et al., 2017).

This sequence is important in the transition *Dinohippus-Equus* because some isolated teeth collected in the locality of Jal Teco 7 Las Gravas present more progressive characters by their grade of hypsodont and curvature that resembles *Equus*, and have been referred to the Blancan age.

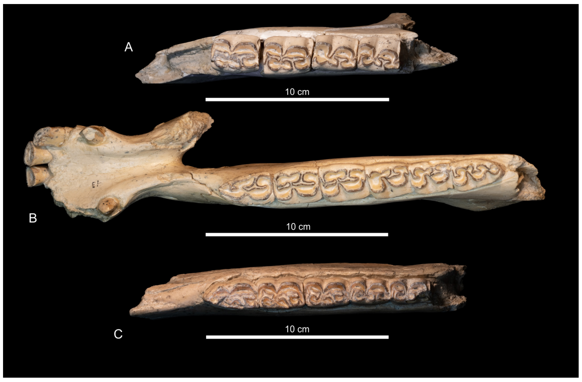

FIGURE 9 | Jaws from GTO 43 Rinconada locality. **(A)** MPGJ 5132 p3-m2. **(B)** 5132 p2-m3. **(C)** MPGJ 5133 p2-m2. The linguaflexid is wide and shallow, the protoconid and hypoconid show inconsistency in the form since flatted to slightly rounded, the symphysis is not complete rounded.

Dinohippus mexicanus (Lance) 1950

Referred specimen

MPGJ 1967 JT 35 late Hemphillian age skull fragment of young individual, with region facial and brain case of the right side well preserved. The M1-M2 first stages of wear, P4-M3 in the alveolus without wear.

Late Hemphillian. Isolated teeth: Jal Teco 1, MPGJ M1 Fragment. JalTeco 48: MPGJ 4044 M1, MPGJ 4045 M1, MPGJ 4046 P4.

Jal Teco 37, MPGJ 5025 M2, MPGJ 5029 p4, JalTeco 26 MPGJ 3541 M1; JalTeco 12 MPGJ 5001 M3, MPGJ 5002 P4. MPGJ 5003 p4, MPGJ 5004 m3. JalTeco 33 MPGJ 5027 p4, MPGJ 5028 m2, MPGJ 5026 M1. JalTeco 35, MPGJ 5102 M1. JalTeco 47 MPGJ 5072 m1-2. MPGJ 5069 m2.

Isolated Teeth. Jal Teco 7 Las Gravas locality Blancan age: Upper Teeth: MPGJ 3227 M1, MPGJ 3698 M3, MPGJ 3699 M12, MPGJ 3987 M1, MPGJ 4021 M1, MPGJ 5057 M3, MPGJ 5022 M1, MPGJ 5058 P4, MPGJ 5059 M3.

Lower Teeth, MPGJ 3246 p4, MPGJ 3226 p34, MPGJ 3985 m3, MPGJ 5052 m2, MPGJ 5049 m1, MPGJ 5050 m3, MPGJ 5051 m1, MPGJ 5052 m1, MPGJ 5053 m2, MPGJ 5054 p4, MPGJ 5136 p4.

Dinohippus mexicanus

Locality, age, and collector

MPGJ 1967 skull fragment, JalTeco 35 Locality, late Hemphillian age collector Mr. Harley Garbani and the author.

Description

Specimen MPGJ 1967 is a skull fragment of a young individual that conserves only the left facial part with the frontal bones and part of the parietals. In the left facial part, in the anterior of the nasal and maxillary bones a well-defined deep dorsal fossa with the delimited edges, pocketed posteriorly with delimited edges; the fossa is wider above the P4. The orbit is complete, the zygomatic apophysis of the temporal bone, the temporal bone and the zygomatic apophysis of the malar are complete. The malar crest is prominent and ends between P4 and M1.

The dentition is reduced to M1 and M2 because P4 and M3 are erupting from the alveolus. The fossettes are simple, almost without plications, the prefossette of M1 presents a small loop, the postfossette has with small plications in the anterior edge and small pli hypostyle. The hypocone is wide with an open and deep furrow. A small and thin plicaballin is present in M1, and the protocone is elongated, without a heel (**Figure 10**).

Locality JalTeco 7

Isolated teeth, the molar MPGJ 3987 M1 has a high crown, but the curvature is pronounced, the protocone larger the lingual border is concave with "wooden-shoe shape," and present a small pointed heel. MPGJ 5022 M1, that correspond to mature individual, the curvature is similar but the protocone is small rounded and without heel. MPGJ 3698 M3 although is an M3 the protocone is larger and the tooth is curved like MPGJ M3 5001 late Hemphillian from locality JT 12 Hilda's late Hemphillian locality of San Jose sequence in Tecolotlán basin.

The specimen MPGJ 5058 P3 from JalTeco 7 Ap 30.32 Tr 26.67 HC 54.25 mm in comparison with MPGJ 5141 P4 GTO 43 Ap 28.08 Tr 26.16, and HC 65.43 mm, they are similar in the structures and the size is less than 10%, however the protocone has the same shape, concave in the lingual border, developed heel, pli caballin in both and fossettes with same plications.

FIGURE 10 | MPGJ 1967 from JalTeco 35, left side, the facial fossa is pocketed with well-defined borders and strong malar crest.

It is important to point out that the JalTeco 7 molars present the overlap of progressive characters, of a primitive *Equus*, with high crown hipsodoncia, protocone with heel and evident curvature, characters of the Blancan molars. In comparison to other teeth from the sequence of Santa María and San Jose, which have more "primitive" characters of *Dinohippus*. The overlap of characters in molars of typical *Dinohippus* to transitional molars of a primitive *Equus*, had already been noticed by MacFadden (personal communication, MacFadden and Carranza-Castañeda, 2002; **Figure 11**).

Lower Teeth. The specimen that have been collected are scarce and damaged, correspond to adult individuals only one is a young premolar. In general, the structures of the occlusal surface have small affinities in comparison with lower molars from the GTO 2 site F, from the Blanco layer in Rancho el Ocote. Hemphillian localities. The linguaflexid is shallow and width in specimens MPGJ 3246 p4, 5050 m2, 5049 p4, 5053 p43, and 5059 p3, all these teeth the most significant difference is the protoconid and hypoconid flat, metaconid lobular and metastylid is smaller and pointed lingually. Deep ectoflexid in molars, short not passing the isthmus in premolars, the paralophid is high until the middle of the metaconid, and some teeth presents a small pli caballinid.

STATE OF HIDALGO

Tepeji del Río Basin

La Plegaria Locality. In the southwestern region of the state of Hidalgo, southwest of the city Tepeji Del Río,

FIGURE 11 | (A) IGCU 11503 P4, from GTO 2 site F Latest Hemphillian. **(B)** MPGJ 3987 M1 JalTeco 7 Blancan age. **(C)** MPGJ 4040 M1 GTO 2 site F. Latest Hemphillian. Comparison in the height of the crown and the curvature of the molars, in **(A)** the height of the crown is more straight than in **(B)**, and in **(C)** the curvature of the crown is greater than in **(A)** and **(B)**, and the height of the crown is also greater than in **(A)** and **(B)**. However, molar **(B)** (Blancan age from Tecolotlán), shows intermediate characters. **(D)** (MPGJ 3698 M3 JalTeco 7 Blancan age) and **(E)** (MPGJ 5001 M3 JalTeco 12 late Hemphillian age) is remarkable the similarity of occlusal surface structures in molars of different ages from the same area.

several localities with fossil remains were found. The most important is La Plegaria.

The mammal fossils are at the top of the lake sediments that have a thickness greater than 100 m and are evidence of the huge lakes that existed in central Mexico during the late Miocene. The fluvial sediments are at the top of the sequence. This is an area of little extension that is covered by vegetation, however, the fossils are found in clay, sand channels and gravel. *D. mexicanus* is an important part of these fauna (Padilla Gutiérrez, 2004).

STATE OF NAYARIT

El Valle del Gigante. At the top of the Sierra Madre Occidental, is the rancheria of El Valle del Gigante, which was initially explored and investigated by Dr. Theodore Downs and Mr. Harley J. Garbani from LACM, in Valle de El Gigante. Years later, the author continued the research in this area and discovered a new locality Nay 1 El Gigante. The continuity of the research in this area, led to the discovery of other localities. In the town of Huajimic Nay 2 El Huichol, there is material of upper and lower molars of *D. mexicanus*, and molars that were referred to as *Rhynchotherium* (?). The research in the north part of Nay 1, a new location Nay 3 El Trapiche, was discovered in the rancheria of the same name. Preliminary results are a collection of upper molars of *D. mexicanus* and fragments of the upper molar of *Teleoceras*, besides fragments of proboscideans. The age of this fauna has been referred to late Hemphillian, by analysis of the volcanic ash collected in the town of El Trapiche was analyzed by the method of U/Pb and gave an age of 5.50 ± 0.3 My.

DISCUSSION AND COMPARISON

All the skulls collected in the early-late and late Hemphillian faunas in central Mexico present a wide range of variability in the DPOF. The skull from Juchipila considered the oldest record of *D. mexicanus* in central Mexico, was compared with a mold 41478-1 of *D. leidyanus* housed in the collection of the University of Texas at Austin. The main differences in *D. leidyanus* cast, the dorsal (DPOF) and malar fossa are well developed. In addition, the protocones are slightly inclined toward the lingual edge.

In the Mexican specimen, the protocone is larger and horizontal to the maxillary lingual border. This is an important characteristic that eliminates the similarity between them (Matthew and Stirton, 1930; Azzaroli, 1988). The comparison with illustrations of *D. interpolatus* (Matthew and Stirton, 1930), also demonstrate important differences because the DPOF is always well developed and bounded at its edges, which does not occur in the skull of Juchipila which has smooth edges and is very shallow. Also in *D. interpolatus* the malar fossa is constant and absent in the skull of Juchipila and all the Mexican skulls. Regarding the curvature of the molars, it is difficult to determine this characteristic in the Juchipila skull because the molars are included in the maxilla. However, the isolated teeth of MPGJ 4067 Zac Juch 47 M12 from El Resbalón, are short and curved, the protocone is rounded, small and slightly oriented to the lingual edge. That reminds us of *D. interpolatus*, but this does not always occur in the molars of Juchipila. Most of the teeth from Juchipila have the anterior border developing a small heel, and the lingual border is flat and horizontal.

The skull from Juchipila was compared with the description of the skull of *D. mexicanus* collected in the Rhino level of Rancho El Ocote locality GTO 2B, (MacFadden and Carranza-Castañeda, 2002). Some similarities are evident in both specimens.

The nasal notch is in the same position, posterior to P2; the infraorbital foramen is 68 mm above P4. The malar fossa is absent, and the malar crest is strong and ends between P4-M1. The biggest difference is the DPOF. In the Guanajuato specimen it is pocketed posteriorly, deeper and the edges are well defined and is 80-mm anterior to the orbit. The specimen from Juchipila has only a faint depression 58 mm in front the orbit, and is shallow, with poorly defined borders. However, when compared the facial region of the Tecolotlán skull, the fossa is like the Rancho El Ocote specimen which is well delimited posteriorly, deep, and the edges are well defined.

The skulls differ in the size of the bar separating the orbit of the DPOF margin. The Juchipila skull is ~58 mm, the specimen from Tecolotlán it is 61 mm, and the Rancho el Ocote is ~80 mm. The skull from the GTO 56 Rinconada area has differences that distinguish it from the other skulls, the DPOF, is a slight depression with soft edges. In addition, the absence of the hypocone and hypoconal grooves possibly represent a primitive form of *Equus* (**Figure 12**).

The skull MPGJ 103 from GTO 75 Arroyo de Emilio, not present evidence of DPOF, as the structures and size

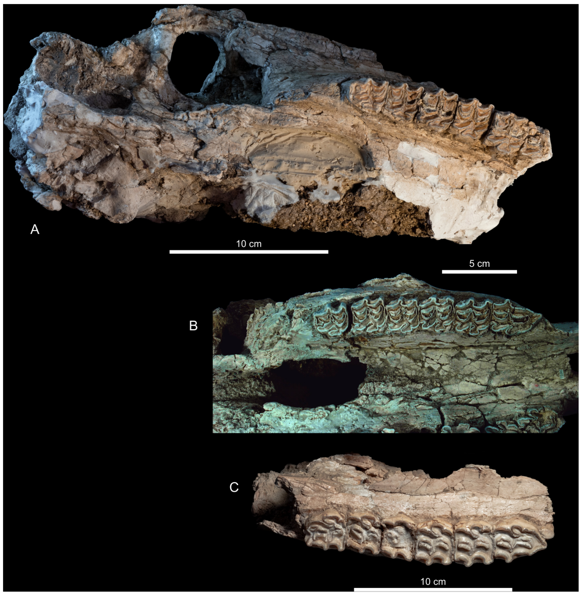

FIGURE 12 | Comparison of the ventral view of the Dinohippus skulls. **(A)** MPGJ 1982 from ZAC Juch 30. **(B)** IGM 7596 Rancho el Ocote. **(C)** MPGJ. 856 GTO 56 Rinconada área. The differences in the structures of the molars are evident, specially observe the variability in the protocone and absence of hypocone in **(C)**.

suggest a transitional form between *Dinohippus* and a primitive *Equus*. However, the upper volcanic ash 4.54 ± 15 My and the associated fauna including Dinohippus mexicanus, *N. eurystyle*, and *N. aztecus* with the jaw MPGJ 857 collected in the lower layer, dated 5.32 ± 0.14 My; these ages undoubtedly encloses all the fauna in late Hemphillian age. Also, the *C. sanmiguelensis* specimen was collected in the same stratigraphic level (Wang and Carranza-Castañeda, 2008).

The comparison between the rows of teeth P2/p2 and M3/m3, shows a similarity in size. When comparing the P2-M3 row in the IGM 7596 from Rancho El Ocote fauna is 157.9 mm, the P2 with a prominent anterostyle. The same measurement in the Juchipila specimen is 150∼, though the anterostyle of P2 is broken. In the skull MPGJ 856 from Rinconada area, the length P2-M3 is 150 mm. The similarity in size of the three specimens is remarkable. The most important differences are the pronounced anterostyle of Rancho el Ocote, and the presence of P1 in the Rinconada maxillary that is not present in the other specimens.

Regarding the protocone, a great variability is also observed in the shape and size of the upper molars. The most noticeable difference is observed when comparing the protocones of the Rancho el Ocote skull where the anterior border is round or very small, the heel is almost non-existent, like the Rinconada specimen. The specimen from Tecolotlán MPGJ 1967 is a young individual, and some differences are observed. The anterior border of the protocone of M1 is rounded, in M2 which is incompletely erupted, the anterior edge is elongated and sharp forming a small heel. The posterior part is elongated and pointed. These variations can be explained because the skull belongs to a young individual. On the contrary, the dentition from Juchipila skull, referred to the early late Hemphillian age, the protocones should be more related to the shape of *D. interpolatus* and *D. leidyanus*, with its axis slightly inclined to the lingual border, and the anterior edge without heel. However, in the skull of Juchipila, the shape of the protocones is elongated with a horizontal and concave lingual border and with a prominent and unexpected heel. Nevertheless, the specimen MPGJ 4067 P4-M1 R and L of the locality Zac Juch 47 El Resbalón of the same age, the protocones are small, lobular without vestiges of a heel and are different from those molars of the Mixtón teeth. These differences show the wide variability that exists in the protocone in individuals of the same age and stratigraphic level.

In comparison the Rancho El Ocote skull of late Hemphillian age, the protocones of the maxilla do not present a heel although the shape is larger. However, strong differences with the specimen MPGJ 131 at locality GTO 75 Arroyo de Emilio, collected in the upper part of the stratigraphic sequence of the Coecillos area were present. These teeth have elongated protocones with concave lingual border. The shape is like a wooden shoe and is remarkable in the R and L M1, but the anterior side is oval without a heel.

The curvature is another important characteristic. The specimen MPGJ 5112 of GTO 2, site F, is larger, in comparison to MPGJ 131 from late Hemphillian of Arroyo Emilio. The contrast between them in curvature and size is outstanding. The specimens MPGJ 5112 M1 site F, is high crowned, the axis Ap 30.84 and Tr 29.12 mm, has been compared with IGCU 5652 M1 referred to *Equus,* an old individual collected in GTO 39 Tlaloc, early Blancan. The measurements Ap 27.56 mm, TR 30.12, show similarity between them.

The Blancan specimen MPGJ 3987 M1 referred to *E. simplicidens* that correspond to a young individual, collected in the locality JalTeco 7 Las Gravas M1 referred to *Equus*, share some features with IGCU 11503 of Rancho El Ocote: the curvature and height crown are similar, both has elongated protocone with an evident triangular heel and concave lingual margin.

The specimens MPGJ 5126 P4 from GTO 2B-F, with minimum wear, the molar is straight and long like IGCU 11503 M1, when compared with MPGJ 4067 P4-M1 R and L from the locality Zac Juch 47, that have lobular and small protocone without vestiges of a heel. It is evident that there is great diversity of shape and size in the protocone of *D. mexicanus* in the faunas of central Mexico, even in young and old specimens of the same locality and stratigraphic level.

Lower Teeth. The jaws, maxillary and isolated teeth, show wide range of variability, but there are no differences from that already mentioned in previous works (Lance, 1950; Quinn, 1955; MacFadden, 1984, 2006, 2016; Carranza-Castañeda, 1992). However, several differences are observed. The metaconid and metastylid are lobular in molars and in premolars, the metastylid is smaller and often the lingual margin is pointed. The entoconid is lobular, the hypoconulid short although it is not constant or very reduced in the jaw MPGJ 857 Arroyo de Emilio and is absent in MPGJ 5136 of Rinconada. The linguaflexid in the MPGJ 5136 from Rinconada is open and shallow, however, the jaw IGCU 6963 that corresponds to a young individual, the linguaflexid is also deep. The specimen MPGJ 857 Arroyo Emilio has a V shape and is more closed, like the mandibula MPGJ 3946 of GTO 2 B level Rhino. The ectoflexid is deep in molars, the protoconid and hypoconid in the jaws GTO 2A MPGJ 5125 and MPGJ 5132 from GTO 43 Rinconada and jaw 310 from GTO 30 Coecillos are horizontal and flat. However, in the specimen MPGJ 5136 and 5132 from Rinconada, the protoconid and hypoconid are horizontal and flat in the premolars. Some of the jaws that are described retain part of the symphysis and the incisors. The differences between them are not significant in relation to their size.

Some of the incisors have an infundibulum limited by enamel and filled with cement, however, others only present a small lake without enamel. The disposition of the incisors is arranged in a circular or flat row, possibly this difference is related to grazing or a mixed feeding (**Figure 13** and **Supplementary Table 2**).

The outstanding result of the research over the material in Rancho El Ocote, without a doubt, is the specimens that have been collected in the GTO 2 sites F and D. These differ in their measurements of the anteroposterior (Ap) and transverse (Tr) axis which are clearly distinguished from those collected in the stratigraphic sequence of the Rhino and White levels. All the teeth from GTO 2 Site F and D, the hypoconid and protoconid have their labial edges more flattened and straight. The ectoflexid is narrow but very deep in the molars,

FIGURE 13 | The structures of the symphysis are compared, **(A)** MPGJ 5129 from GTO2B, **(B)** MPGJ 5126 from GTO 43, **(C)** MPGJ 857 from GTO 75, and **(D)** MPGJ 1683 from Zac Tab 34. Observe the infundibulum of the incisors that do not present enamel. The row of the incisors is rounded in **(C)**, in **(A)**, and **(D)** the row is more flatted.

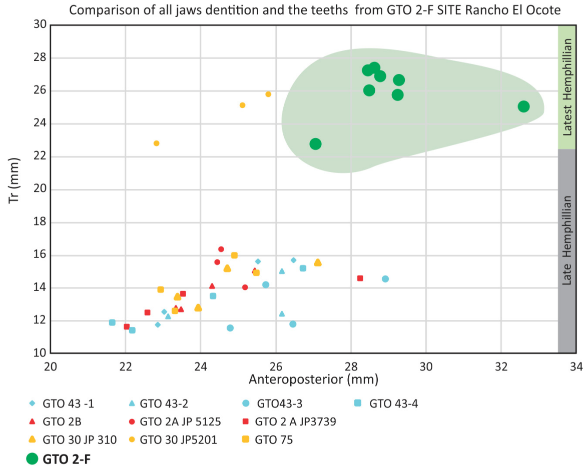

FIGURE 14 | All the teeth p3-m2 of the jaws are plotted in the graph, including those of GTO2 site F. Is remarkable the separation all the teeth from site F. The result suggests that the molars of GTO 2 F and D correspond to a group of individuals different from those found in the late Hemphillian localities.

almost touching the inner edge of the linguaflexid and less deep in the premolars. The linguaflexid is wide and shallow. Another difference is the metastylid that tends to be small and more pointed at its lingual edge. In addition, Pli caballinid is frequent but very small.

All the measurements of the teeth in the jaws described in this paper were plotted on a graph. It is remarkable that all the material from GTO 2 site D-F are separated from the typical Hemphillian teeth, and suggest a transitional group between *Dinohippus* and primitive *Equus*, as seen in the **Figures 6, 14**.

CONCLUSION

(1) *Dinohippus mexicanus*, has a wide geographical distribution in the central region of Mexico between the parallels 19° and 22°, only the most important localities due to the number of specimens, presence of skull, jaws and isolated upper and lower teeth by the variability they present in their structures and the stratigraphic position have been mentioned in this work. The main localities: early-late Hemphillian of Juchipila Zacatecas, late Hemphillian of Arroyo de Emilio Rinconada, Coecillos and Rhino layer of Rancho El Ocote; and latest Hemphillian in the Blanco layer, at Rancho El Ocote, basin of San Miguel de Allende, Guanajuato, late Hemphillian-early Blancan of Tecolotlán basin, Jalisco. The associate fauna always with stratigraphic indexes of late Hemphillian age and confirmed by radiometric ages.

(2) In *D. mexicanus* the morphology of the fossa dorsal (DPOF), was considered an important character in the diagnosis and systematics of the *Pliohippus* group of the Hemphillian age. However, the new records of skull collected in the faunas of early-late Hemphillian and late Hemphillian of the central region of Mexico, have shown that this structure has a wide variation in shape and size.

(3) The greatest differences observed in the skulls are more evident in the MPGJ 103 specimen of Arroyo de Emilio older individual, which has the largest facial region without evidence of DPOF, and the hypocone is not clear because the natural wear. These differences are comparable with the skull MPGJ 856 old individual from Rinconada, where the DPOF is reduced to a narrow and shallow groove and the hypocone is absent. It is possible to argue that these variants are determined by the ontogenetic age and natural wear. However, it is remarkable that these skulls were collected in deposits of 4.5 ± 15 My, (MPGJ 103) and in 4.4 ± 0.3 My (MPGJ 856), and in both the affinity with *Equus* is noticeable. However, the associated fauna of these two compared specimens, undoubtedly contains stratigraphic indices of the late Hemphillian age (**Supplementary Table 1**).

(4) The sample of skulls referred to *Dinohippus* mentioned in this work is the largest that has been described the differences observed in the DPOF induce to reconsider its value in the diagnosis of *Dinohippus*. The malar fossa is never present or insinuated in the facial region in the sample of skulls.

(5) The height of the crown in upper and lower molars is greater than 82.34 mm (MPGJ 4040, GTO 2B), 76.65 (MPGJ 5143, GTO 43) and in lower molars is 82.73 mm (MPGJ 5116 GTO 2 site F), these values are higher than the Yepomera samples and those mentioned for the fauna of Bone Valley, Florida (MacFadden, 2016). Always the cement covers the crown.

(6) The protocone has a wide variation of shape and size, even in molars collected at the same stratigraphic level vary from rounded to elongated although always the lingual edge is horizontal to the jaw. The anterior edge very often forms a heel that is not constant in all molars inclusive from the same locality, such as the molars of the skull of Juchipila and the molars MPGJ 4607 (ZJ 47).

(7) The MPGJ 856 skull from the Rinconada area, with shallow DPOF, very simple fossettes and absence of hypocone

are features that make it distinctive to another skull. Also, the jaws: MPGJ 5136 P2-M3, MPGJ 5132 P3-M2, and MPGJ 6963 P2-M3 of the locality GTO 43 Rinconada, with the wide and shallow linguaflexid, protoconid and hypoconid are more flattened and straight; are features distinguish them from the mandibles of El Ocote and Coecillos. These differences suggest that the skull MPGJ 856 and the mandibles of GTO 43 Rinconada have significant affinity with *Equus*.

(8) The upper and lower molars collected in the Rhino and Blanco layers, have differences in size compared to those collected in the GTO 2 site D and F, on their AP and Tr axes and the height of the crown, indicating a "Group" with transitional characters between *Dinohippus* and a primitive *Equus*.

(9) The Graphs 6 and 14 have been plotted the measurements Ap, Tr and crown height of the upper and lower molars that have been discussed in this work, including the upper and lower molars of the sites GTO 2 site D and F. The result of this analysis suggests that *D. mexicanus* makes up a distinctive group closer (transitional) to *Equus*.

(10) In this work it has been shown the variability of the *D. mexicanus* collected in the Hemphillian localities from Zacatecas, Guanajuato and Jalisco localities: the curvature of the upper molars, the height of the crown in upper and lower molars besides the complexity of the DPOF and the variability of characters of the teeth. All these variations are evidences of the transition from *D. mexicanus* to *Equus*, in the faunas of the central region of Mexico in the boundaries Hemphillian-Blancan of Rancho El Ocote and Tecolotlán faunas.

Also, this has been observed too in the fauna of Yepomera (late Hemphillian) and La Concha (early Blancan) in the state of Chihuahua, where some lower molars cannot be reliably referred to *Dinohippus* (Lindsay, 1984).

(11) The specimens referred to *D. mexicanus* collected in the boundaries of late Hemphillian-early Blancan age, are the last records of *D. mexicanus* in Mexican faunas.

AUTHOR CONTRIBUTIONS

OC wrote the manuscript, conceived, interpreted, and collected the data for the graphics, and it is the main collector of the fossil material.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2019.00089/full#supplementary-material

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Evolution of Early *Equus* in Italy, Georgia, the Indian Subcontinent, East Africa, and the Origins of African Zebras

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We report here ecological and morphological characterization of the main Old World *Equus* in North America, Asia, Europe, and Africa, by comparing the studied fossil forms with the living *Equus grevyi* zebra. *Equus simplicidens* from North America, *Equus livenzovenzis*, *Equus stenonis,* and *Equus stehlini* from Italy, *Equus sivalensis* from India, *Equus* cf. *stenonis* and a small *Equus* from Georgia (Caucasus), *Equus oldowayensis*, *Equus koobiforensis,* and *Equus* cf. *tabeti* from Kenya and the extant *Equus grevyi* are described in their cranial and dental features and are compared in morphological postcranial dimensions by means of log10 ratio analysis. The occurrence of the two horses at the Dmanisi *Homo* site in Georgia is reported here for the first time. Our comparative analyses allow to confirm the primitive lineage of the ancient zebras as derived from *Equus simplicidens*, and the successive evolution of the stenonine horses in Asia, South Asia, and Europe during the Plio—Pleistocene. The morphological analysis has reveals a clear trend in third metacarpals and third metatarsals of *E*. *simpicidens*, the small *Equus* from Dmanisi and *E*. *grevyi*, suggesting a close relationship between these species. The trend of the stenonine *Equus* from Europe and Asia confirms the possible derivation from the North America *Equus simplicidens*. The description of all the Old World *Equus* is integrated with an overview of their paleoecological context, with a referred section for each locality where these fossils were found. This contribution represents a comprehensive review of the present knowledge of the Old World *Equus* evolutionary history, with some new important data in deciphering the deep origin and evolution of ancient and living zebras.

Keywords: ***Equus*, evolution, African zebras, North America, old world, Plio–Pleistocene, Villafranchian**

INTRODUCTION

The genus *Equus* includes extant species of horses, asses (and donkeys) and zebras. Wild *Equus* species live in Africa and Asia. A fundamental subdivision of *Equus* is caballine horses (including the domesticated horse) and non-caballine horses that include zebras and asses. African species include the zebras *Equus grevyi* (Ethiopia and Kenya), *Equus quagga* (south of Ethiopia to southern Africa), *Equus zebra* (southern Africa), and the African ass *Equus asinus* (Ethiopia, Somali, Horn of Africa) from which the domestic donkey is derived. Asian horses include *Equus hemionus* (Asiatic ass ranging from Iran to China) and *Equus kiang* (Tibetan Plateau). *Equus ferus* is the wild (caballine) horse of Eurasia. Bernor et al. (2010) recently reviewed the fossil and extant African horses and followed closely Groves (2002) taxonomy of living horses citing extensive conflicts between ethological, morphological, and molecular interpretations of *Equus* taxonomy and phylogeny. We follow traditional morphological criteria herein. Bernor et al. (2010) further drew extensively upon Churcher and Richardson's (1978) as well as Eisenmann's (1983) taxonomy of African *Equus* and herein we also rely upon the *Equus* phylogenetic interpretations of Azzaroli last presented by him in 2003 and again in Bernor et al. (2018).

MATERIALS AND METHODS

Skeletal elements studied herein originate from the Smithsonian Institution (USNM), University of Florence, Italy (IGF), the Georgian National Museum (Dmanisi, D numbers), Natural History Museum, London (NHMUK), Panjab University (PU), and the National Museums of Kenya (KNM numbers). Anatomical nomenclature, osteological landmarks, and ligament attachment interpretations are according Bernor et al. (1997). Measurements are all given in millimeters and rounded to 0.1 mm. Measurement numbers (M1, M2, M3, etc.) refer to those published by Eisenmann et al. (1988) for the skulls and postcrania, reiterated and augmented for dentition by Bernor et al. (1997). In various studies, Eisenmann (see Eisenmann, 1995 for a comprehensive summary) has used log 10 ratio diagrams to evaluate differences in equid long bone proportions, in particular, as a basis for recognizing taxa and their evolutionary relationships. (Bernor et al., 2003a,b), Bernor et al. (2017, 2018), Bernor and Harris (2003), and Sun et al. (2018) have used log10 ratio diagrams for analyses of postcranial proportions which we apply herein for comparing metacarpal III (MCIII) and metatarsal (MTIII) proportions of *Equus* species under consideration. We use the mean values for the Hoewenegg Horse Quarry sample of *Hippotherium primigenium* (Bernor et al., 1997) for these log10 comparisons.

DESCRIPTION

We undertake a brief description and comparison of the following *Equus* species which are relevant to our study of early Old World *Equus.* From North America we provide observations and measurements on the 3.3 Ma sample of *Equus simplicidens* from the Hagerman Horse Quarry, Idaho. From Eurasia and Africa: *Equus* cf. *livenzovensis, E. stenonis,* and *E. stehlini* from Italy with comments on the earliest small *Equus* from Italy; *Equus sivalensis* from India with comments on the earliest small *Equus* from the Indian Subcontinent; *Equus* cf. *stenonis* from Dmanisi, Georgia; *Equus "oldowayensis," E. koobiforensis* and *E.*cf. *tabeti* from Kenya; extant African *Equus grevyi.* **Figure 1** includes the localities under consideration. **Figure 2** is a chronology of the localities under consideration.

Equus simplicidens (Figure 3)

The Hagerman Horse Quarry, Glenns Ferry Formation, is within the Hagerman Fossil Beds National Monument located west of Hagerman, Idaho (McDonald, 1996). The Hagerman is an extremely rich deposit discovered by a local rancher, Elmer Cook in the late 1920s. He reported this find to Dr. Harold T. Steam of the United States Geological survey who in turn reported it to Dr. James W. Gidley of the Smithsonian Institution. The Smithsonian Institution's field crew excavated three quarry beds during 1929–1931 and 1934 (McDonald, 1996; Richmond et al., 2002). Gidley (1930) published the first description of the Hagerman Horse Quarry sample as *Plesippus shoshonensis* and followed by Gazin (1936) who described and illustrated samples of the dentitions of various ontogenetic stages. Skinner and Hibbard (1972) assigned the Hagerman horse to the taxon *Equus simplicidens* which we follow herein. McDonald (1996) undertook a demographic study of the Hagerman Horse quarry. The Smithsonian Institution accumulated the largest sample of the Hagerman horse which is currently under study by us.

Figures 3A–C is of an adult male skull and mandible of *Equus simplicidens*, USNM12573. In lateral view (**Figure 3A**) the skull is somewhat deformed but would appear to have a preorbital fossa well anterior to the orbit; nasal notch is retracted to mesostyle of P2, infraorbital foramen is placed high on the maxilla reflecting the horses great cheek tooth crown height. In ventral view (**Figure 3B**) the snout is elongate, with arcuate incisor arcade, canine is large indicative of a male individual. The maxillary cheek teeth (**Figure 3D**) have P2 with relatively short anterostyle; M3 is just coming into wear; protocones are elongate, mostly flattened lingually and on P2-M1 are connected to the protoloph; mesostyles are pointed. **Figure 3C** is the mandible in lateral view. **Figure 3E** renders the left cheek tooth row in occlusal view with the following salient features: p2 anterostyle is short; metaconids and metastylids are predominantly rounded; linguaflexid on premolars is a shallow V-shape, being deeper V to U-shape on the molars; ectoflexids are shallow on p2 and p3, deeper on p4 and extend very deeply into the metaconid-metastylid isthmus on m1-m3. Azzaroli and Voorhies (1993) have proposed that North American *Equus simplicidens* is the source for first occurring Old World *Equus.*

Equus livenzovensis

Bernor et al. (2018) reported the first occurring *Equus* in Italy at the locality of Montopoli, ca. 2.6 Ma which they referred to *E.* cf. *livenzovensis.* This sample is represented by very large anterior and posterior 1st and 2nd phalanges III closely comparable to *E. livenzovensis* from Khapry, near the Azov Sea and a sand pit

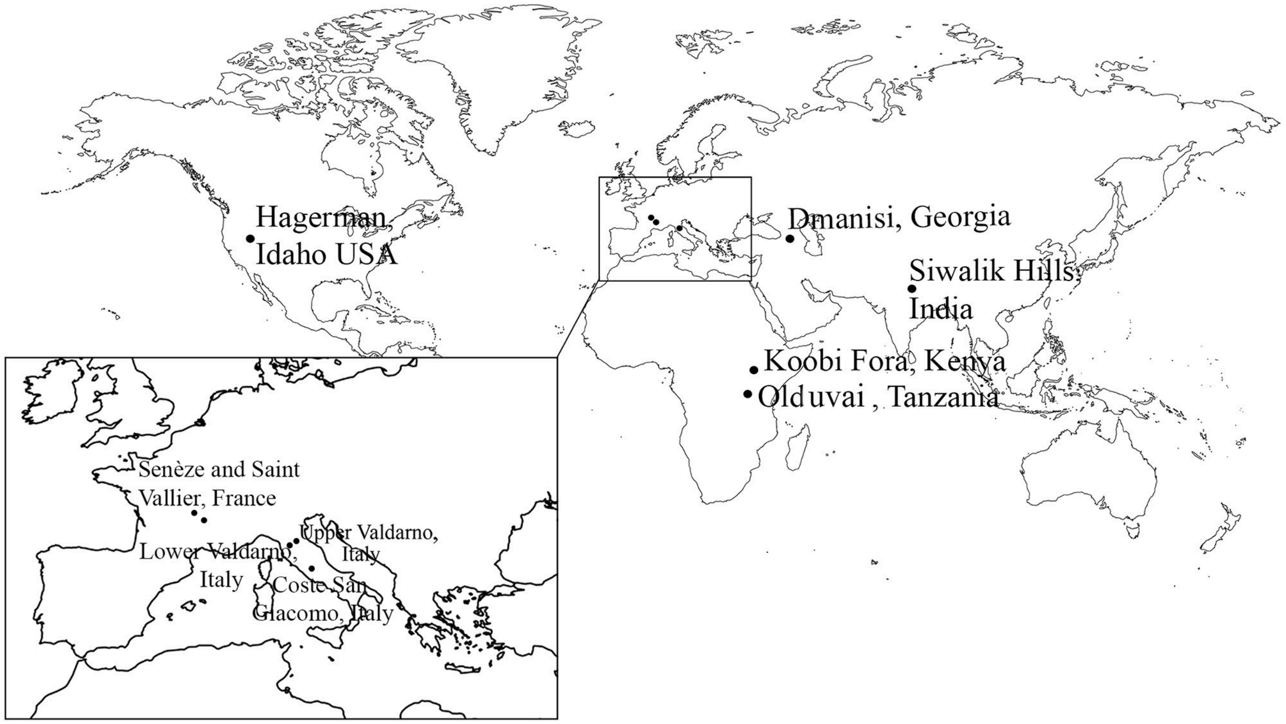

FIGURE 1 | Map of the localities discussed in the text.

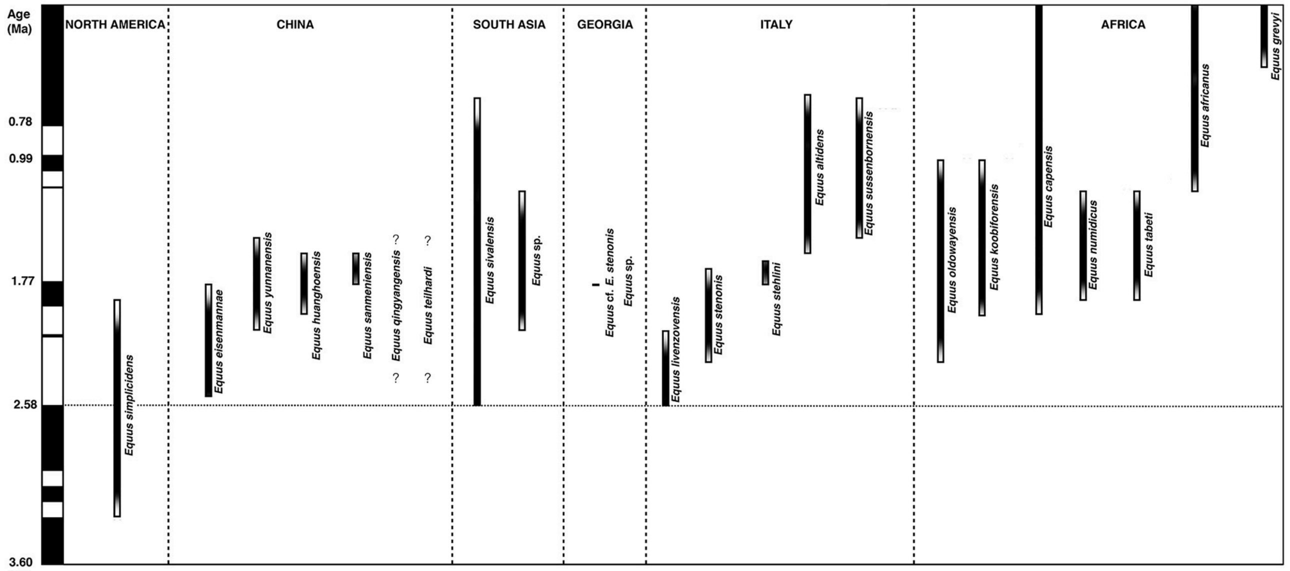

FIGURE 2 | Chronology of the taxa in North America, Asia, South Asia, Georgia, Italy, and Africa.

at Livensovka near Rostov on Don (Bajgusheva, 1971, 1978). Azzaroli (1982) noted that the skulls of *Equus livenzovensis* are somewhat larger than *E. namadicus* and *E. stenonis*, but otherwise similar. Azzaroli (1982) has reported that the Khapry skull has a well developed preorbital fossa (POF). Bernor et al. (2018) described a large anterior and posterior 1st and 2nd phalanges III *Equus* cf. *livenzovensis* from the 2.6 Ma locality of Montopoli and reported that they were larger than a large suite of Eurasian, African and North American *Equus,* validating the species identification.

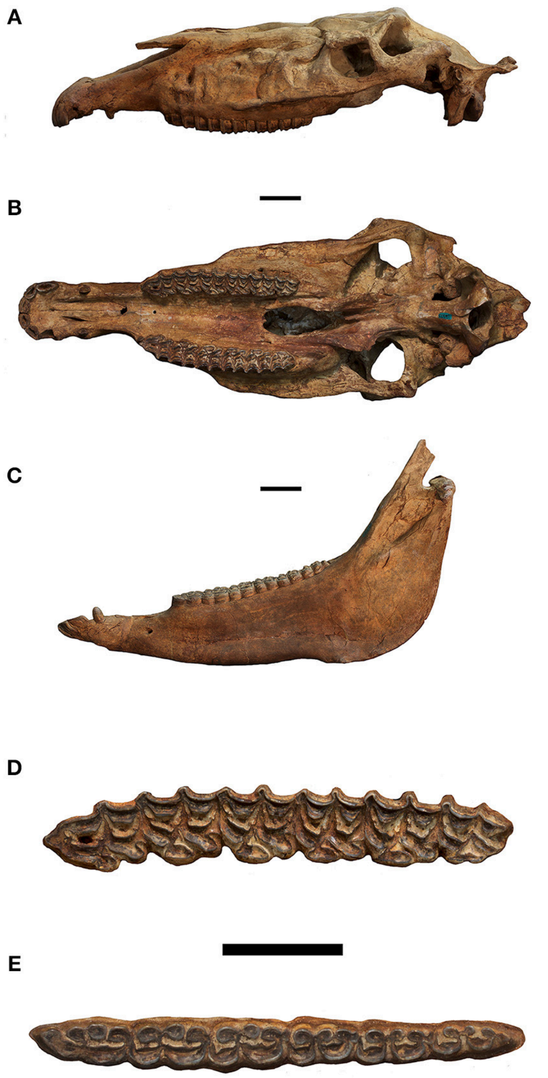

FIGURE 3 | *Equus simplicidens*. **(A)** Skull in lateral view; **(B)** Skull in ventral view; **(C)** Mandible in lateral view; **(D)** Upper tooth row in occlusal view; **(E)** Lower tooth row in occlusal view.

Equus stenonis (Figure 4)

Equus stenonis type skull (IGF 560) comes from Terranova (Arezzo, Tuscany), a 1.8 Ma fossil locality in the Upper Valdarno basin in Central Italy, housed in the Natural History Museum in Florence. Cocchi (1867) named the new species and the holotype was described by Forsyth Major (1877–1880) and later, in much detail, by Azzaroli (1964). The oldest occurrence of *Equus stenonis* in Europe is recorded in France, from the fossil locality of Saint Vallier, ca. 2.2 Ma (Eisenmann, 2004); its chronologic range is known until Tasso FU, 1.6 Ma. The Upper Valdarno basin yielded a relevant number of specimens referable to *Equus stenonis*, from various fossil localities; one of these, Matassino, located near the town of Figline (Arezzo), has been calibrated as being 1.8 Ma (Napoleone et al., 2001), and the fossil horse collection from this site shows features and proportions of *Equus stenonis* (Mazza et al., 2004). This locality, both with the type skull from Terranova (Azzaroli, 1964) and the other specimens from Olivola (Val di Magra basin; De Giuli, 1972), demonstrate the presence of *Equus stenonis* in central Italy during the Early Pleistocene (Alberdi and Palombo, 2013). According to several researchers (Azzaroli, 1982, 2003; Alberdi et al., 1998; Forsten, 1999; Palombo and Alberdi, 2017; Palombo et al., 2017), the primitive lineage of *Equus livenzovenzis* co-occurs with *Equus stenonis* in Europe. *Equus stenonis* has some morphological features close to *Equus livenzovenisis*, but is a slightly smaller in size. The European Middle to Late Villafranchian horses referred to *Equus stenonis* differ in size and body proportions, even if they show a similar bauplan. For this reason, several subspecies have been proposed, including: *Equus stenonis livenzovenzis*, *E. s. stenonis*, *E. s. olivolanus*, *E. s. vireti*, *E. s. pueblensis*, *E. s. guthi*, *E. s. senezensis*, *E. s. mygdoniensis*. The validity of these subspecies is matter of debate (re: Forsten, 1999).

The type specimen of *Equus stenonis* is IGF560, a skull with an associated mandible. The original mandible is missing and in its place is a plaster cast painted to match the color of the original skull. The skull is viewed from its left side (**Figure 4A**) which is the least distorted, but nevertheless crushed in the maxillary region. The skull has an elongate snout with a large canine indicative of a male individual. The nasal bones are retracted to the level of P3 mesostyle. There is a faintly delimited preorbital fossa depression on the postero-superior aspect of the maxilla. The facial maxillary crest is strongly developed. In ventral view (**Figure 4B**) the snout is elongate with an arcuate incisor arcade. In occlusal view the incisors have well demarcated infundibula that are open. The maxillary cheek teeth (**Figure 4D**), are inclusive of dP1-M3 and M3 is in wear; dP1 is remarkably still in place being well in wear. The maxillary cheek teeth have the following salient features in occlusal view as seen on the left side row: dP1 is small and rounded; P2 has a short anterostyle; all cheek teeth have protocone short with linkage to the protoloph; pli caballins are single on all cheek teeth; fossettes are well developed on P2–P4 and M2, lesser developed on M1 and M3; hypoglyph is moderately deep on P2–M2 and not expressed on M3.

The mandible (cast) is complete on the left side (**Figure 4C**). In occlusal view (**Figure 4E**) the incisors are complete, worn, have infundibula, are slightly procumbent and form an arcuate arcade. The mandibular canine is placed very close to i3 and is large as in the maxilla. The left side occlusal view of the cheek teeth reveals the following salient features: p2 has a short anterostyle; whereas metaconids are rounded, metastylids exhibit some distal squaring; linguaflexids are uniformly V-shaped as is diagnostic of stenonine horses; ectoflexid is shallowest on p2, somewhat deeper in p3 and p4, and deeper on the molars, but not separating metaconid and metastylid; pre- and postfossettes for the most part have simple enamel margins.

Equus stehlini (Figure 5)

Equus stehlini is the second most common horse occurring in the Upper Valdarno deposits after *Equus stenonis*. The species is represented by the type skull housed in the Natural History

FIGURE 4 | *Equus stenonis*. **(A)** Skull in lateral view; **(B)** Skull in ventral view; **(C)** Mandible in lateral view; **(D)** Upper tooth row in occlusal view; **(E)** Lower tooth row in occlusal view.

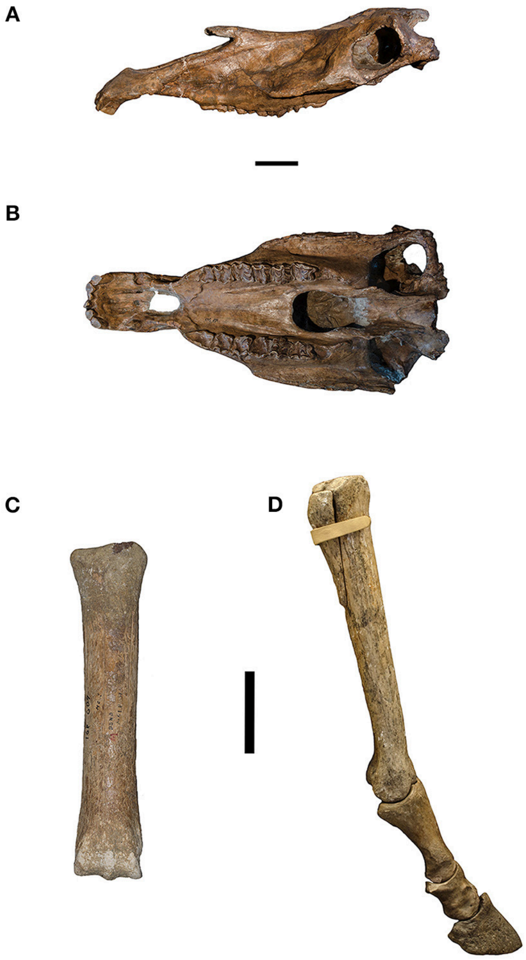

FIGURE 5 | *Equus stehlini*. **(A)** Skull in lateral view; **(B)** Skull in ventral view; **(C)** MCIII in dorsal view; **(D)** Forelimb in lateral view.

Museum in Florence (IGF 563); it comes from the same level as the *Equus stenonis* Type skull (IGF 560). The occurrence of a smaller species associated with *E. stenonis* in the Upper Valdarno was recognized for the first time by Stehlin and Graziosi (1935) basing their observation on a jaw found in the locality of Terranova (and kept in the Basel Naturhistorisches Museum collection), which they ascribed to *Equus* cf. *hydruntinus*. Later, Azzaroli (1964) formalized the species *Equus stehlini* based on the IGF 563 skull and on several postcranial specimens. This taxon is less common than *Equus stenonis* in Upper Valdarno even if is the only horse species that characterize the Casa Frata locality, which is correlative with the Tasso Faunal Unit, 1.6 Ma (De Giuli and Masini, 1986). The presence of *Equus stehlini* is documented in the Upper Valdarno basin (Azzaroli, 1964, 1982; De Giuli and Masini, 1986; Alberdi and Palombo, 2013), its phylogenetic relationships are not yet fully understood. Azzaroli (1964) recognized some asinine and stenonine features on the type skull and interpreted this species as derived from *Equus stenonis*. Later (Azzaroli, 1990), noted that *Equus stehlini* shares many cranial specializations with *Equus senezensis* from the French fossil locality of Senèze. Alberdi et al. (1998) considered this horse as a subspecies of *Equus senezensis*. De Giuli (1972) and Delson et al. (2006) both reported the presence of *Equus stehlini* from Senèze in association with *Equus senezensis*.

Recently, Palombo et al. (2017) described a small horse from the 2.1 Ma locality of Coste San Giacomo, Central Italy (Bellucci et al., 2012, 2014) as *Equus senezensis* aff. *Equus senezensis stehlini*. The origin and evolution of small horses in Europe, including *Equus stehlini*, is not yet well understood. The recent findings at Coste San Giacomo extends back in time the presence of these small horses, suggesting a different interpretation of their

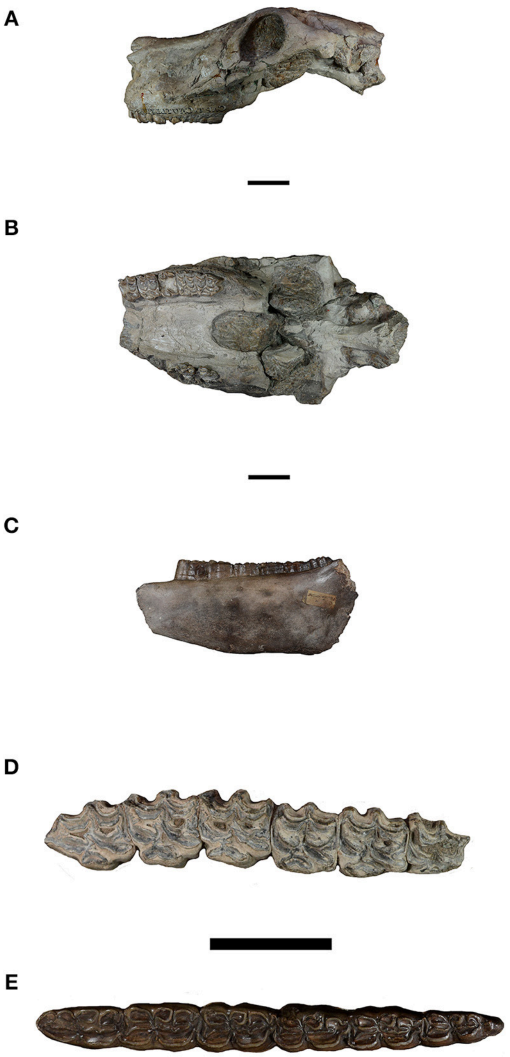

FIGURE 6 | *Equus sivalensis*. **(A)** Skull in lateral view; **(B)** Skull in ventral view; **(C)** Mandible in lateral view; **(D)** Upper tooth row in occlusal view; **(E)** Lower tooth row in occlusal view.

evolution, in contrast to the old theories that they originated from the "*Equus stenonis* group."

IGF563 is the type skull of *Equus stehlini,* which is an old adult individual. In lateral view (**Figure 5A**), the skull has a complete snout and orbit and is missing the posterior braincase. The nasal notch is as in *E. stenonis* being retracted to P3 mesostyle. The maxilla is crushed and may have had a faintly developed preorbital fossa high and posteriorly placed on the maxilla. In lateral view, the cheek teeth can be seen to be very worn and the cusps are blunt from wear. In ventral view (**Figure 5B**) the snout is relatively short and broad. The incisor arcade is arcuate and incisors are heavily worn not preserving infundibula; right and left I1 are severely worn with broken buccal margins. On both the right and left side, the occlusal surfaces are so worn as to not preserve any meaningful morphological details except on M2 and M3 that have simple fossette ornamentation.

The MCIII (**Figure 5C**) is elongate and slender, as is the anterior first phalanx. **Figure 5D** is an image of a forelimb (lateral view) referred to *Equus stehlini.*

Oldest Italian Small Horse

Upper Valdarno small horses are found from Tasso FU (1.6 Ma), where *Equus stehlini* has previously been recognized (Azzaroli, 1964; De Giuli and Masini, 1986). The recent discovery of a small horse in the site of Coste San Giacomo (ca. 2.1 Ma) reopened speculation about the origin and evolution of these small horses (Palombo et al., 2017). Our ongoing review of the Villafranchian horses housed in the collection of the Natural History Museum in Florence, is revealing some important information in this regard. An important discovery by OC is an incomplete third metatarsal (IGF 566) from Montecarlo (a site dated 2.4–2.2 Ma; Ghinassi et al., 2005), reported here for the first time. The Montecarlo locality has yielded few fossil vertebrates specimens, fishes, small mammals ascribed to *Mimomys polonicus* and gomphothere remains (*Anancus arvernensis*). This new discovery allows us to increase the faunal assemblage from this locality and share new insights into the distribution of early middle Villafranchian horses. This specimen has been catalogued as an MTIII and referred to "*Equus stenonis.*" Its metric dimensions and morphological comparison reveals that it is similar to the *Equus stehlini* sample of Casa Frata, and smaller than *Equus stenonis* from Olivola and Matassino (M3 = 30.8; M4 = 30; M5 = 46.7; M6 = 39; M7 = 32.7; M8 = 11.1. Eisenmann et al., 1988; Bernor et al., 1997). The attribution of IGF 566 is not yet formalized and more data from *Equus stenonis* and *Equus stehlini* are needed to compare this specimen with these two Italian Villafranchian species, however this new finding is congruent with the occurrence of a small horse from Coste San Giacomo (Palombo et al., 2017).

The first occurrence of these small horses seems to be earlier than 1.6, in contrast with the classical view of *Equus stehlini* as the horse indicator of Tasso Faunal Unit (1.6 Ma); this hypothesis needs to be tested with more data and analysis of coeval localities, such as Senèze and Saint Vallier.

Equus sivalensis (Figure 6)

Equus sivalensis is a large species of horse found in the Siwaliks of the Indian Subcontinent, ranging from the Potwar Plateau in the west to the Nepal Siwaliks in the east. It was first discovered by Hugh Falconer and Proby Cautley in the foothills of the Himalayas between the rivers Yamuna and Sutlej in the 1830s (Falconer and Cautley, 1849). The type series, which includes 27 cranial and postcranial specimens housed at the Natural History Museum, London (Falconer and Cautley, 1849; Lydekker, 1886). Other referred material is housed at the American Museum of Natural History (Colbert, 1935b), Naturalis Biodiversity Center (Hooijer, 1951), Wadia Institute of Himalayan Geology (Nanda, 2015), Panjab University (Sahni and Khan, 1988), Indian Museum (Lydekker, 1885), Saketi Fossil Park (Mishra et al., 2013), Geological Survey of Pakistan (Dennell, 2004), Science and Art Museum, Dublin (Lydekker, 1884), and the Museum of Natural History, Ludlow (Baker, 1850).

Falconer and Walker (1859) described a few specimens housed in museum of the Asiatic Society of Bengal (collection now housed in the Indian Museum) but never formally described the species. Lydekker (1882, 1886) described these species in the Palaeontologia Indica and Catalogue of Fossil Mammalia in the British Museum (Natural History). When Falconer and Cautley documented *Equus* from the Subcontinent, they named three species: *Equus sivalensis* from the Siwaliks, and *Equus namadicus* and *Equus palaeonus* from the Narmada Valley. Because the holotype of *Equus palaeonus* was a series of lower milk molars, Lydekker (1882) synonymized this species with *E. namadicus*. Matthew (1929) provisionally considered *E. namadicus* as a junior synonym of *E. sivalensis* or derived from it, because the distinguishing character used by Lydekker (longer protocones on both premolars and molars) was too variable, an observation reiterated by Hooijer (1951). Lydekker (1882) further stated that the small protocones on the premolars were indicative of a relationship with *E. hemionus*. Later, Lydekker (1891) stated that *E. sivalensis* was intermediate between *E. stenonis* and *E. caballus*, and was similar to early Pleistocene horses recovered from Yunnan. Similarly, Forsyth Major (1885) also closely compared *E. sivalensis* with *E. stenonis* from the Val d'Arno. In contrast, Hopwood (1936) suggested that the lectotype of *E. sivalensis* was a caballine horse, but erected a new species *E. cautleyi* based on a large partial mandibular ramus with p2-m3 (NHMUK PV OR 23107), which showed typical zebrine features (see description below). However, this view was rejected by Azzaroli (1966). Azzaroli studied the then known skulls of *E. sivalensis* and concluded that in the features of the orbits and zygomatic arches were typical of hippotigrine zebras rather than caballine horses. A skull (PU A/639) and mandibular rami (PU A/601 and PU A/602) described by Sahni and Khan (1961) show similar zebrine characteristics as well. These morphological observations led researchers like Badam and Tewari (1974), Sahni and Khan (1961), and Azzaroli (1966) to conclude that extinct species of Pleistocene *Equus* from South Asia were exclusively zebrines.

The exact stratigraphic range of *E. sivalensis* was ascertained several decades after the original discovery. Pilgrim (1910, 1913) determined that *Equus* is found in the Upper Siwaliks, and later Colbert (1935a) demonstrated that *E. sivalensis* would have made its first appearance in the Siwaliks during the Pleistocene in the Pinjor faunal zone. With the advent of modern paleomagnetic studies in the region, the biostratigraphy of Siwalik mammals was further refined. It is now known that *Equus sivalensis* first appears just above the Gauss-Matuyama boundary in the early Pleistocene (ca. 2.58 Ma), and ranges through until about 0.6 Ma, the upper end of the fossiliferous Siwalik depositional sequence (Patnaik, 2013).

NHMUK PV M.16160 is the Lectotype of *Equus sivalensis* Falconer and Cautley. It is a skull lacking the snout. **Figure 6A** shows that this specimen preserves the nasal notch that is incised to the mesostyle of P3 and there is a faint depression high dorsally and posteriorly on the maxilla for a weakly defined preorbital fossa. **Figure 6B** reveals that NHMUK PV M.16160 is an old individual with P3–M1 occlusal surfaces severely worn. Of these, P3–M3 preserve protocones with P4, M2, and M3 having weak connections to the protoloph and P3 and M1 having broader connections due to their more advanced wear; protocones are moderately elongate on P4–M1, longer on M2 and M3; hypoglyph is preserved on P3, P4, and M2 and is only moderately deeply incised; P4, M2, and M3 preserve fossettes that are slightly to moderately ornamented; all mesostyles are pointed buccalward. **Figure 6C** is a right mandible, NHMUK PV OR 23107, labial view. **Figure 6E** is the mandible's occlusal view and reveals the following salient features: premolars have elongate metaconid and squared metastylid; p3 and p4 have a prominent mesiolabial pli directed labialward on the preflexid; premolar linguaflexids are a deep narrow V-shape; premolar ectoflexids are all shallow, not invading the space between opposing borders of the pre- and postflexids; molar teeth likewise have rounded metaconids and squared metastylids with deep V-shaped linguaflexids; ectoflexids are as in the premolars not being deep or invading the pre- and postflexids; the premolar and molar teeth all have distinct to diminuitive pli caballinids.

Within the stratigraphic range of *E. sivalensis*, remains of a smaller horse with slender metapodials have also been found. Gaur and Chopra (1984a) were the first to document a smaller subspecies of equid from the Siwaliks of South Asia which they named *Equus sivalensis minor*, owing to its small size, but overall morphological similarity with *Equus sivalensis*. These fossils were found ∼3.0 km N.E. of the town of Mirzapur in northwestern India in the Pinjor Formation. The exact age of the Pinjor Formation at this site is unknown, therefore the age of these specimens can only be constrained to the entire range of the formation, 2.58–0.6 Ma. However, given the age of the Pinjor Formation ∼13 km away at a parallel location along the Patiali stream (Gaur and Chopra, 1984b; Ranga Rao et al., 1995), this locality is likely from the middle-upper Pinjor Formation. Subsequently, other remains of small horses were discovered on the Mangla-Samwal anticline (Hussain et al., 1992), and in the Pabbi Hills (Dennell, 2004; Dennell et al., 2006). Hussain et al. (1992) document both a large horse, which they refer to as *Equus* cf. *sivalensis* which ranges in duration from 2.35 to 1.9 Ma, and a small horse at locality HGSP 4460 (ca. 2.1 Ma), which is referred to as *Equus* sp. A. The Pabbi Hills specimens are all referred to as *Equus* cf. *sivalensis* and the metapodials are metrically similar to the smaller horses from the Mangla-Samwal anticline (Dennell, 2004; Dennell et al., 2006). Small equid remains are also present in the Falconer and Cautley collection at the Natural History Museum, which includes the type series of *E. sivalensis* (Lydekker, 1882; Forsten and Sharapov, 2000). However, a detailed morphometric analysis (beyond the scope of this paper) is necessary to determine the taxonomic identity and relationships of this smaller taxon.

Equus cf. *stenonis,* Dmanisi, Georgia (Figure 7)

The site of Dmanisi is located about 65 km southwest of Tbilisi (Georgia, South Caucasus), in the Kvemo Kartli region (Gabunia et al., 2000). Today the site is situated at an elevation of 910 m

MSL on a promontory that is isolated on two sides by the deeply entrenched Mashavera and Pinesauri rivers. Radiometric ages and paleomagnetic data provide a chronology for all the deposits at Dmanisi bracketing the age of the fossiliferous deposits in a chronologic range between 1.85 and 1.77 Ma (Ferring et al., 2011). Well-preserved bones have been recovered from throughout the succession although the great majority are from stratum "B1." The latter has a complex, very brief, depositional history and has yielded an exceptionally well-preserved fauna occurring as dense accumulations. In addition to its unique paleoanthropological record, Dmanisi is one of the richest Early Pleistocene palaeontological sites of Eurasia's temperate zone. More than three decades of excavation have uncovered a highly diverse fossil vertebrate fauna with 49 taxa, inclusive of *Homo*. The large mammal record from Dmanisi indicates a biochronology positioned at the very early Late Villafranchian (Vekua, 1995; Lordkipanidze et al., 2007; Rook and Martínez-Navarro, 2010), while the occurrence of the water vole *Mimomys pliocaenicus* correlates with the Late Villanyan of the micromammal biochronology (Fejfar et al., 1998). The *Equus* collection is sizeable and growing annually from an active excavation program. Our observations herein are strictly preliminary and intended to give some early insight into the equids present at Dmanisi.

D353 (**Figure 7A**) is a partial skull lacking the snout, nasals, posterior orbit, and posterior cranium. One cannot determine the nasal notch position for this individual. There is no discernible preorbital fossa for this individual. **Figure 7B** illustrates an occlusal view of specimen D66, an adult individual with M3 in early wear. This specimen has a very small, worn right dP1 with a socket still present for a missing right dP1. Salient features of the remaining cheek teeth include: P2 has an elongate, bucco-lingually constricted anterostyle; protocone on P2 is short and rounded, whereas P3 and P4 are progressively longer; M1 protocone is as in P4, whereas M2 is longer and M3 is long but labiolingually compressed; protocones are lingually flattened on all cheek teeth and P3–M2 prefossettes have a distinct lingually directed mesial pli; protocone has a weak connection to the protoloph on P2, P3, M1, and M3, but not so on P4, M2; pli caballin is only clearly expressed on M1; hypoglyph is deeply incised on all cheek teeth encircling the hypocone on P3 and P4; mesostyles are pointed on M2 and M3 and more rounded on P2-M1.

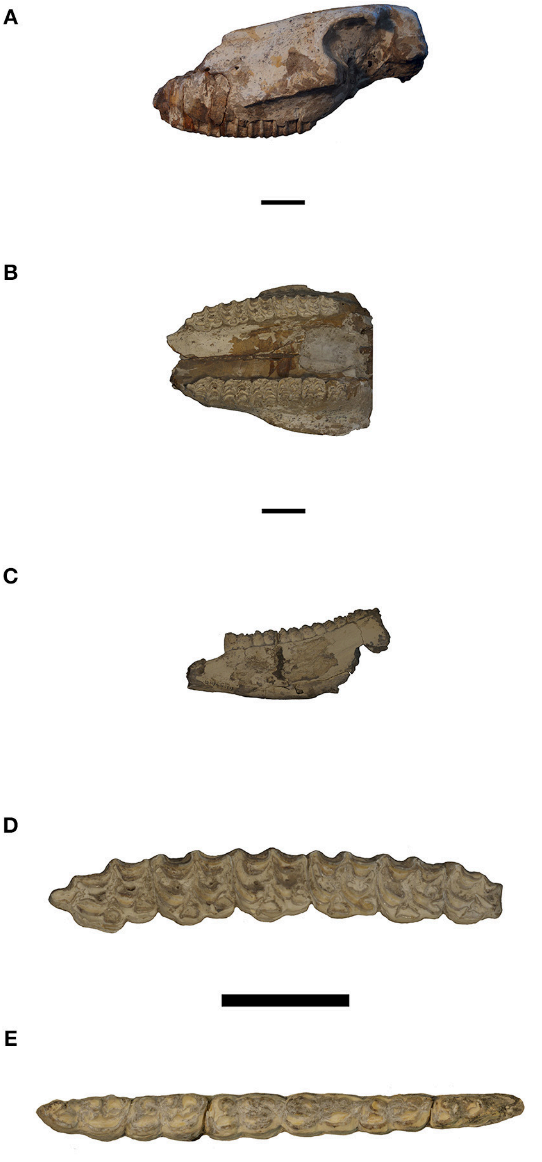

FIGURE 7 | Dmanisi *Equus*. **(A)** Skull in lateral view; **(B)** Skull in ventral view; **(C)** Mandible in lateral view; **(D)** Upper tooth row in occlusal view; **(E)** Lower tooth row in occlusal view.

Equus oldowayensis (Figure 8)

Churcher and Hooijer (1980) reviewed the taxonomy of *E. oldowayensis* which Bernor et al. (2010) closely followed. Hopwood (1937: **Figures 1**, **2**) designated a lower jaw from an animal about 2 years old (Catalogue Number VIII, 353 m in the Bayerische Palaeontologische Staatsammlung, Munich) as the holotype of *E. oldawayensis.* Hopwood (1937) also designated a lower incisive region with left incisors and right i1 (BMNH14199) as the paratype. The type was destroyed by bombing in World War II leaving the paratype to represent the species; this in itself, is an inadequate element for species recognition in horses.

Cooke (1963: Table 4) assigned a large equid from the Omo deposits to *E. oldowayensis* (Hopwood, 1937), or possibly *Equus grevyi*, but without discussion. Hooijer (1976) reported a large *Equus* from the Omo that he considered to be indeterminate. Churcher and Richardson (1978) identified *Equus* (*Dolichohippus*) *oldowayensis* from the Omo Shungura F through J explicitly recognizing it as being a member of the Grevy's zebra clade. Coppens (1971) earlier recognized that the earliest *Equus* occurred in Omo Shungura G (not as early as member F), ca. 2.3 Ma. which is our current understanding (J.-R. Boissierie, personal communication to Bernor) Churcher and Hooijer (1980) reported an extensive *Equus* material currently on loan to the Rijksmuseum van Natuurlijk Historie Leiden and nominated a mandible, BMNHM14184, as a Neotype.

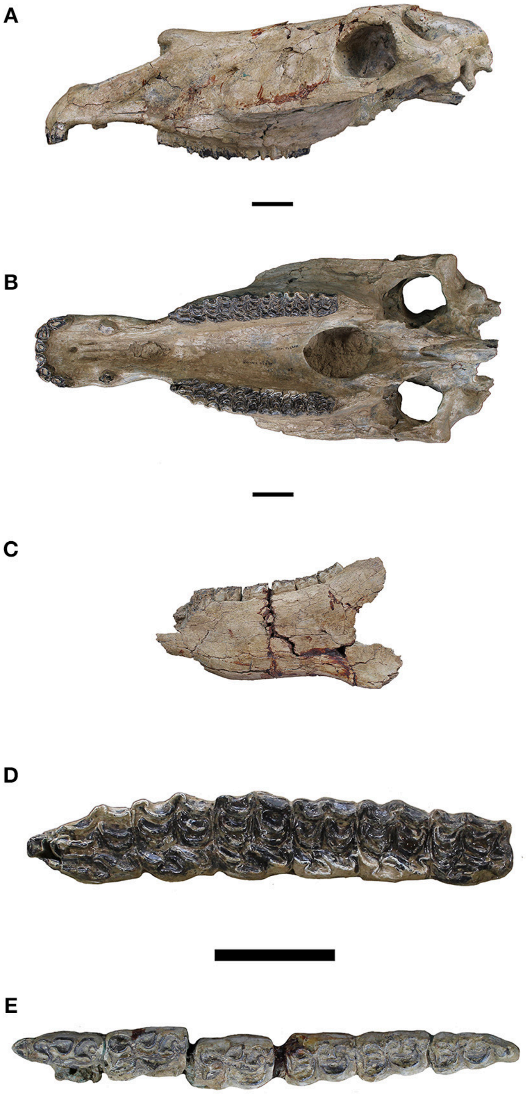

FIGURE 8 | *Equus oldowayensis*. **(A)** Skull in lateral view; **(B)** Skull in ventral view; **(C)** Mandible in lateral view; **(D)** Upper tooth row in occlusal view; **(E)** Lower tooth row in occlusal view.

Eisenmann (1983) noted the likely similarity of Koobi Fora *Equus koobiforensis* to *Equus oldwayensis.* Bernor et al. (2010) followed these arguments and in review again here we find that while *E. koobiforensis* and *E. oldowayensis* may overlap in their morphology and temporal distribution, *Equus oldowayensis* presents a very confusing and uncertain taxonomy whereas *Equus koobiforensis* is clearly characterized and defined and brings stability to our understanding of this large East African horse. We agree with Eisenmann's decision to characterize and define *Equus koobiforensis* as a legitimate species. Clearly, the Olduvai and Omo *Equus* material needs a comprehensive revision with the benefit of Eisenmann's (1983) study of the Koobi Fora *Equus* assemblage.

Our clearest understanding of the morphological basis for *Equus oldowayensis* comes from Churcher and Hooijer's (1980) diagnosis of *Equus oldowayensis*, the salient features are summarized after them briefly herein: *Equus* (*Dolichohippus*) *oldowayensis* is a large horse overlapping in size with *Equus grevyi*; with a large, broad, incisor arcade; infundibula present on I1 and I2, possibly absent on I3; canine large in males, may be absent in females; P2 and P3 protocones shorter and rounder than on P4 and persistently longer on molars; protocone strongly linked to protoloph; pli caballins vestigial or absent; fossette plications simple. Mandibular incisors as in maxillary incisors having distinct infundibula; lower cheek teeth have vestigial metaconid on p2 and rounded or slightly elongate on p3-m3; metastylids are rounded to square shaped; linguaflexids very shallow on p2 and V-shaped on p3-m3. Metapodial IIIs reportedly variable in length and slenderness. Bernor et al. (2010) reviewed these characters and particularly in the case of metapodial III variability, suggested that there is likely more than one *Equus* species represented in this sample. Eisenmann (1983) recognized species specific variability in the Koobi Fora equid assemblage so it is reasonable to expect similar variability in the Olduvai and Omo assemblages. A relatively complete cranium (**Figure 8**) and mandibular specimens from upper Member 1 Olorgesailie Formation, ca. 1.0 Ma, have also been assigned provisionally to *E. oldowayensis* based large overall size, a broad incisor arcade, and a P2–M3 tooth row longer than in male *E. grevyi* (Potts, 1998; Potts et al., 2018).

Olorgesailie, Kenya has yielded a 1.0 Ma skull referred to herein as *Equus "oldowayensis"* (KNMOG22833; **Figures 8A–C**). The skull is in pristine condition and in lateral view (**Figure 8A**) exhibits a moderately long snout with nasal notch retracted to P2 mesostyle, preorbital fossa is lacking; broken canines are large revealing that this individual was male; P2–M3 are clearly worn and all paracone cusps are extremely low and blunt suggesting an abrasive diet likely composed largely of grass. In ventral view (**Figure 8B**) the incisor arcade is arcuate with right I1 having a broken buccal margin and all incisors and canines being heavily worn; incisors have round infundibula occlusally; no dP1 is present. **Figure 8D** provides a closeup of P2–M3; P2 has an elongate anterostyle; P2, P3, M1, and M2 have protocone strongly connected to protoloph, P4 and M3, less so; hypoglyphs range from being slightly incised on P2–M2, being more strongly incised on M3; all protocones are flattened lingually; protocones show slight serial increase in length from P2–M3; all pre- and postfossettes have slightly to non-plicated margins; mesostyle is rounded on P2–M2 and pointed labially on M3; pli caballins are not apparent on P2–M3. **Figure 8C** is a partial mandible in lateral view, and discovered within the same stratum as the cranium, ∼80 m away **Figure 8E** is a closeup of p2-m3 with the following salient features: the cheek teeth are typically stenonine/zebrine with p2-m3 having rounded metaconid, squared, and often distolingually pointing metastylid; shallow linguaflexid on p2 and V-shaped on p3-m3; preflexid has a strong, labially directed pli on the mesiolabial border; pre- and postflexids are distinct and separated except for the p4 postflexid which is highly complex labially, connecting mesially with the metaconid; ectoflexid is shallow on p2-p4 and deep separating metaconid from metastylid on m1-m3; pli caballinids are absent on all cheek teeth.

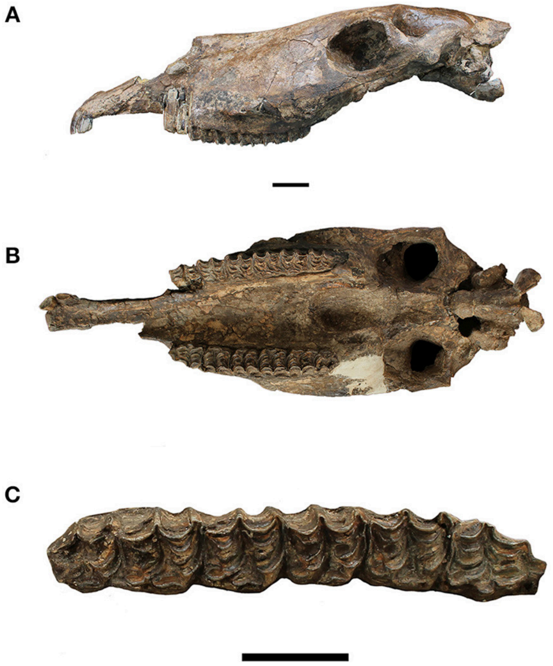

FIGURE 9 | *Equus koobiforensis*. **(A)** Skull in lateral view; **(B)** Skull in ventral view; **(C)** Upper tooth row in occlusal view.

Equus koobiforensis (Figure 9)

Eisenmann (1983: 178) named *Equus koobiforensis* for a skull of a young mare, KNM-ER1484 originating from the *Notochoerus scotti* zone, below the KBS Tuff, in Area 130. Other specimens were reported from the *Notochoerus scotti* and *Metridiochoerus andrewsi* zones of Koobi Fora and questionably from the Omo Shungura Formation and Olduvai Gorge.

The skull is large with P2–M3 length being 202 mm. In lateral view (**Figure 9A**) the skull has a moderate length snout, nasal notch is retracted to mesostyle of P3 and there is no apparent depression for a preorbital fossa. The lacrimal bone is clearly defined anteriorly by its suture. The facial-maxillary crest is modestly developed. In ventral view (**Figure 9B**) the right half of the snout is broken away with only left I2 and I3 in place with open infundibula. The left premaxilla has a very small alveolus for the diminutive female canine. The maxillary cheek tooth dentition has the following salient features: P2 with a short anterostyle and short ovate protocone not connected to protoloph; P3 is triangular shape with a slight connection to protoloph and protocone is likewise triangular shaped with no connection to the protoloph; P2 has a labially squared mesostyle, while P3 and P4 have mesiodistally constricted and labially pointed mesostyles; all premolars have weakly developed fossette ornamentation; P2 has a moderately deeply incised hypoglyph and P3 and P4 have deeply incised hypoglyphs; M1–M3 have elongate, lingually flattened protocones with only M1 having a clear connection to the protoloph; all molars have labially pointed mesostyles and weakly developed fossette ornamentation.

Eisenmann (1983, p. 179–180) reported one lower cheek tooth series that she found matched the holotype cranium, KNM-ER4051, which she characterized as having teeth like those of *E. stenonis* with rounded metaconids and metastylids, deep and pointed lingual grooves (= linguaflexids), short vestibular grooves (= ectoflexids) on at least some of the molars, and a relatively long p2. The presence of a protostylid on p2 evokes a comparison with *E. grevyi* but the shallow nature of the vestibular grooves is rare in the later species.

Equus cf. *tabeti* (Figure 10)

Eisenmann (1983, p. 188) referred a smaller *Equus* skull, KNM-ER 1211 of a young adult (**Figure 10** herein) to *Equus* cf. *tabeti*. As she pointed out: "*E. tabeti* is a North African early Pleistocene species of moderate size, mostly characterized by slender limb bones, asinine upper teeth and stenonine lowers." In lateral view (**Figure 10A**) the skull is seen to lack the pre-maxilla and nasals, has a broken distal right maxilla, partial orbit, and almost complete brain case. The lateral view also shows that M3 is not yet fully emerged from its crypt and hence this individual is a sub-adult. **Figure 10B** is a ventral view of KNM-ER 1211. Eisenmann (1983, p. 188) reports that h P2–M3 tooth row length is 169 mm. The salient features of the upper cheek teeth are: P2 with a short anterostyle, rounded protocone with lingually flattened surface and weak connection to the protoloph; P3 with longer, lingually flattened protocone, and weak connection to protoloph; P4 with still longer and flattened protocone and no connection to the protoloph. M1-M3 show increased bucco-lingual flattening serially, with M1 having a weak connection to the protoloph while M2 and M3 have no connection to the protoloph; m3 protocone lenticular shaped; hypoglyph is deep on P2, P3, and M1, being very deep on P4 and M2 and not discernible on M3 due to its very early wear stage; pli caballins are not developed on any of the cheek teeth; mesostyle is labially squared on P2 and pointed labially on P3–M3; cheek tooth fossettes are mostly weakly ornamented on all cheek teeth.

Equus grevyi (Figure 11)

Equus grevyi is the largest living zebra, exceeding the size of the plains and mountain zebras. It is the sole living member of the subgenus *Dolichohippus*.

We characterize *Equus grevyi* using a pristine adult female skull with associated mandible, USNM163228. The skull has a P2–M3 dimension of 185.7 mm. The skull in lateral view (**Figure 11A**) has nasal notch reflected to P2 metastyle. The infraorbital foramen is prominent, placed slightly higher than midway between the occlusal level of distal P4 and the superior surface of the posterior nasal bone. The lacrimal bone is large, square shaped, and extends from the anterior orbit to the level of the mesostyle of M3. Paracone cusps of P4–M2 are low and blunt and reflect a grazing diet. In ventral view (**Figure 11B**) the snout is elongate with a rounded incisor arcade; all incisors have distinct, open infundibulae; canines are small and just emerging from their crypts. The left cheek tooth series (**Figure 11D**) with dP1 small and worn; P2–M2 have mesostyles squared labially; all maxillary cheek teeth have moderately to poorly developed pre- and postfossette plis; pli caballins are absent on all cheek teeth;

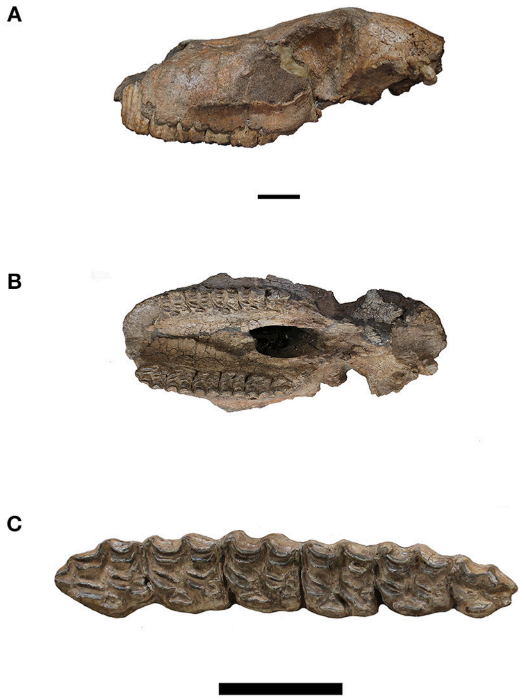

FIGURE 10 | *Equus* cf. *tabeti*. **(A)** Skull in lateral view; **(B)** Skull in ventral view; **(C)** Upper tooth row in occlusal view.

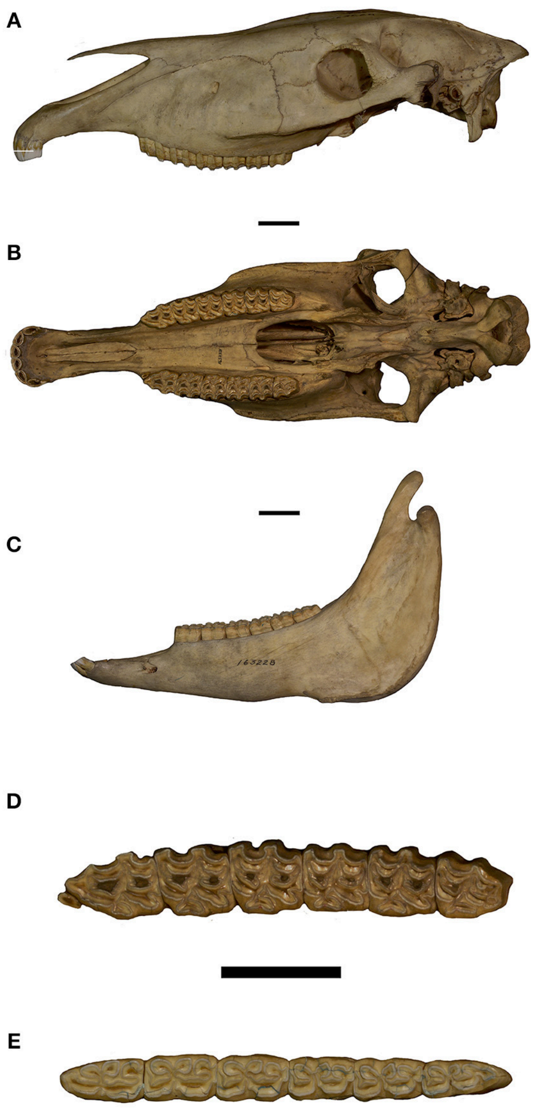

FIGURE 11 | *Equus grevyi*. **(A)** Skull in lateral view; **(B)** Skull in ventral view; **(C)** Mandible in lateral view; **(D)** Upper tooth row in occlusal view; **(E)** Lower tooth row in occlusal view.

P2 has a moderately elongate, mesially rounded anterostyle; P2 protocone is the shortest, P3-M3 being longer; P3-M3 protocones are longer than P2 and have a flattened lingual border with a buccally-directed inflection midway along its margin.

As seen in the lateral view (**Figure 11C**) the mandible is pristine, incisors are moderately procumbent, canine is lacking and symphysis is moderately long. The left p2-m3 cheek tooth series (**Figure 11E**) has p2 with short anterostylid; premolars have rounded metaconids, and square metastylids, all mandibular premolars have a V-shaped linguaflexid; ectoflexids are very shallow on p2, and deeper on p3-4, but not coursing between the pre- and postflexids; p2-p4 have pli caballinids that become reduced serially through the premolar series; pre-and postflexid margins are mostly not plicated; p3 and p4 have a labially directed pli on their mesio-labial margin. Mandibular molars have metaconids and metastylids as in the premolars; linguaflexid is U-shaped on m1 but as in the premolars V-shaped for m2 and m3; ectoflexids are deeply inflected separating metaconid and metastylid on all of the molars; the molars lack pli caballinids; pre- and postflexids are smaller, have simple margins and are more labio-lingually compressed than in the premolars and have a weakly developed mesio-buccal pli. The lower cheek teeth retain the so-called *stenonine* occlusal pattern, especially with regards to metaconid-metastylid and linguaflexic morphologies.

Figures 12A,B are log10 ratio diagrams of metacarpal IIIs (MCIII) and metatarsal IIIs (MTIII), respectively, of many of the *Equus* species we have discussed in this contribution; the Hoewenegg *Hippotherium primigenium* log10 mean is used as our comparative sample because of its large sample size and clear proportional differences with our *Equus* sample.

Figure 12A MCIII shows that all *Equus* species under consideration herein have longer MCIIIs than Hoewenegg (Ho) *Hippotherium primigenium* except for *Equus stehlini*, which is shorter. The largest (M5 and M6 proximal articular dimensions and M10 distal supra-articular dimension) horse in our sample is *Equus stenonis.* The large Dmanisi *Equus* plots closely to *E. stenonis* having similar midshaft (M3 and M4) dimensions, and slightly smaller proximal articular facet (M5 and M6) and trans- distal suprarticular (M10) dimensions; this supports our referral of the large Dmanisi form to *Equus* cf. *stenonis*. *Equus sivalensis* has the longest MCIII (M1), has strongly contrasting

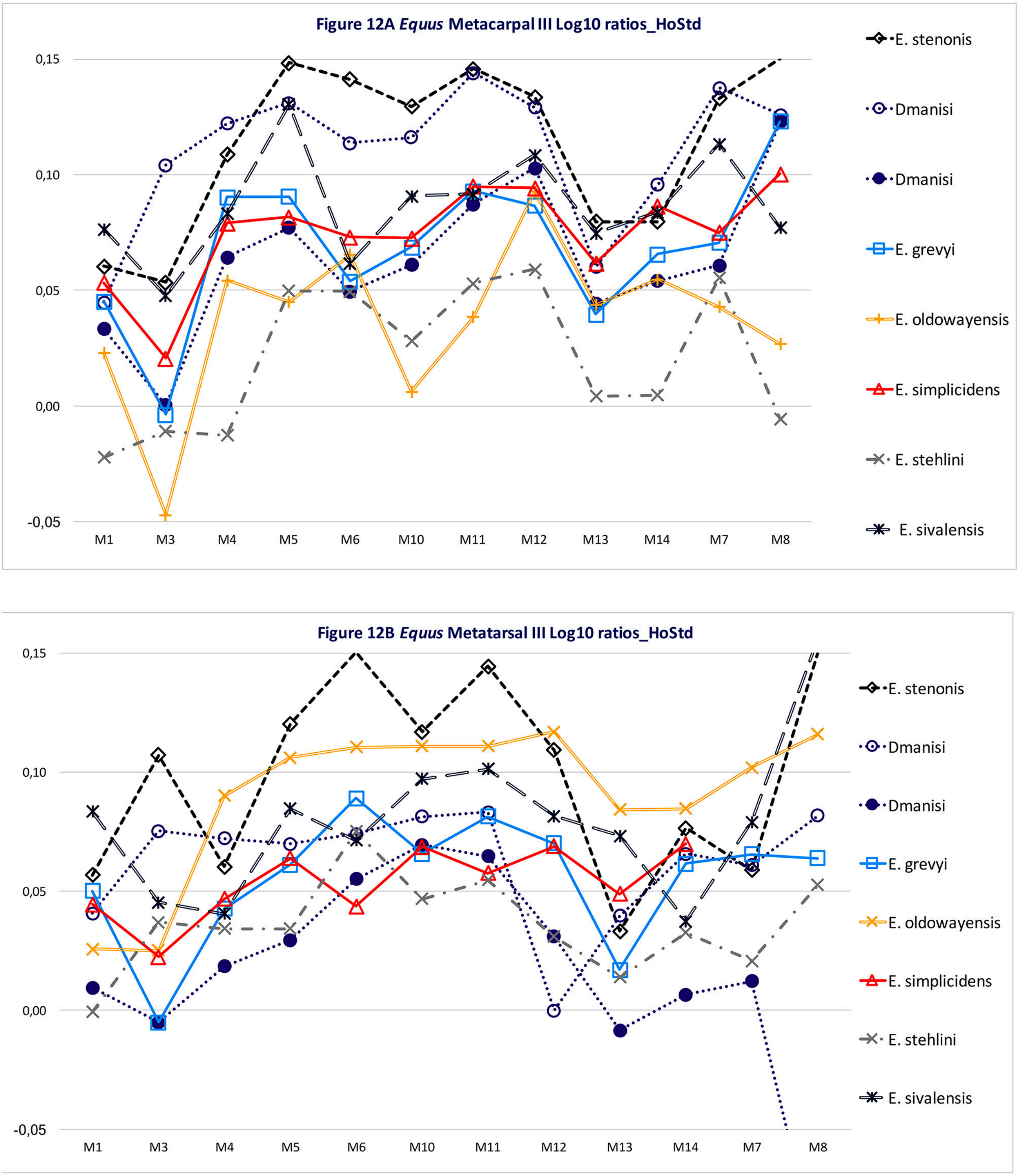

FIGURE 12 | Log10 ratio diagrams; the specimens are analyzed on the Hoewenegg *Hippotherium primigenium* sample. **(A)** Log10 ratio diagram of third metacarpal; **(B)** Log10 ratio diagram of third metatarsal.

large midshaft width (M3) and depth (M4) dimensions as in *E. stenonis* and narrower trans- supraarticular (M10) dimensions but otherwise plots with species in the central portion of the figure. *Equus simplicidens, E. grevyi,* and the smaller Dmanisi *Equus* sp. are in the center of the plot and have close trajectories to one another. *Equus "oldowayensis"* likewise plots close to this group except for the narrow midshaft (M3) and supraarticular (M10) dimensions. *Equus stehlini* is the shortest MCIII and overall and is the smallest *Equus* in this sample but generally has a plot trajectory similar to the *E. simplicidens, E. grevyi,* and smaller Dmanisi *Equus* triad.

Figure 12B again shows that all *Equus* species under consideration herein have longer MTIIIs than Hoewenegg (Ho) *Hippotherium primigenium* except for *Equus stehlini* and the smaller *Equus* from Dmanisi which are approximately the same as each other and the Hoewenegg mean sample. The most remarkable feature of this plot, again is how close the log10 ratios are between Hagerman *E. simplicidens*, extant *E. grevyi* and the smaller form of *Equus* sp. from Dmanisi, except for the short length of the Dmanisi small form. *Equus stenonis* has a similar length as a majority of specimens, but its log10 trajectory shows large size peaks for midshaft width (M3), proximal articular depth (M6) and distal articular width (M11). *Equus "oldowayensis"* length (M1) and midshaft width (M3) is as in other specimens, but is larger approaching *E. stenonis* for M4-M12 measurements and has the largest relative dimensions for M12–14. *Equus sivalensis* is the longest MTIII of our sample and its log10 trajectory largely resembles *E. simplicidens, E. grevyi* and the large and small Dmanisi *Equus. Equus stehlini* and the smaller Dmanisi *Equus* have the shortest MCIIIs. This log10 ratio diagram on MTIII supports the interpretation than *E. stehlini* is in fact a different species than *E. stenonis,* and that our referral of the larger Dmanisi *Equus* to *E.* cf. *stenonis* is warranted on skull, dental and now MCIII and MTIII grounds. Our limited sample of *Equus "oldowayensis"* suggests that this "species" is somewhat shorter (M1), has wider midshaft (M3), and distal width (both M10 and M11) than *E. grevyi, E. simplicidens* and both Dmanisi *Equus* sample; a survey of a larger sample of *E. "oldowayensis"* is needed.

PALEOECOLOGICAL CONTEXT

Hagerman Fossil Beds Paleoecology—4.18 to 3.11 Ma

The fossils from the Hagerman beds are best known from the Hagerman Fossil Beds National Monument, Idaho (McDonald et al., 1996). These beds are located on the Snake River Plain, and are currently under the protection of the U.S. National Park Service. The beds are part of the Glenns Ferry Formation (Repenning et al., 1995), and consist of fluvial, flood plain, and lacustrine deposits (Ruez Jr., 2009a). The age of the beds exposed in the National Monument range from 4.18 to 3.11 Ma (Ruez Jr., 2009a), and corresponds to the Blancan Land Mammal Age (Bell et al., 2004). The Hagerman Horse Quarry is arguably the most famous fossil locality in the beds, where scores of *Equus simplicidens* remains have been recovered (Gazin, 1936). This quarry is roughly 3.19 Ma in age. It is thought that either a flood killed a herd of horses and subsequently buried them (McDonald, 1996), or drought stricken horses died at a dwindling watering hole and were then subsequently buried by a flash flood (Richmond and McDonald, 1998). The paleoclimate at the National Monument is interpreted to have been warm and wet, with a short cool interval between 3.6 and 3.2 Ma (Ruez Jr., 2006). The climate of the Hagerman Horse Quarry is interpreted to be very warm, providing some support for the drought hypothesis (Ruez Jr., 2006). A diverse assemblage of mammals has been recovered from the Hagerman beds, including a mix of small and large taxa from various guilds (Ruez Jr., 2009b).

Italy—2.6 to 2.0

Palaeoecological data, from the comparison of Montopoli fauna (the site recording the *Equus* Datum in Italy) with other Plio-Pleistocene mammal assemblages of Europe, show that the *Equus* event is related to the faunal turnover and palaeoenvironmental change that occurred at the early–to–middle Villafranchian transition, chronologically corresponding to 2.6 Ma. Furthermore this time coincides with one of the major shifts in δ_{18}O isotopic oscillations (cf. Miller et al., 2005), and the setting of 40 Ka obliquity-forced thermal glacial/interglacial cyclicity (Bertini, 2010) with strong effects on seasonality, and the first record of cool winters and drier climates as testified by the diffusion of herbaceous steppe vegetation (Fortelius et al., 2006).

Several paleoecological analyses (Pradella and Rook, 2007; Rivals and Athanassiou, 2008; Valli and Palombo, 2008; Strani et al., 2015, 2018) stress a trend toward more open environments, both in terms of taxonomical composition (at family and genus levels), ungulate hypsodonty, and dietary categories. This is consistent with the faunal turnover known as "Elephant-Equus event" (Azzaroli, 1983), that occurred at 2.5 Ma in Europe, an event that produced a faunal composition with predominance of grazing species and grass-dominated mixed feeders, among which the most representative taxa are the monodactyl horse, *Equus* cf. *livenzovensis*, and the first true elephant, the primitive *Mammuthus gromovi*, and the disappearance of the extinction of numerous woodland dwellers like *Mesopithecus monspessulanus, Mammut borsoni*, *Tapirus arvernensis*, *Sus minor,* and *Ursus minimus* (Azzaroli et al., 1986; Eronen and Rook, 2004; Pradella and Rook, 2007).

Dmanisi, Georgia—1.85 to 1.77 Ma

The large mammal record from Dmanisi includes several of the herbivore faunal elements also known from Middle Villafranchian contexts of Western Asia and Europe, but a significant number of genera, especially of artiodactyls, reflect the early Late Villafranchian faunal renewal, the composition of the carnivore guild also points to an early Late Villafranchian age (Vekua, 1995; Lordkipanidze et al., 2007), correlative with a geochronologic age range between 1.85 and 1.77 Ma (Ferring et al., 2011). Overall the large mammal assemblage is characterized by a preeminence of open woodland adapted herbivores. The small mammal association is dominated by steppic or dry-adapted rodents, while woodland with fluviatile elements are very rare (Lordkipanidze et al., 2007; Furió et al., 2010). The herpetofaunal assemblage from Dmanisi indicates an important water stress environment suggesting a period of increased aridity and supports a reconstruction of open, relatively dry environments and climate as dry and warm as the Mediterranean type (Blain et al., 2014). The Dmanisi mammal fauna points to a mosaic-like landscape with

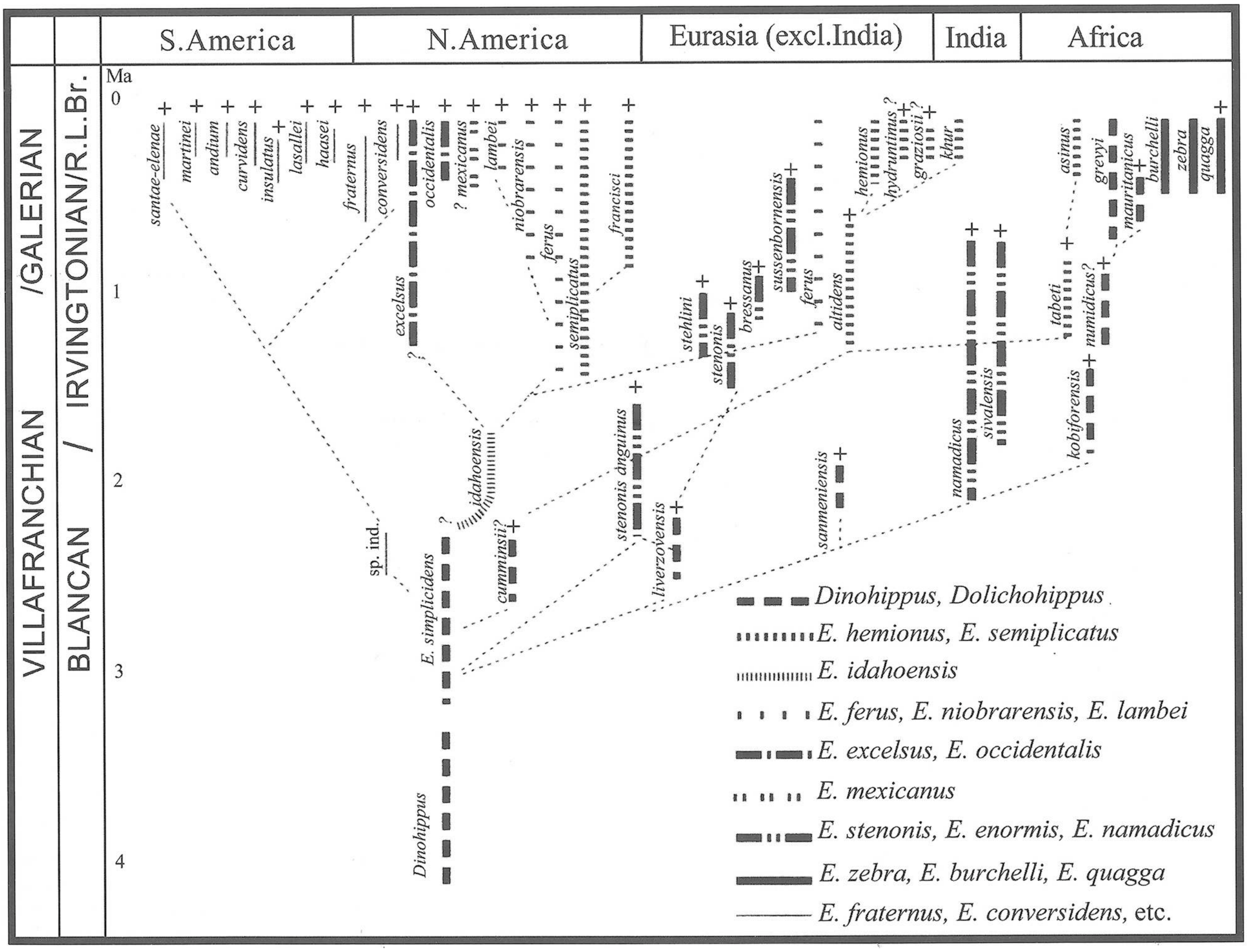

FIGURE 13 | Phylogeny of the genus *Equus* with species geographical and stratigraphical distribution from Azzaroli (2003).

remarkable differences in humidity and vegetation across its terrain. Although the immediate vicinity of the fossil site was situated in a more or less forested valley, the wider region was largely made up of drier open tree savanna and grassland and by mountainous to semi-arid rocky terrains.

Indian Subcontinent—2.6 to 0.6 Ma

Siwalik *Equus* is known to be a grazer based on the flat occlusal surfaces (also, low and blunt paracones of P4–M2 mesowear terminology) and enamel isotopic data (Patnaik, 2015). Carbon isotopes from dental enamel and soil carbonates show the presence of grasslands in the Siwaliks during the Pleistocene, albeit with patches of woodland within grasslands (Quade et al., 1993; Quade and Cerling, 1995; Patnaik, 2015). *Equus* appears in the Siwaliks along with other hypsodont grazers such as the alcelaphine *Damalops palaeindicus*, the reduncine *Sivacobus palaeindicus*, and bovines *Bos acutifrons*, *Bubalus platyceros*, *Leptobos falconeri*, and *Hemibos triqueticornis* and the elephantid *Elephas hysudricus* and mesodont mixed feeders such as cervids and rhinocerotids (Jukar, 2018). *Equus* also replaces the smaller and less hypsodont hipparionines across the Plio-Pleistocene boundary (Jukar, 2018). The causes of this ecological replacement are still unclear since both hipparionines and *Equus* were adapted to a grazing lifestyle in open habitats.

East Africa—2.3 to 0.6 Ma

The first record of East African Equidae, the C_4-grazing *Eurygnathohippus*, coincided with a sharp 3.1‰ enrichment in $\delta^{13}C$ values connoting C_4 grassland expansion at ca.10 Ma, based on n-C_{35} alkane terrestrial plant wax biomarkers recovered from Somali Basin and Red Sea drill cores (Uno et al., 2016). Pedogenic carbonate $\delta^{13}C$ values across sub-Saharan African fossil sites suggest, however, that C_4 grasses were a minor component of the environment until the early Pleistocene (Ségalen et al., 2007). The earliest appearance of *Equus* in East Africa, currently dated at 2.3 Ma in the base of Member G Shungura Formation of the Omo-Turkana basin, and its subsequent numerical increase are associated with further expansion of C_4 grass-dominated habitats (Cerling et al., 2015). Omo-Turkana equids, as represented by *Equus* and *Eurygnathohippus*, range from 1.5 to 11% of all large

TABLE 1 | Measurements of the specimens reported in **Figure 12A**.

SPEC_ID	SPECSHORT	Quarry	AGE	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
12828	*E. stenonis*	Upper Valdarno	1.8	244.6	240.2	35.6	28.7	56.2	38.2	37.1	16.6	6.8	52.9	51.6	38.0	29.5	31.6
D810	Dmanisi	Dmanisi	1.8	236.0	224.5	40.0	29.6	54.0	35.8	47.6	15.7	8.1	51.3	51.4	37.6	28.2	32.8
Pa62/63B2a12133	Dmanisi	Dmanisi	1.8	229.8	220.1	31.5	25.9	47.7	30.9	39.9	15.6	8.2	45.2	45.1	35.4	27.2	29.8
USMN49944	*E. grevyi*	Kenya	0.0	236.2	228.2	31.2	27.5	49.2	31.2	40.8	15.6		46.0	45.7	34.1	26.9	30.6
RMNH933	*E. oldowayensis*	63 BKII	1.2	224.4	216.9	28.2	25.3	44.3	32.0	38.3	12.5		39.8	40.3	34.6	27.2	29.9
USNM222034	*E. simplicidens*	Hagerman Horse Quarry	3.3	240.6	233.4	33.0	26.8	48.2	32.6	41.2	14.8	5.3	46.4	45.9	34.7	28.3	32.1
IGF 605V	*E. stehlini*	Upper Valdarno	1.6	202.3	199.5	30.7	21.7	44.8	30.9	29.4	11.6	4.7	41.9	41.7	32.0	24.8	26.6
NHMUK PV M.2671	*E. sivalensis*	Siwalik Hills	2.58-0.6	253.9	246.9	35.1	27.1	53.9	31.8	45.0	14.0	7.8	48.4	45.6	35.9	29.2	31.9

Codes M1 to M14 indicate standard measurements for third metacarpal referred to Eisenmann et al. (1988) and Bernor et al. (1997).

TABLE 2 | Measurements of the specimens reported in **Figure 12B**.

SPEC_ID	SPECSHORT	Quarry	AGE	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
15231	*E. stenonis*	Upper Valdarno	1.8	277.5	272.2	39.5	32.6	55.7	47.7	35.1	14.4	5.4	52.3	52.5	39.4	27.3	32.2
N17Pa	Dmanisi	Dmanisi	1.8	267.5	261.8	36.7	33.5	49.6	40.0	45.3	12.3	10.4	48.2	45.6		27.7	31.4
Pa66/60 V 162 2622	Dmanisi	Dmanisi	1.8	248.9	241.2	30.5	29.6	45.2	38.3	40.5	8.0	8.7	46.9	43.7	32.9	24.8	27.4
USMN49944	*E. grevyi*	Kenya	0.0	273.3	266.2	30.5	31.3	48.6	41.4	45.8	11.8	7.2	46.5	45.4	36.0	26.3	31.1
RMNH2660	*E. oldowayensis*	63 BKII	1.2	258.4	248.2	32.7	34.9	53.9	43.5	49.8	13.3	10.1	51.6	48.6	40.1	30.7	32.8
USNM 13791	*E. simplicidens*	Hagerman Horse Quarry	3.7	269.8	266.1	32.5	31.6	48.9	37.3				46.8	43.0	35.9	28.3	31.7
IGF 1680V	*E. stehlini*	Upper Valdarno	1.6	243.1	241.7	33.6	30.7	45.7	40.1	31.3	11.5	4.1	44.5	42.7	32.9	26.1	29.1
NHMUK PV OR 16681	*E. sivalensis*	Siwalik Hills	2.58-0.6	280.7	274.7	34.5	30.8	49.7	36.4	45.1	15.0	14.8	46.6	45.8	31.3	25.4	28.8

Codes M1 to M14 indicate standard measurements for third metatarsal referred to Eisenmann et al. (1988) and Bernor et al. (1997).

mammal specimens between 2.3 and 1.35 Ma (Bobe and Eck, 2001; Hernández Fernández and Vrba, 2006). Between 2.3 and 1.8 Ma, *Equus* accounts for roughly 30% of all Omo-Turkana equids, increasing to around 50% of all equids from 1.8 to 1.35 Ma (Bobe and Leakey, 2009). The appearance of *Equus* in the Omo-Turkana record coincided with an overall transition in mammalian herbivore diets as a C_4-grazer-dominated fauna supplanted an herbivore community of C_3-C_4 mixed-feeders by 2.3 Ma. Early Pleistocene *Equus* of Turkana was a C_4 grazer with an average $\delta^{13}C$ value of $-0.1 \pm 1.1‰$ ($n = 39$), only slightly less enriched than that of extant East African *Equus* with an average $\delta^{13}C$ value of $1.3 \pm 1.4‰$ ($n = 147$) (Cerling et al., 2015).

In 2 Ma sediments at Kanjera South, Kenya, *Equus* accounts for 6–10% of the excavated large mammal specimens from three stratigraphic levels, all of which are associated with pedogenic carbonate $\delta^{13}C$ values indicative of $>75\%$ C_4 grassland habitat (Plummer et al., 2009; Ferraro et al., 2013). In the excavated fauna of Bed I Olduvai Gorge, Tanzania, dated ∼1.9–1.8 Ma, *Equus* ranges from 3 to 14% of the large-bodied mammals (percent minimum number of individuals); the genus increases in representation relative to all herbivores after 1.8 Ma in the faunas of Bed II Olduvai, associated with increased pedogenic $\delta^{13}C$ values and open habitat (Leakey, 1971; Cerling and Hay, 1986; Potts, 1988). Although the spread of grasslands has often been attributed to increased aridity, East African vegetation and moisture varied independently; instead, the transition to open habitat favoring *Equus* and other grazing herbivores now appears to have been more closely related to decreasing atmospheric CO_2 concentration rather than climatic aridification (Blumenthal et al., 2017; Faith et al., 2018).

After 1.35 Ma, the best-preserved evidence of fossil *Equus* in East Africa comes from the Olorgesailie Basin, southern Kenya. Comprising 44% of the large mammals, *Equus* is the dominant taxon in the bovid-depauperate fauna dated ca. 1.0 Ma, and is associated with a nearly 100% C_4 grassland. The relative abundance of Olorgesailie *Equus* decreases to 10% of the herbivore fauna after this time (Sikes et al., 1999; Potts, 2007). In modern East African game reserves, *Equus* typically comprises 10–25% of the large mammal fauna (data compiled in Potts, 1988). Based on faunal representation from the Omo-Turkana, Olduvai, and Olorgesailie basins, the number of non-ruminant C_4-grazing ungulate genera ranged between five and ten during the interval between 2.3 and 0.6 Ma. However, most species in those large ungulate clades either became extinct or switched to browsing and mixed-feeding such that only four non-ruminant C_4-grazing taxa, including *Equus*, currently survive in East Africa (Potts, 1988; Cerling et al., 2015; Potts et al., 2018). While a major ecological shift in African mammal communities occurred after 0.6 Ma, the resilience of *Equus* appears to relate to a dietary strategy that involves C_4 grazing and the ability to adopt a mixed-feeding mode in situations where graze is scarce (Kaiser and Franz-Odendaal, 2004).

DISCUSSION AND CONCLUSION

We have provided a brief review of *Equus* evolution including samples of North American Hagerman *Equus simplicidens*, Italian *Equus stenonis,* and *Equus stehleni, two* apparent species of *Equus* from Dmanisi, Georgia, *Equus sivalensis* from the Indian Sub-Continent and Kenyan *Equus koobiforensis, Equus “oldowayensis”* and *Equus* cf. *tabeti*.in comparison to extant Grevy's zebra. We consider this an initial evaluation of a restricted sample of these species skulls and dentitions meant to evaluate the plausibility of their evolutionary relatedness. We find that traditional views on the relationships of stenonine horses and zebras are upheld: that Azzaroli and Voorhies (1993) were correct that Hagerman Quarry *E. simplicidens* is a likely phylogenetic source for Old World stenonine horses; that McDonald (1996) was justified in referring to Hagerman horse *Equus simplicidens* as a zebra; that *Equus grevyi* and, more broadly, African zebras are the descendants of stenonine horses. We have reported remarkable similarities in skull, tooth and metapodial III log10 proportions between *E. simplicidens,* smaller Dmanisi *Equus* sp. and *Equus grevyi*. Both *Equus simplicidens* and its likely descendant *Equus stenonis* exhibit the basic bauplan of other Eurasian early *Equus* species and *Equus grevyi.* The revelation herein is that African zebras would appear to have a genuine deep-time origin in North American *Equus* through the Eurasian *Equus stenonine* lineage. This hypothesis needs future testing with large sample sizes of *E. simplicidens*, Eurasian and African fossil and extant *Equus.* We refigure (**Figure 13**) herein Azzaroli (2003) last version of his phylogeny of *Equus* for ready reference.

DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

RB and OC conceived the paper. RB, OC, AJ, RP, and MB provided data. RB, OC, and AJ carried out analyses. RB wrote the manuscript with support from OC, AJ, RP, and LR. All authors equally contributed to discussion and conclusions.

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Assessing the Causes Behind the Late Quaternary Extinction of Horses in South America Using Species Distribution Models

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At the end of the Pleistocene, South America witnessed the loss of an 83% of all megafaunal genera that inhabited the continent at that time. Among the taxa that disappeared were all the representatives of the Equidae family, including several species of *Equus* and *Hippidion*. Previous studies have investigated the causes behind the extinction of horses in South America using radiocarbon data sets to set the time of extinction and compare it to the timing of major climate changes and human arrival. While these studies have shown to be informative, they are available only for some regions of the continent. In the present work we use paleo species distribution models to estimate the potential distribution of *Equus neogeus*, *Hippidion saldiasi*, *Hippidion devillei* and *Hippidion principale* in South America from the Last Glacial Maximum (LGM) through the early Holocene. The main goal is to track changes in the potential area of distribution for these taxa as they approached to the time of their extinction between 12 and 10 kyr BP, to test the role of climate changes in the process of extinction. The distribution models show the Pampas, El Chaco and Central Chile as major areas of distribution for *E. neogeus* and *H. principale* during the LGM. The high Andes and central Argentina appear as potential areas for *H. devillei* and southern South America as the potential area of distribution for *H. saldiasi* during the LGM. A major contraction of the potential areas of distribution is observed toward the beginning of the Holocene for all species of horses, occurring along with a shift of these areas toward higher latitudes and higher altitudes. The moments of major changes in the potential areas of distribution happened at times when humans were already present in most of the different areas of South America. Even if a reduction in the potential area of distribution is not probe for a main role of environmental changes in driving the demise of horses, the models presented here suggest an increased risk of extinction for these taxa during the late Pleistocene which was accompanied by a spread of humans in the continent.

Keywords: megafauna, *Equus*, *Hippidion*, PSDM, extinction

1. INTRODUCTION

Two genera of horses are recognized for the Pleistocene of South America: *Equus* and *Hippidion*. The genus *Equus* is also present in the fossil record of North America, Eurasia, and Africa, and corresponds to the only genus with living representatives of the family Equidae. *Hippidion*, on the other hand, is endemic to South America and it is not known if it originated in this continent or somewhere else (Prado and Alberdi, 2017). Hoffstetter (1950) established the subgenus *Equus (Amerhippus)*, based mainly on morphological characteristics of the skull, to denote a different clade for the South American lineage of the genus. The validity of this subgenus has been questioned in more recent times based on morphological (Eisenmann, 1979; Alberdi and Prado, 2004; Prado and Alberdi, 2017) and genetic studies (Orlando et al., 2008), therefore, the subgenus category will not be used here. Historically, several species for both genera have been established from the study of South American fossils. For *Equus*, Prado and Alberdi (2017) propose, based on the morphology of cranial and postcranial elements, the presence of three species: *E. neogeus*, *E. andium*, and *E. insulatus.* This classification has been challenged by more recent studies that suggest a single species of *Equus* for South America, which shows a gradient of morphological variation following different environmental conditions (Machado et al., 2018). Less debated at the moment is the presence of three species of *Hippidion*: *H. saldiasi*, *H. devillei* and *H. principale* (Prado and Alberdi, 2017).

The recorded occurrences from the fossil record of the different species of horses suggests that they occupied different habitats in the continent (**Figure 1** for the species used here). *Equus neogeus* is the most broadly distributed species of the genus occupying environments both in the Atlantic and Pacific coasts of the continent, the Andes and the interior, from the subtropics to the north and even reaching the Caribbean (Prado and Alberdi, 2017). The smaller forms, *E. insulatus* and *E. andium* are exclusively found in the western side of the Andes, from southern Chile to the north (Prado and Alberdi, 2017). The largest form of *Hippidion*, *H. principale*, is mainly distributed in the eastern part of the continent from the subtropics to north east Brazil (but there is one late Pleistocene finding of *H. principale* in central Chile Alberdi and Frassinetti, 2000). *Hippidion devillei* is found in the Andean region, Pampas and eastern Brazil, while *H. saldiasi* is the horse with the southernmost distribution in the continent which is restricted to the southern cone, ranging from the tropics to Tierra del Fuego (Prado and Alberdi, 2017). All the representatives of the two genera became extinct at the end of the Pleistocene as part of the Late Quaternary Extinction event (LQE) that affected South America and almost every other continent in the planet (Koch and Barnosky, 2006). In South America, this event was particularly severe and around an 83% of all the genera considered megafauna (over 44kg) in the continent disappeared during the late Pleistocene and the beginning of the Holocene (Brook and Barnosky, 2012). As for most of the taxa that became extinct during the LQE, the debate about the causes behind the extinction of horses revolves around the role of climate changes happening at the end of the last ice age, the role of humans entering the continent and combinations of both drivers of extinction.

1.1. Horse Extinction in South America: Human vs. Environmental Drivers

Until now, what we know about the possible causes behind the extinction of horses in South America comes from regional analyses. In these studies (Prado et al., 2015; Barnosky et al., 2016; Villavicencio et al., 2016; Villavicencio and Werdelin, 2018) the radiocarbon chronology of megafaunal extinction is compared to the chronology of human presence and to the timing of major environmental changes in the areas under study, giving an idea of the possible role of the different factors in driving some of these extinctions. The most complete radiocarbon record for the presence and demise of *Equus neogeus* comes from the Pampas region of Argentina, Uruguay and Southern Brazil, and shows spatial coexistence between humans and horses for around 3,000 yr, dismissing a scenario of rapid overkill or "blitzkrieg" scenario [rapid extinction; Mosimann and Martin (1975)] in the area. At around 12 kyr BP (calendar years before present), *E. neogeus* disappears from the record, during a time of major vegetation changes in the Pampas (Prado et al., 2015; Barnosky et al., 2016). A similar situation is observed for the area of Última Esperanza in Southern Patagonia where the radiocarbon record for the presence of *Hippidion saldiasi*, the only horse inhabiting this region, shows at least 2,000 yr of spatial coexistence between humans and this species. This coexistence is followed by the disappearance of *H. saldiasi* from the record during a time of vegetation changes in the landscape from a grass steppe to *Nothofagus* forests (Villavicencio et al., 2016). A different situation is observed from a less robust chronology coming from the Andean Altiplano that records the existence in this area of *Hippidion devillei* during the late Pleistocene (Villavicencio and Werdelin, 2018). This record shows little evidence of temporal overlap between humans and horses in the area, with *H. devillei* disappearing from the record during a time of drying conditions. In summary, the chronology of horse disappearance in different regions shows no evidence of overkill of members of this group by human hunters, although it does not discard a more protracted role of humans in the process of extinction. At the same time, it shows a temporal coincidence of changes in the environment and the demise of horses, suggesting a possible important role for climatic changes in driving their extinction.

To explore the role of environmental changes in driving extinctions, we use paleo species distribution models (PSDM) to explore the dynamics of the climatic niche and the potential range of distribution of different species of horses as South America was transitioning from the Last Glacial Maximum (LGM) to the Holocene. Species distribution models have proven to be useful for determining the current distribution of common and rare species (Peterson et al., 2011; González-Salazar et al., 2013; Breiner et al., 2015), forecasting future distributions of species (Peterson et al., 2018; Raghavan et al., 2019), hindcasting the past distribution of extinct and extant species (Nogués-Bravo,

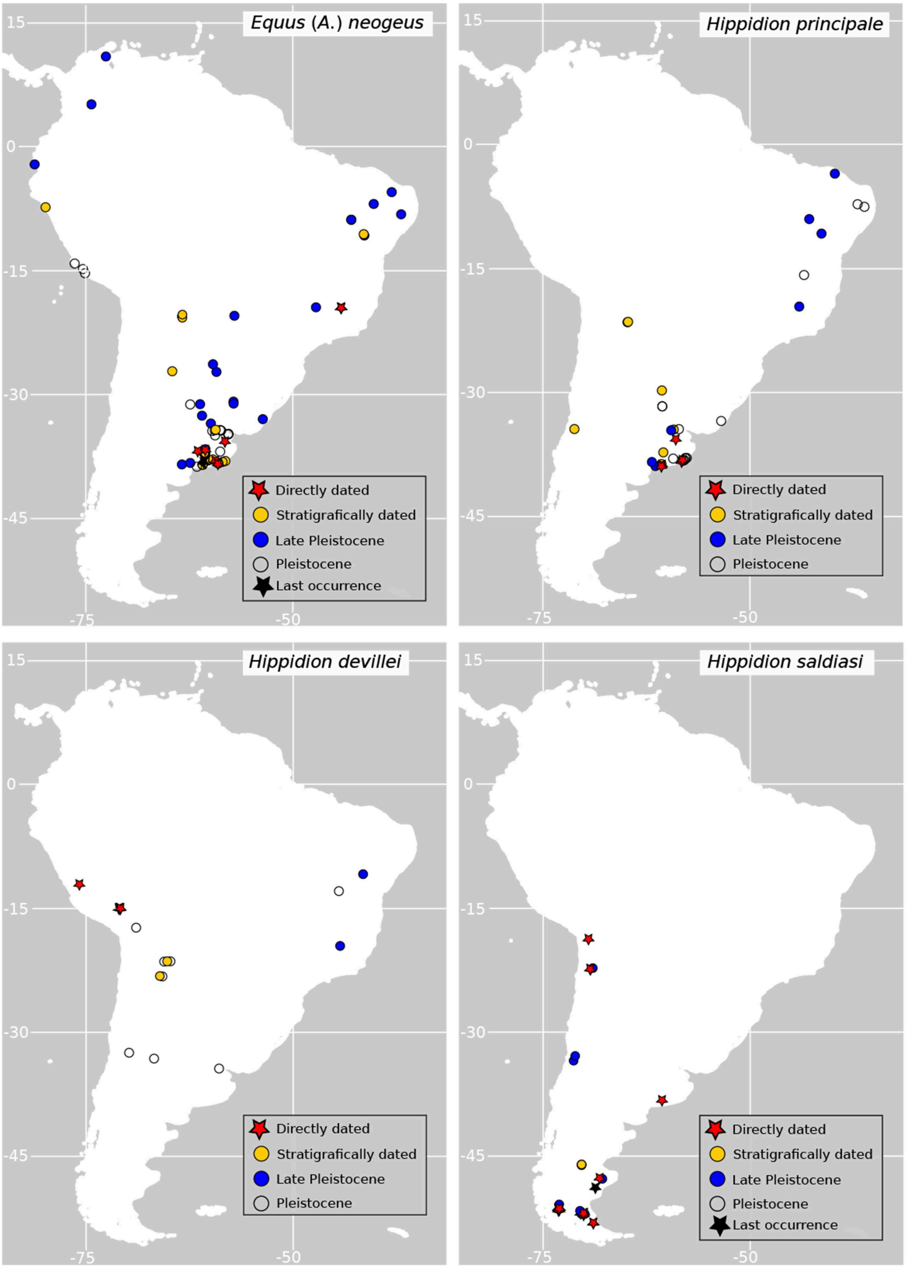

FIGURE 1 | Geographic distribution of fossil records of horses used in this study. Directly dated records (red stars) are those corresponding to fossil specimens directly dated using radiocarbon dating; stratigraphically dated records (yellow dots) are those dated according to associated radiometric dates (i.e., ^{14}C, ^{234}U/^{230}Th) on sediments or other stratigraphic features; Late Pleistocene (blue dots) and Pleistocene records (empty dots) are those fossil specimens which are tentatively assigned to the Pleistocene epoch or Late Pleistocene times according to the literature.

2009), predicting the yield of crops (Hannah et al., 2013; Ramírez-Gil et al., 2018) among other applications. Niche modeling, and PSDM in particular, is a powerful tool for the study of the potential distribution (its spatial and temporal dynamics) of extinct horses in South America, which will allow us to assess the role of environmental changes in the extinction of South American horses.

2. MATERIALS AND METHODS

Occurrence data of the species of *Hippidion* and *Equus* was compiled from the literature and the Paleobiology Database (https://paleobiodb.org/). The compilation consists of direct radiocarbon dates on different specimens as well as stratigraphically dated specimens. All the data was checked in the pertinent references and cleaned to avoid repetitions in the data. Only presences occurring from 21 kyr BP onwards and species with more than 5 records available were used to build the models. Even when species distribution models can be developed with a lower limit of three presences, we decided to be conservative and place a minimum of five occurrences to run the models (van Proosdij et al., 2016). Following these criteria, we were able to develop models for four taxa: *Equus neogeus* (26 presences), *Hippidion principale* (10 presences), *Hippidion devillei* (6 presences) and *Hippidion saldiasi* (23 presences). The geographic distribution of the fossil data used is presented in **Figure 1** and **Data Sheet 1**, along with occurrences assigned tentatively to the late Pleistocene and the Pleistocene in the literature. Most of the occurrences used are assigned in the literature to the species level. Just three occurrences for *Hippidion saldiasi* are assigned to the species level with some uncertainty. This information is specified in the **Data Sheet 1**.

2.1. Climatic Layers

We generated downscaled (2.5 min) bioclimatic layers based on the layers from the software PaleoView (Fordham et al., 2017). We use average high and low monthly temperature and average monthly precipitation represented as a difference from present conditions, and for the period from 21 kyr BP to 8 kyr BP, between the latitudes of 15 degrees north to 60 degrees south, and between longitudes 87.5 degrees west to 27.5 degrees west. These layers were then used to apply the delta method modified to consider the changes in sea level (Schmatz et al., 2015). Past sea levels were estimated from previous publications (Fleming et al., 1998; Milne et al., 2005), coupled with the Gebco database for bathymetry and topography (Weatherall et al., 2015) and using the Worldclim 1.4 as current conditions for the delta method (Hijmans et al., 2005). We used Worldclim 1.4 instead of 2.0 since version 1.4 uses 1975 as reference to calculate differences in climate, the same as Paleoview and unlike Worldclim 2.0 (Fick and Hijmans, 2017). After generating the downscaled average high and low monthly temperature and average monthly precipitation, we used the biovars function from the dismo package (Hijmans et al., 2017) to generate the 19 biolcimatic variables usually used for Species Distribution Models. We used all the bioclimatic variables to build the species distribution models following (Phillips et al., 2006; Elith et al., 2011), using the regularization method to avoid overfitting (Allouche et al., 2006; Hastie et al., 2009; Merow et al., 2013). This method allows machine learning algorithm techniques to decide which biolclimatic variables are important to model the distribution of the different species analyzed. The variable selected for each of the species we used in this study can be found in the **Supplementary Material** section.

2.2. Modeling

The Maxnet package was used to model the distributions of all species (Phillips et al., 2004, 2017; Merow et al., 2013). For each species the bioclimatic conditions of the presences in each time slice plus the bioclimatic conditions of a thousand random background points were extracted. As mentioned above, only species with more than five presences were modeled. We used 5-fold cross validation to fit the models when they had more than 10 presences a three fold cross-validation if they had 10 or less presences. After the models were fit, True Skill Statistic (henceforth TSS) was used to select the threshold criteria (Allouche et al., 2006).

In order to get a confidence interval for the size of the geographic distribution, we used the TrinaryMaps package (Merow, 2019) to get high and low confidence interval on the threshold. This method detected the areas where the sensitivity is prioritized and thus detects most of the presences giving a larger distribution (Low confidence interval), and areas where the specificity is prioritized (High Confidence Interval) which means it will detect most of the false negatives resulting in a smaller range (Merow, 2019).

The predictive capacity of the models was evaluated using AUC (Area https://www.overleaf.com/3886381414dchghrxpdvrw Under the Curve) values obtained from the ROC curves (Fawcett, 2006).

3. RESULTS

The predictive capacity of our models was high with values of AUC close to 0.9 (**Table 1**). The potential distributions for the four species analyzed here are presented as trinary maps (**Figures 2–5**, see section 2 Materials and Methods for more details) where blue represents areas of 0 probability of finding the species, white represents the potential distribution calculated using the low confidence interval (LCI, **Table 1**) of the threshold and red represents areas calculated from the high confidence interval (HCI, **Table 1**) of the threshold. These last are places with the highest probability of finding the species.

During the LGM (21 kyr BP), the predicted potential distribution of *Equus neogeus* (**Figure 2**) shows the highest probability of occurrence (red) in the Pampas region, central Chile and some very small patches in south-east Brazil and the northern Altiplano. The potential distribution estimated from the LCI (white area) shows a great potential extension of the area inhabited by *E. neogeus* covering from the Santa Cruz province in southern Argentina to the southern portion of north-east Brazil and forming a corridor to the west through central Chile. It is also present in the high Andes, going from the eastern Cordillera in Bolivia all the way north until the end of the Andean mountain range in Colombia. From the LGM through the early Holocene there is a reduction in both, areas calculated from the HCI (red) and the ones calculated from the LCI (white) of the potential distribution. Interesting is to notice that as the highly suitable

TABLE 1 | Model evaluation parameters.

Low CI	High CI	TSS threshold	AUC	Species name
0.009	0.487	0.106	0.963	*Equus neogeus*
0.001	0.169	0.017	0.974	*Hippidion devillei*
0.134	0.421	0.304	0.963	*Hippidion principale*
0.001	0.397	0.028	0.978	*Hippidion saldiasi*

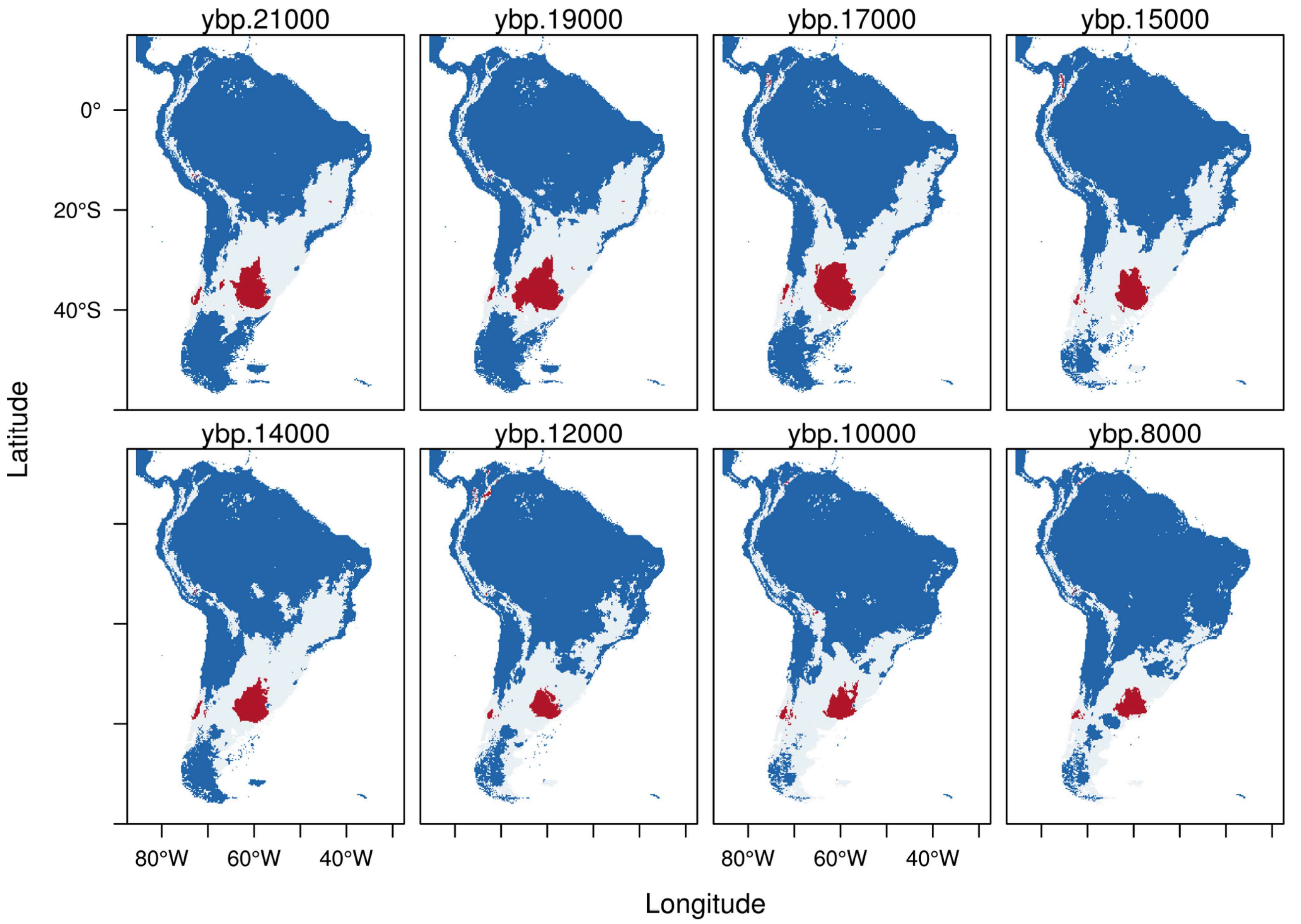

FIGURE 2 | Trinary maps showing the potential distribution of *Equus neogeus*, calculated from the Last Glacial Maximum (LGM, 21 kyr BP) to the early Holocene (8 kyr BP). The different colors represent blue: areas where *E. neogeus* is not present; white: potential distribution of *E. neogeus* calculated from the low confidence interval of the threshold and red: potential distribution of *E. neogeus* calculated from the high confidence interval of the threshold. See methods for more details.

areas of the Pampas became clearly reduced, the smaller one in central Chile persisted and some small patches became available in the Altiplano, eastern Bolivia and the northernmost portion of the Andean cordillera. At the same time, suitable environments suffer a southward shift during the early Holocene, reaching the southernmost portion of the continent in the Atlantic coast.

Hippidion principale exhibits a potential distribution mainly restricted to the southern cone during the LGM (**Figure 3**). The potential distribution estimated from HCI (red) goes from the Pampas extending south to the Santa Cruz province of Argentina. *Hippidion principale* also has an Andean distribution mostly situated in the high and western side of the Andes from north to south Chile. Further, between 17-15 kyr BP the model predicts the existence of a large pocket of potential area of distribution in the Amazon basin, which becomes an area of high probability of presence for *H. principale*. As we approach the transition to the Holocene, the potential distribution of *H. principale* becomes reduced and more displaced to the southern portion of the continent, as well as more fragmented. During the early Holocene, the remaining area of potential distribution estimated from the HCI (red) of the model calculations is located in the Pampas and extended to the adjacent western Andes. Some small portion remain in Southern Brazil and Southern Chile.

Hippidion devillei and *H. saldiasi* exhibit a small potential distribution during the time lapse analyzed, especially when we only consider the areas calculated from the HCI denoted in red (**Figures 4**, **5**).

Hippidion devillei (**Figure 4**) during the LGM presents a fragmented distribution which includes a small portion of central Argentina and patches located in the Altiplano and central Peru. Some areas of the Amazon basin and south east Brazil are also assigned as places of potential distribution (red). All of these areas became reduced as we approach the Holocene and the last remnants that persist until 8 kyr BP are some patches in the Altiplano and in western Brazil.

Hippidion saldiasi (**Figure 5**) during the LGM has a potential distribution calculated from the LCI (white) located in the southern portion of the continent from Tierra del Fuego, covering all Argentina, central and northern Chile, and extending in the high Andes as far as northern Ecuador. There are very few

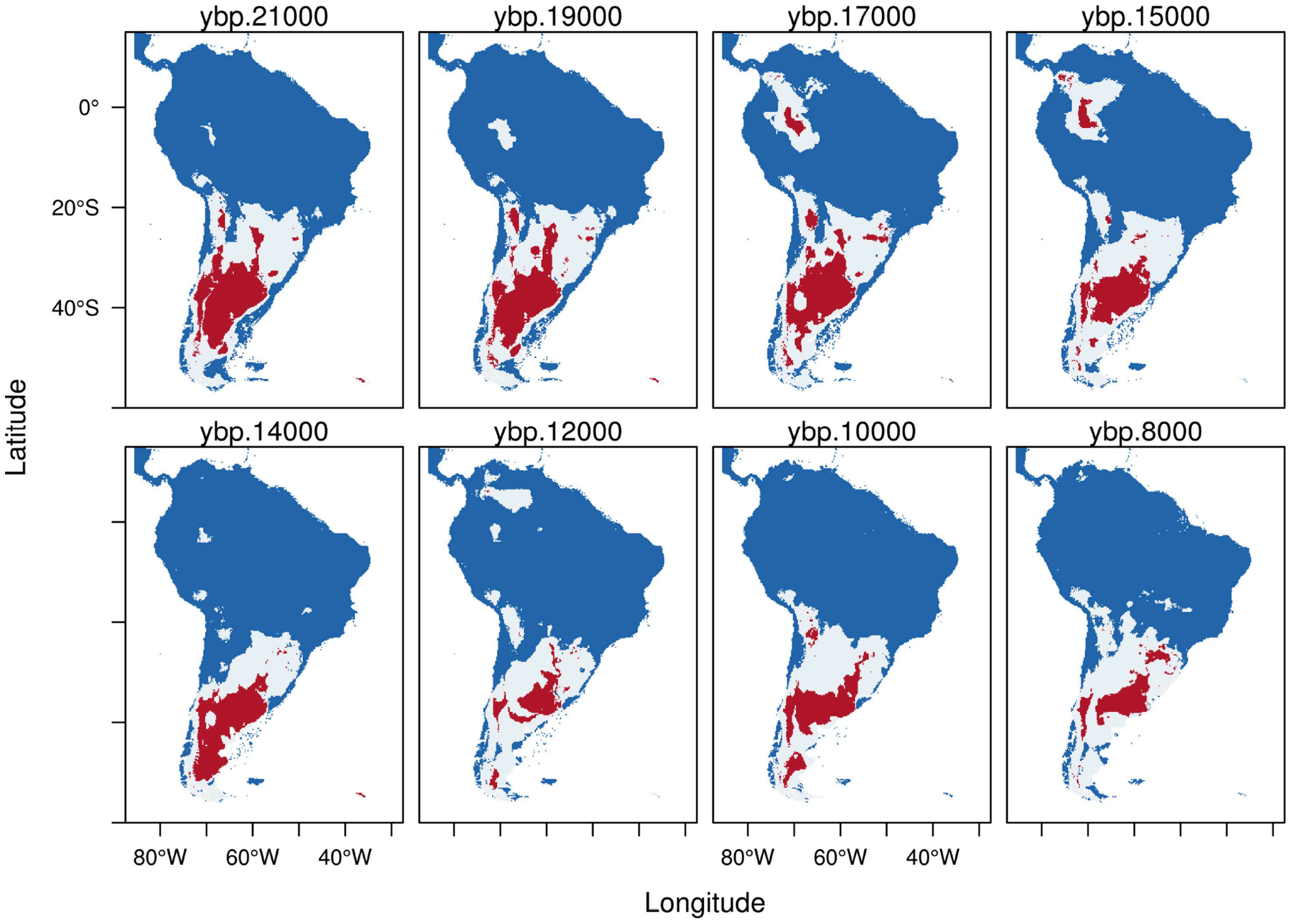

FIGURE 3 | Trinary maps showing the potential distribution of *Hippidion principale*, calculated from the Last Glacial Maximum (LGM, 21 kyr BP) to the early Holocene (8 kyr BP). The different colors represent blue: areas where *H. principale* is not present; white: potential distribution of *H. principale* calculated from the low confidence interval of the threshold and red: potential distribution of *H. principale* calculated from the high confidence interval of the threshold. See methods for more details.

areas of potential distribution estimated from the HCI during the LGM, which becomes bigger after about 16 kyr BP in southern Patagonia, reaching its highest extension between 13 and 11 kyr BP. While the rest of the potential area of distribution (white) becomes smaller as we approach the early Holocene, the areas of potential distribution estimated from the HCI (red) persist up to 8 kyr BP in the southern portion of the continent.

The dynamics of the potential area of distribution (in km^2) calculated for the four different taxa using the TSS threshold through time is shown in **Figure 6**. *Equus neogeus* and *Hippidion principale* are the ones with the broadest distribution during the LGM with an estimated area close to 2.7 million km^2 for both of these taxa, while *H. saldiasi* potentially occupied an area of 1.4 million km^2 and *H. devillei* an area 7.9 thousand km^2. For all species there is a reduction in the potential areas of occupancy through time, and by 8 kyr BP *Equus neogeus* has lost a 61% of its potential area of distribution, *H. principale* a 36%, *H. devillei* a 55%, and *H. saldiasi* a 35%.

The diversity of horses at different times is shown in **Figure 7**. From the LGM to 14 kyr BP, it is possible to observe areas in central Argentina and the Pampas where the four species of horses potentially coexisted. The potential distribution of the four species together has its greatest extension at around 18 kyr BP. After 13 kyr BP, only a small area with a diversity of three species of horses is located in the southern portion of the Pampas, which remains until the end of our analyses at 8 kyr BP. By 10 kyr BP, new potential areas with a diversity of three species appear in the Altiplano and in portions of Southern Patagonia, disappearing by 8 kyr BP. An estimation of the change in biodiversity through time was calculated by subtracting the diversity at 8 kyr BP from the one calculated at 21 kyr BP (Δ Diversity in **Figure 7**). From this analysis we can see how the diversity is reduced in areas of central Argentina, the Pampas and Central Chile while increases in the southern portion of the continent and in some areas of the high Andes, north east Argentina and south east Brazil.

4. DISCUSSION

We have shown that the potential distribution of the analyzed species drastically decreased from the late Pleistocene through

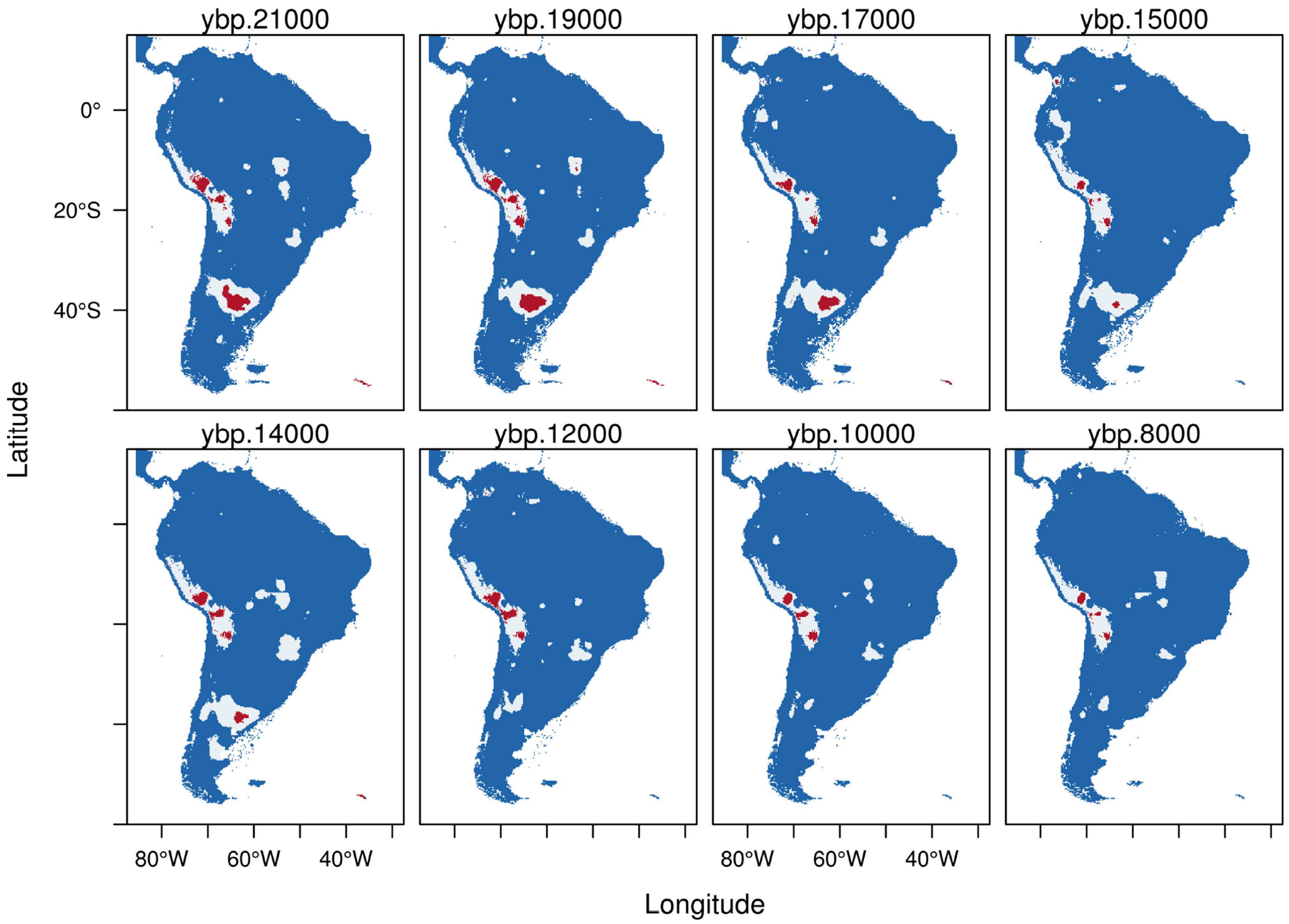

FIGURE 4 | Trinary maps showing the potential distribution of *Hippidion devillei*, calculated from the Last Glacial Maximum (LGM, 21 kyr BP) to the early Holocene (8 kyr BP). The different colors represent blue: areas where *H. devillei* is not present; white: potential distribution of *H. devillei* calculated from the low confidence interval of the threshold and red: potential distribution of *H. devillei* calculated from the high confidence interval of the threshold. See methods for more details.

the Holocene and, according to the PSDM, no one was evidently driven to extinction due to changes in climate, suggesting that climate alone is not enough to explain the extinction of these taxa.

The PSDMs presented in this work correspond to presence only climatic models which use climatic information to establish the set of abiotic conditions that determine where the modeled species potentially could be present. Since only climatic variables are considered to model the potential distribution of these taxa, this model is suitable to assess the contribution of climate in affecting the potential distribution. But other contributing factors,associated to biotic interactions, for example, cannot be ruled out.

According to the above, what is being modeled by the PSDMs could be interpreted as the fundamental niche of the species; the set of abiotic conditions that determine the area where the species potentially could be present (Soberón and Peterson, 2005). In reality, however, at least two other major drivers can impact the distribution of a species, migration and biotic interactions (Soberón and Peterson, 2005). The idea that what is being modeled is the fundamental niche, instead of the realized niche, possibly leads to an overestimation of the potential area of distribution calculated by the models (Peterson et al., 2011). However, Varela et al. (2011) suggest that, due to the low number of presences commonly available to produce paleo species distribution models, it would be more common to underestimate the potential area of distribution of a species, due to the fact that fewer recorded occurrences imply a more sparse sampling of the conditions where the species was actually present according to the fossil record. Fortunately both potential biases compensate each other. However, further analyses with a larger dataset of species and of occurrences by species are required.

In order to take into account possible over estimation and under estimation of the potential areas of distribution calculated in this study we employ the trinary maps package (Merow, 2019). With the use of trinary maps, we were able to obtain scenarios where the sensitivity was prioritized (using the LCI of the threshold) which gave larger distributions, and scenarios where the specificity was prioritized (using the HCI of the

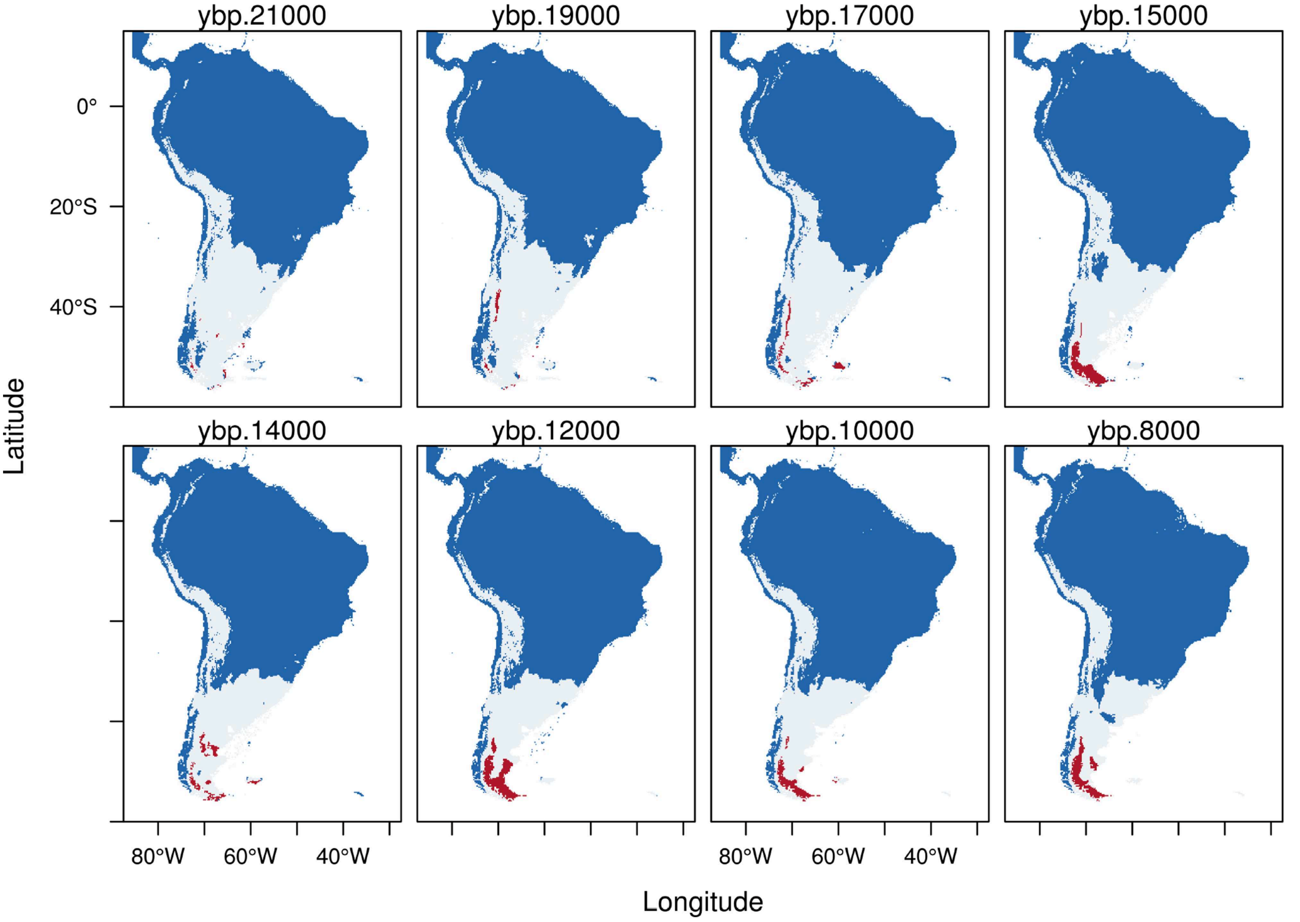

FIGURE 5 | Trinary maps showing the potential distribution of *Hippidion saldiasi*, calculated from the Last Glacial Maximum (LGM, 21 kyr BP) to the early Holocene (8 kyr BP). The different colors represent blue: areas where *H. saldiasi* is not present; white: potential distribution of *H. saldiasi* calculated from the low confidence interval of the threshold and red: potential distribution of *H. saldiasi* calculated from the high confidence interval of the threshold. See methods for more details.

threshold), which resulted in a smaller ranges. Having two scenarios is important in the case of study presented here, where taphonomic and preservation issues can introduce an important bias especially in the form of false negatives.

As it is expected in a scenario of global warming, like the one experienced during the transition from the LGM to the current interglacial, the potential distribution calculated for the late Pleistocene horses in South America became reduced in tropical and subtropical latitudes and persisted or shifted toward geographic areas where cooler conditions persisted longer. In this context, for example, the potential distribution of *E. neogeus*, which initially extended toward north-east Brazil, appears to be more shifted toward Patagonia and persistent in the high part of the Andes at 8 kyr BP (**Figure 2**). *Hippidion devillei*, which exhibits a small potential distribution during the LGM in the Pampas and the high Andes, persisted only in the last one at 8 kyr BP and disappeared from more tropical latitudes (**Figure 4**). Along this same line of argument, less evident are the changes observed for the distribution of *H. principale* and *H. saldiasi* as none of them experienced great shifts in the entire range of its potential distribution (**Figures 3**, **5**). One main observation that can be drawn however, is that by the last time slice of our analysis only the areas located in the southernmost part of the calculated distributions and in the high Andes persisted.

Changes in diversity from the LGM to the early Holocene show a significant reduction in biodiversity in subtropical and tropical areas and an increase in Patagonia and some high Andean places, which also reflects a preference toward the areas of the continent where cooler conditions persisted longer (**Figure 7**, Δ Diversity).

It is important to acknowledge that the displacement and the changes in size of the potential distribution of horses could be related to more variables than just temperature (see **Supplementary Material**). In this sense, vegetation changes that were happening all over the continent during the Pleistocene Holocene transition could have had an important role in driving some of the changes in distribution observed in this study. These vegetation re-configurations, in turn, are ultimately related to changes in precipitation and temperature patterns.

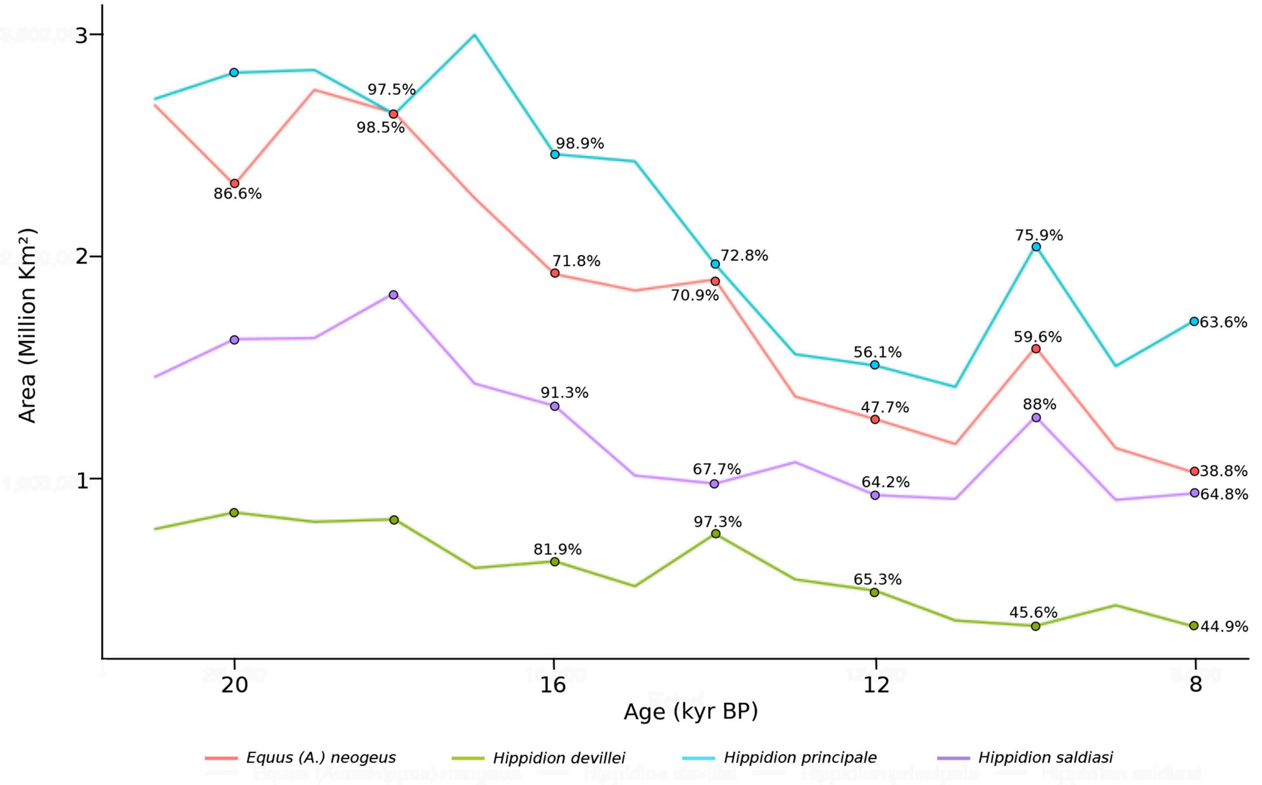

FIGURE 6 | Estimated potential area (km^2) of *Equus (Amerhippus) neogeus*, *Hippidion principale*, *Hippidion devillei* and *Hippidion saldiasi*, calculated from the LGM (21 kyr BP) to the early Holocene (8 kyr BP), every 1,000 yr interval. Percentage from the initial area calculated at 21 kyr are indicated at 20, 18, 16, 14, 12, 10, and 8 kyr BP. Percentages representing more area than the initial area omitted. This values are calculated from the TSS estimation. For the other values, see **Data Sheet 2**.

4.1. Potential Distribution and Ecological Preferences of South American Horses

The potential distribution calculated for *Equus neogeus* during the LGM included areas with grassland steppe and temperate semi-deserts in the Pampas and more tropical savanna environments in east Brazil, as some environmental reconstructions suggest for this time (Ray and Adams, 2001; de Melo França et al., 2015). This observation does not contradict what is known about the diet and the environments inhabited by *E. neogeus* derived from stable isotopes studies, which suggest the occupancy and consumption of plants from the entire spectrum of C3 plants, C4 plants, and mixed C3-C4 diet (Prado and Alberdi, 2017 and references there). *Hippidion principale* would have occupied areas of grasslands and temperate deserts according to the potential distribution calculated by our models and the vegetation reconstructions for the continent during the LGM (Ray and Adams, 2001; de Melo França et al., 2015). In the case of *H. devillei* and *H. saldiasi*, their potential distribution indicates they occupied areas with temperate deserts and semi-deserts during the LGM, as well as colder areas in the high Andes and in the southern tip of the continent (Ray and Adams, 2001; de Melo França et al., 2015). This agrees with the results from stable isotope analyses showing that all species in the genus *Hippidion* during the Pleistocene preferred woodlands or C3 wooded open areas, with a diet of C3 plants or C4-C3 mixed [Prado and Alberdi (2017) and references there].

The area with the highest diversity of horses during the LGM is the Pampas (**Figure 7**). End Pleistocene Pampas was a C3- dominated grassland steppe, representing a sub-humid and arid environment which changed, starting at 12 kyr BP, to a major proportion of C4 vegetation, as the climate became more humid and warmer (Prieto, 1996; Iriarte, 2006; Suárez, 2011). These changes would have been negative for the species of *Hippidion* in the area given their habitat preferences discussed above. Accordingly, the timing of changes in vegetation coincides with a major reduction in the potential distribution of *Hippidion principale* between 13 and 12 kyr BP in the area (**Figure 3**) and with the timing of a drop in biodiversity in the area from four to three species of horses at around 12 kyr BP (**Figure 7**).

4.2. Area of Potential Distribution: Body Size and Extinction Risk

It is interesting to notice that the species of horses with the greater calculated area of occupancy (**Figure 6**) are the ones with greater body size. *Hippidion principale*, with an estimated body size of 460 kg (Alberdi et al., 1995) and *Equus neogeus* with a body size of 370 kg (Prado and Alberdi, 1994) had a potential area of distribution of around 2.7 million km^2. On the other

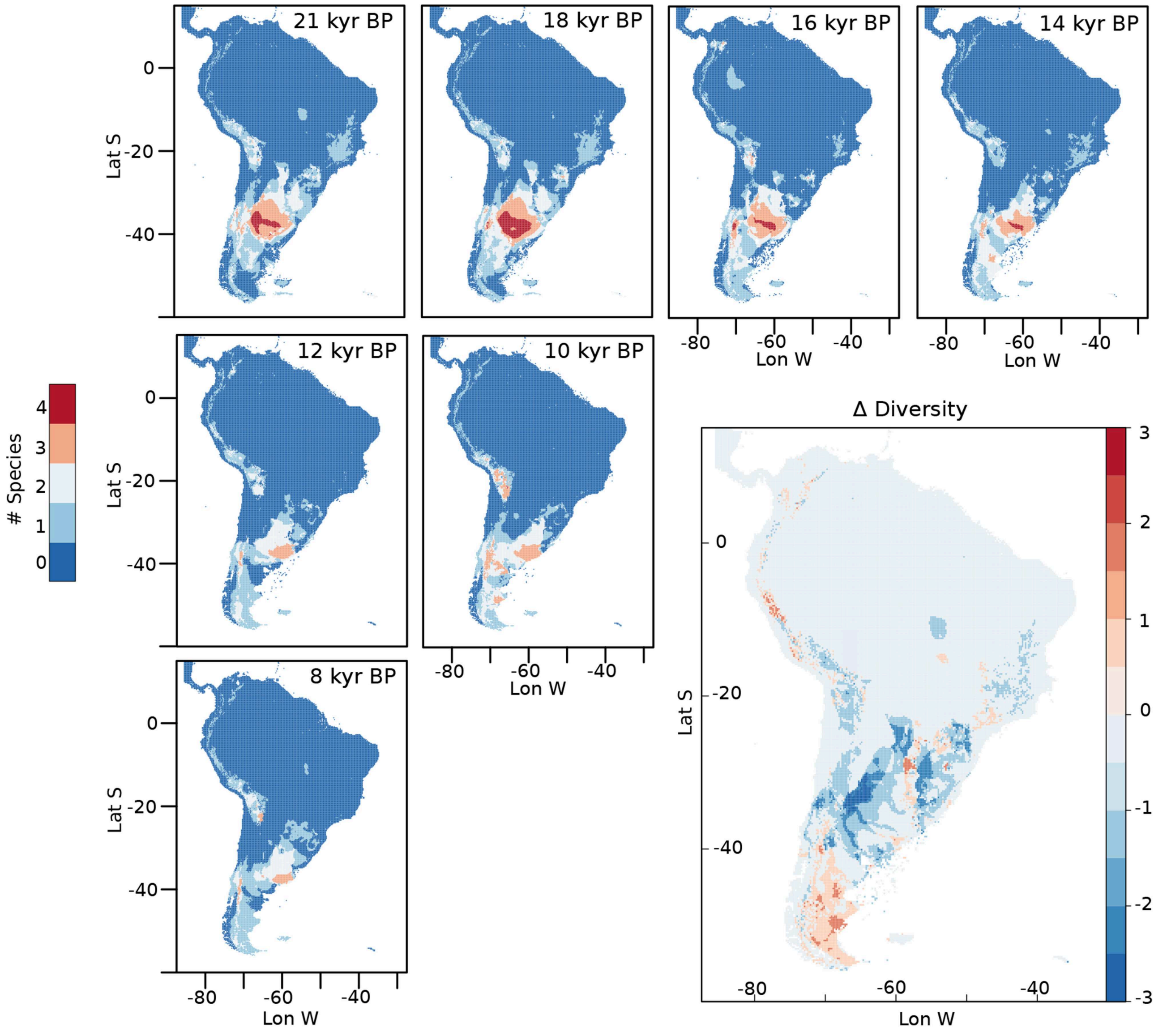

FIGURE 7 | Diversity calculated for different moments from the LGM to 8 kyr BP. Delta diversity was calculated by subtracting the summed diversity at 8 kyr BP from the one calculated at 21 kyr BP.

hand, the smallest species *Hippidion devillei* (250 kg, Alberdi et al., 1995), has the most reduced potential area of distribution with an estimate of around 793 thousand km^2 during the LGM. *Hippidion saldiasi*, with an estimated body size of 265 kg (Alberdi et al., 1995), has a potential area of occupancy of 1.4 million km^2.

All taxa of horses analyzed here experienced a significant reduction in the area of potential occupation according to the information in **Figure 6**. *E. neogeus* experienced the greatest reduction losing 61% of its distribution from the LGM to 8 kyr BP. According to the radiocarbon chronology for this taxon, it disappears from the record of South America at around 11.7 kyr BP (Rio Quequen Salado, Argentina, Prado et al., 2015), a time that coincides with a reduction of its potential area of distribution by half. This last appearance date (black star, **Figure 1**) is located in the area calculated for the distribution of *Equus neogeus* at 12 kyr BP (red, **Figure 2**). Something slightly different is observed for *H. saldiasi*. The greatest reduction of the potential area of distribution for this taxon occurs at 9 kyr BP and corresponds to a

TABLE 2 | Minimum Viable Area (MVA).

Species name	Mass (kg)	Home range (km^2)	MVA (km^2)
E. neogeus	370	11.33	49330.82
H. principale	460	14.14	61565.56
H. saldiasi	265	8.06	35093.24
H. devillei	250	7.59	33046.86

loss of a 37% of the area calculated. This result could suggest that the potential area of distribution of *H. saldiasi* was less affected by the climatic changes of the late glacial and early Holocene when compared to *E. neogeus*, for example. Interestingly, the radiocarbon record for *H. saldiasi* shows the last appearance date close to 10 kyr BP (Cerro Bombero, Argentina, Paunero et al., 2008), being the last horse species becoming extinct in the continent according to the information available at the moment.

Hippidion devillei and *H. principale* had the greatest reduction in their potential distribution at 11 kyr BP, with a reduction of 51% and 47%, respectively. The radiocarbon record for these two taxa shows last appearance dates of 12.8 kyr BP and 15.3 kyr BP, respectively, however, it is still scarce in terms of the total number of dates to make conclusions about the timing of extinction of these horses.

A deeper analysis about the impact that a reduction in the potential area of occupancy from the LGM to the early Holocene was performed.To begin with, we calculated the minimum area needed to have a population of horses that could persist in time and compare that calculation with the potential areas of occupancy estimated from the PSDM (**Figure 6**). We used the following information: there is evidence that for mammals, the number of individuals that can inhabit in a certain area is affected by body size (Marquet and Taper, 1998) and that the minimum viable population for ungulates in natural conditions is 4,354 individuals (calculated using the information and methods provided in Traill et al., 2007). We used the estimations for body size available in the literature (first paragraph, section 4.2) to determine the home range needed for each of the different species of horses knowing that home range scales positively with body size (Lindstedt et al., 1986). Following the work carried out by Marquet and Taper (1998) on body size and extinction risk of mammalian species in islands, we then multiplied these home range values by the minimum viable population size (4,354 individuals) to finally calculate the minimum viable area (MVA) for each taxon. The results of these calculations are in **Table 2**. From the values presented there and the ones from **Figure 6** we can conclude that by 8 kyr BP *E. neogeus* has an estimated area of occupancy 20.3 times larger that its MVA, *H. devillei* 9.5 times its MVA, *H. principale* close to 29.4 times its MVA, and *H. saldiasi* 31.8 times it MVA. A more conservative approach was to calculate MVAs using only the potential areas of distribution

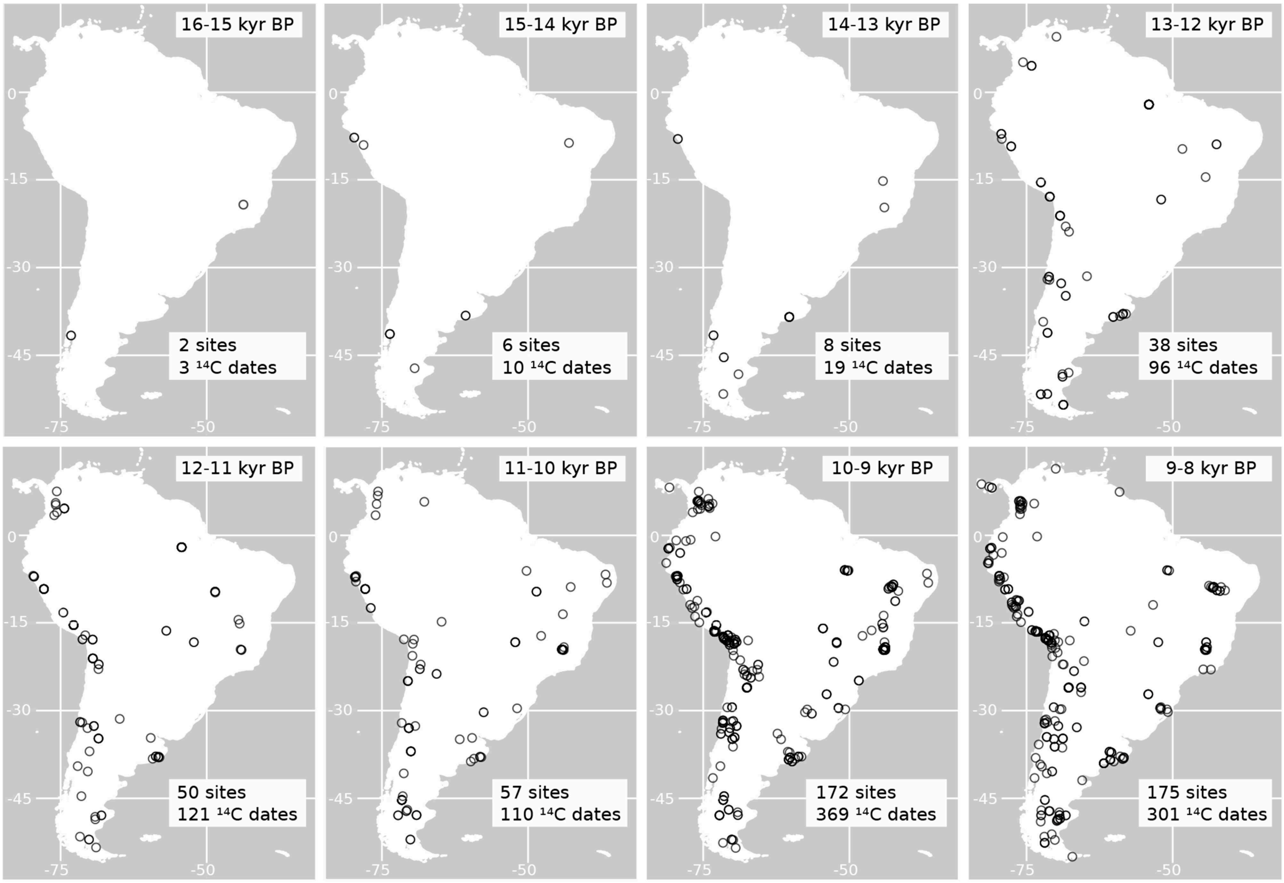

FIGURE 8 | Maps of the geographic distribution of radiocarbon dates on archaeological sites indicating the presence of humans in South America. The number of archaeological sites and radiocarbon dates graphed per time bin are indicated in each map. All dates were calibrated using Calib 7.02 and the calibration curve SH13 (Hogg et al., 2013). Dates where obtained from the databases published by Gayo et al. (2015) and Goldberg et al. (2016).

calculated from the high confidence interval from the trinary maps, which in turn results in smaller potential areas. Also, we left out every contiguous patch of area that was smaller than the calculated MVA for the different species. As a result, by 8 kyr BP, *E. neogeus* has an occupancy area 6.18 times its MVA, *H. devillei* one 1.08 times its MVA, *H. principale* an area 15.1 times its MVA, and *H. saldiasi* an estimated area of occupancy 6.83 times the MVA needed for its survival. This conservative scenario leaves *H. devillei* as the only species under a very high risk of extinction under these conditions. In summary, all these calculations suggest that the inferred climate-driven changes in the potential distribution of horses are not sufficient to explain the extinction of these taxa at the end of the Pleistocene in South America, thus other causes to explain their extinction should be invoked.

In **Figure 8** is shown the distribution of radiocarbon dates on archaeological sites from the time of human arrival into South America at around 16 kyr (Monte Verde, Chile, in Dillehay, 1997) to the early Holocene. As shown in this figure, from the time of colonization, there is a constant increase in the estimated number of sites and radiocarbon dates recording the presence of people in the continent. At the same time, from the time interval between 13 and 12 kyr BP, the presence of humans is evident in most of the regions in the continent, which could have led to an increase in human impacts in the main different ecosystems of South America. Some of these ecosystems may have been particularly more vulnerable to human impacts as well (Pires et al., 2015). Comparing these observations with the changes in the potential distribution of horses we can see, for example, that reductions close to a 50% of the potential area occupied by *E. neogeus* and *H. principale* happened around 13 kyr BP, a time when humans where already present in almost every environment (**Figure 8**). The major increase in the number of sites with evidence of humans is recorded between 10-9 kyr BP, time at which all the horse species studied had already experienced a major reduction in their potential distribution.

5. CONCLUSIONS

According to the models presented here, there is an evident reduction in the potential distribution of the four species of horses from the LGM to 8 kyr BP in South America. In general, the reduction in the size of the areas of potential distribution is accompanied by a shift in the location of the estimated distribution toward southern latitudes and higher altitudes where cooler conditions persisted longer compared to tropical and subtropical latitudes. The changes in diversity of horses follow the same pattern of shifts toward areas of cooler conditions at the beginning of the Holocene, experiencing a decrease in the number of horse taxa in tropical and subtropical latitudes and an increase in the number of species in the high Andes and Patagonia when we compare the LGM diversity with the one calculated at 8 kyr BP.

It is possible to suggest an increasing extinction risk through time for the species of horses studied as we noticed major reductions, between a 50% and 37%, of the potential area of distribution when we compared the LGM to the time slice at 8 kyr BP.

An important statement to make is that, even if there are major reductions in the potential areas of distribution from the LGM toward the early Holocene according to the PSDM, these do not reach levels indicating high extinction risks, suggesting that climate change, alone, is not able to explain the extinction of late Pleistocene horses in South America but for one species (*Hippidion devillei*). In this line of argument is important to recall that the reductions in area happened at times when humans where already present in most of the environments of the continent with increasing presence (and maybe impacts) in the landscape. This opens once more the possibility of synergistic effects between humans and environmental changes in driving some of the late Quaternary extinctions in South America.

DATA AVAILABILITY

The datasets for this study can be found in the **Supplementary Material**.

AUTHOR CONTRIBUTIONS

NV: conceived original idea, data gathering, data analysis, discussion, and manuscript preparation. DC: data gathering, data analysis, discussion, and manuscript preparation. PM: data analysis, discussion, and manuscript preparation.

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SUPPLEMENTARY MATERIAL

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The Diversity of South American *Equus*: Did Size Really Matter?

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The extant horse genus *Equus* originated in North America, probably during the late Miocene/early Pliocene, and its entrance into South America was possibly related to one of the last four stages of the Great American Biotic Interchange. Nonetheless, the genus had a broad geographic distribution throughout South America. Five species of *Equus* were traditionally recognized on this continent, although recently they have been synonymized into three: *Equus neogeus*, *E. insulatus*, and *E. andium*. However, the diagnoses of the three species are still unclear and a recent study showed that the characters previously used are not taxonomically valid, with the implication that in South America, *Equus* was represented by a single species, *E. neogeus*. This contribution is intended to update current knowledge on the diversity of South American *Equus*. Accordingly, a synthesis of prior knowledge as well as an update on the fossil distribution of *Equus* is presented here. Dental analyses were carried out, and the results revealed a clear overlap among the currently recognized species. Characters of the autopodia were also reanalyzed with greater sampling, and the results once again confirmed that a single species was present in South America. The update of fossil occurrences increased knowledge of the geographical distribution of the genus in South America. There are records throughout almost the entire continent, except for regions in the Amazonian rain forest, at latitudes south of 40°S, and at altitudes above 3,000 m. Furthermore, evaluating the new data with reference to geography revealed that *E. neogeus* formed a smooth cline, in which variation was gradual and continuous. It is also inferred that observed phenotypic variation is probably related to topography.

Keywords: ***Equus*, South America, autopodia, paleobiogeography, cline**

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INTRODUCTION

The genus *Equus* originated during the Early-Middle Pliocene in North America, probably in the Blancan North American Land Mammal Age (NALMA), but it was during the Pleistocene that the group reached its widest geographical range, with records on all continents except Antarctica and Australia (MacFadden, 1994; Eisenberg and Redford, 1999; Alberdi and Prado, 2004; Prado and Alberdi, 2017). However, very recently the genus *Equus* was retricted to its traditional crown-group, which included only the diversity from the early Pleistocene to the Recent (Barron-Ortiz et al., in press). Currently the genus is restricted to Eurasia and Africa, and its extinction in the Americas is probably related to negative selection against the megafauna at the end of the Pleistocene and the beginning of the Holocene (MacFadden, 1994).

The invasion of *Equus* into South America was possibly related to one of the dispersion events of the Great American Biotic Interchange (GABI) which occurred from the end of Pliocene to the terminal Pleistocene (Webb, 1978; MacFadden, 1994; Woodburne, 2010; Bacon et al., 2016).

Nonetheless, the genus had a widespread distribution throughout South America and survived into the Late Pleistocene (MacFadden and Azzaroli, 1987; Alberdi and Prado, 2004; Prado and Alberdi, 2017). Traditionally, five species have been recognized on this continent (Prado and Alberdi, 1994; Alberdi and Prado, 2004), but recently the number has been reduced to three: *Equus neogeus*, *E. insulatus*, and *E. andium* (Prado and Alberdi, 2017). However, Machado et al. (2018) suggested the possibility that South America might have had only a single species of native *Equus*, namely *E. neogeus*.

The traditional taxonomy of South American *Equus* has always relied on the length of the autopodium, which was considered to be greatest *E. neogeus*, smallest in *E. andium*, and intermediate in *E. insulatus* (Prado and Alberdi, 2017). Owing to the difficulty of finding taxonomically significant differences in qualitative dental characters, the current taxonomy of South American *Equus* also relies on tooth proportions (Prado and Alberdi, 1994, 2017; Alberdi and Prado, 2004). However, dental analyses alone have been unable to fully distinguish between the putative species, instead identifying a group with smaller teeth dimensions corresponding to *E. andium* and a larger group encompassing the other species (Prado and Alberdi, 1994, 2017; Alberdi and Prado, 2004).

No clear, objective and certain basis for distinguishing between the three species has been established and Machado et al. (2018) and Machado (2018) showed that the characters used previously are not taxonomically valid. Furthermore, when a larger dataset is analyzed, there is a great overlap among all three *Equus* species in morphospace (Machado, 2018; Machado et al., 2018). The most plausible interpretation is that *Equus* was probably represented in South America by only a single species, *E. neogeus*. Morphological variation in autopodia, perhaps representing a type of cline, might then be expected.

The aim of this contribution is to critically update current knowledge of the diversity of South American native *Equus*. An historical background is presented, mainly in order to establish when the paradigm of the importance of size for the taxonomy of South American native *Equus* was assumed and why it must be forsaken. Additionally, tooth analyses are performed, autopodial characters are reanalyzed with greater sampling and new inferences are drawn.

MATERIALS AND METHODS

The historical background of South American *Equus* studies presented here is a compilation from a detailed survey of the literature, beginning with the first record of the genus in South America (Owen, 1840).

The tooth analyses incorporated 1,409 dental specimens of South American *Equus*, including (lower and upper) molars and premolars at an intermediate wear stage (Solounias and Semprebon, 2002). Dental elements were analyzed both qualitatively and quantitatively, using data acquired with digital calipers with 0.01 mm precision, following the recommendations of Eisenmann et al. (1988), **Figure 1**. We relied on photos for information on 144 out of the 1,409 specimens analyzed, and in these cases we followed the procedures of Mariano and Romano (2017) and took measurements using ImageJ (Rasband, 1997).

When dealing with isolated *Equus* teeth, only the second premolar (P2/p2) and the last molar (M3/m3) are easily identified (Eisenmann et al., 1988). Since most of this sample analysis relied on isolated teeth, upper and lower cheek teeth were divided into three categories: P2/p2; M3/m3; and P3, P4, M1, M2/p3, p4, m1, and m2.

Bivariate and multivariate analyses were performed. The bivariate analysis was carried out on the tooth measurements that are more related to the dimensions of occlusal surface and was run in Microsoft Excel (2010 version). Multivariate analyses included PCA and CVA, and for the PCA the problem of missing data was handled by the Iterative Imputation method (Hammer, 2012; Machado et al., 2018).

The methodology used in the autopodial analysis took into consideration the latest proposition of Prado and Alberdi (2017) and followed the methods and reasoning of Machado et al. (2018). We analyzed 29 metatarsi (MTIII), 33 metacarpi (MCIII) and 54 first phalanges (IPHIII) of *E. andium*; 53 MTIII, 47 MCIII, and 70 IPHIII of *E. insulatus*; and 20 MTIII, 14 MCIII, and 28 IPHIII of *E. neogeus*. Since the North American *E. occidentalis* used to be included in the same subgenus as the South American *Equus* (Hoffstetter, 1950), the northern species was used here as a control group and 32 MTIII, 40 MCIII and 56 IPHIII of *E. occidentalis* from Rancho La Brea, California were also analyzed.

Comparative morphological, morphometric and statistical analyses were performed, using measurements taken according to the recommendations of Eisenmann et al. (1988, **Figure 1**) with digital calipers with 0.01 mm precision.

The bivariate analyses were performed in Microsoft Excel (2010 version), based on the dimensions of the autopodial elements as captured by measurements 1, 3, and 4 of MTIII and MCIII, and measurements 1, 3, and 5 of IPHIII. The PCA and CVA were based on all the measurements recommended by Eisenmann et al. (1988), but measurements 10, 11, 12, and 13 of IPHIII were omitted due to the difficulty of distinguishing between some examples of this bone as being left or right. All analyses were performed in Past version 3.16 (Hammer, 2012).

The statistical analysis consisted of a variance analysis using the non-parametric Kruskal-Wallis test, with Dunn's method as a *post-hoc* test, and was executed in BioEstat 5 (Ayres et al., 2007). The only measurements used in this analysis were those related to the Gracility Index (Alberdi and Prado, 2004) and to the biomechanical properties of the distal limb bones measurements 1, 3, 4, 5, and 10 of MTIII and MCIII, and measurements 1, 3, 5, 7, and 8 of IPHIII (Machado et al., 2018).

All the specimens represent adult individuals and are deposited in the paleontological collections of the following institutions: Museu Nacional (MN) and Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCL), Brazil; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-Pv) and Museo de La Plata (MLP), Argentina; Museo de Historia Natural "Gustavo Orcés V" (V and MECN), Ecuador; Museo Nacional Paleontología y Arquiología de Tarija (TAR), Bolivia; Museo de Historia Natural (UNMSM), Peru; Museo de Ciencias Naturales Federico Carlos

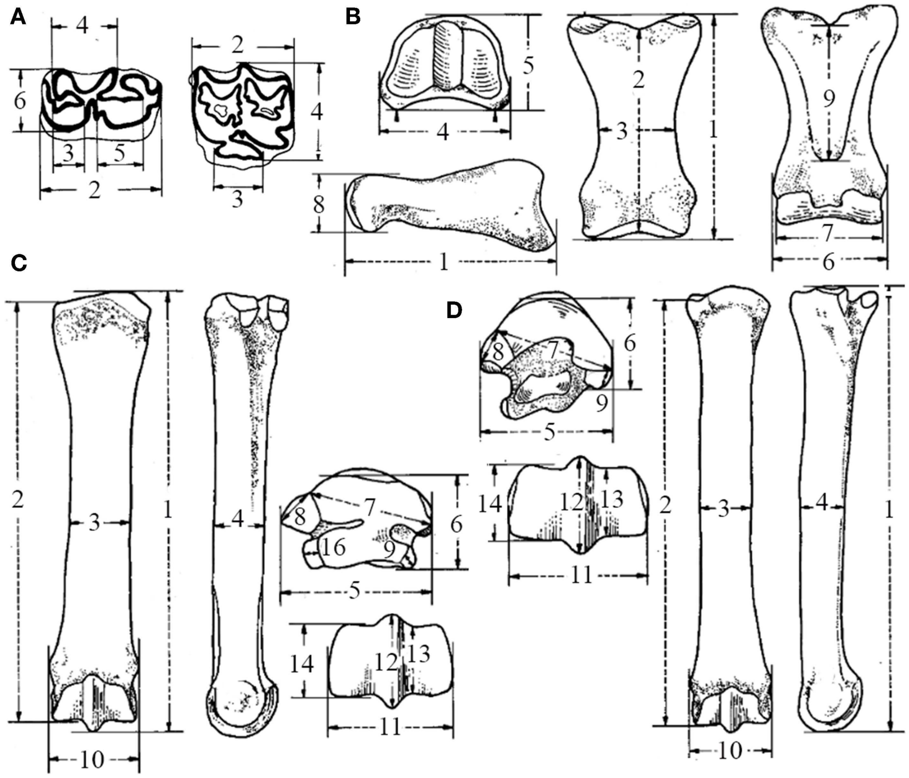

FIGURE 1 | Dimensions used for teeth and autopodial analyses, according to the *Hipparion* Conference (Modified from Eisenmann et al., 1988): **(A)** Lower dentition (left) (2) occlusal length, (3) length of the preflexid, (4) length of the double-knot, (5) length of the postflexid, (6) maximal width; upper dentition (right) (2) occlusal length, (3) occlusal length of the protocone, (4) occlusal width; **(B)** IPHIII (2) anterior length, (3) minimal breadth, (4) proximal breadth, (5) proximal depth, (6) distal breadth at the tuberosities, (7) distal articular breadth, (8) distal articular depth, (9) minimal length of the trigonum phalangis; **(C)** MCIII and **(D)** MTIII (2) medial length, (3) minimal breadth, (4) depth of the diaphysis, (5) proximal articular breadth, (6) proximal articular depth, (7) maximal diameter of the articular facet for the third tarsal/carpal, (8) diameter of the articular facet for the fourth tarsal/carpal, (9) diameter of articular facet for the second tarsal/carpal, (10) distal maximal supra-articular breadth, (11) distal maximal articular breadth, (12) distal maximal depth of the keel, (13) distal minimal depth of the lateral condyle, (14) distal minimal depth of the medial condyle, (16) diameter of the posterior facet for the fourth carpal.

Lehman, Colombia; and American Museum of Natural History (AMNH) and La Brea Tar Pits and Museum (previously the George C. Page Museum; GCPM), USA.

An updated tabulation of the distribution of fossil *Equus* in South America was made through a survey of the literature. Catalog cards from the Museo de La Plata (MLP) and Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-Pv) were also consulted as a source of information on localities where *Equus* fossils have been found, as was the catalog of fossil-types and figures from the paleo vertebrate collection of the Museu Nacional (MN).

RESULTS

Comments on the State of Knowledge of South American *Equus* Taxonomy: Did Size Really Matter?

The urgency of a new taxonomic arrangement for South American *Equus* becomes clear when its taxonomic history is reviewed. Most of the traditional taxonomy was founded on poor samples and superficial diagnoses, which mainly used differences in size to characterize the various putative species. Thus, most taxonomic revisions of South American *Equus* neglected the fact that morphological variations can reflect non-taxonomic factors, such as ontogeny, sexual dimorphism and individual/population differences, and particularly adaptation driven by exposure to different environments (lowlands vs. highlands and within distinct altitudes in the Andes). However, the taxonomic *zeitgeist* of the mid-nineteenth to mid-twentieth century favored splitting, which generated many poorly diagnosed species and resulted in a distorted view of ancient diversity. South American native *Equus* taxonomy conformed to this pattern.

The history of the taxonomy of native fossil horses in South America could not have had a more special beginning than at the hands of one of the greatest scientists of all time, Charles Darwin. The survey expedition of the *HMS Beagle* brought Darwin to the Province of Santa Fé, Central-Eastern Argentina, where he found a horse molar at the locality of Bajada de Santa Fé in October 1833 (**Figure 2A**; Lister, 2018).

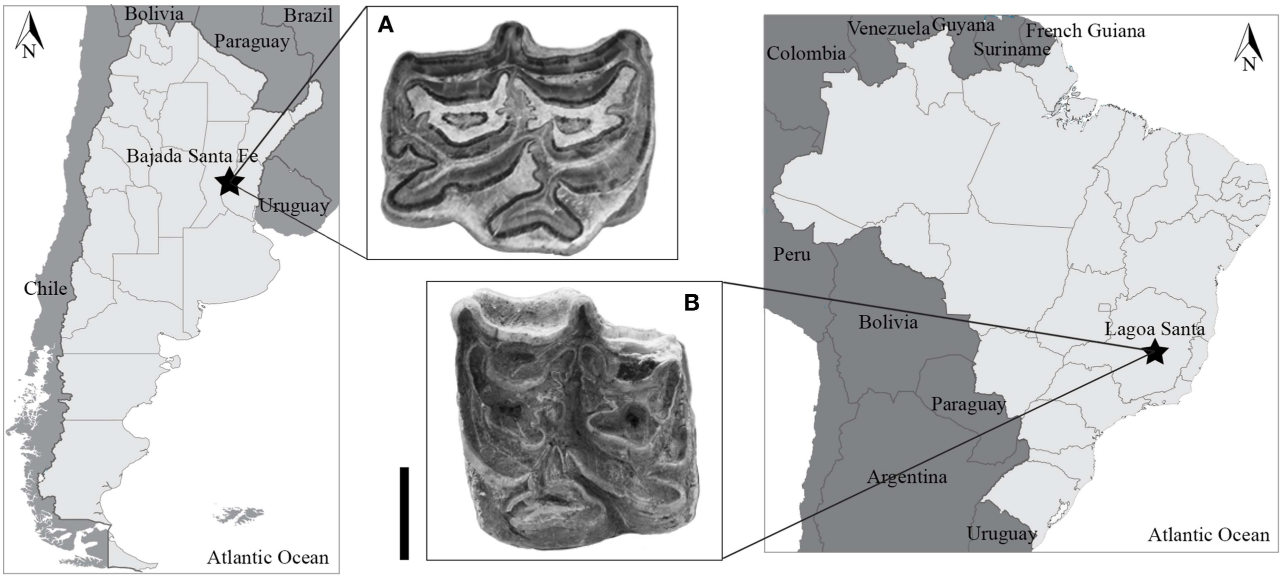

FIGURE 2 | Molars associated with the first records of *Equus* from South America: **(A)** right M2 collected by Darwin in Entre Ríos, Santa Fé (Argentina) and identified by Owen; **(B)** left M1 found in association with the holotype of *E. neogeus* in Lagoa Santa, Minas Gerais (Brazil) and used in the original description by Lund. Scale 1 cm.

Although other South American Holarctic mammals, such as proboscidean gomphotheres (Cuvier, 1806), had previously been found and published, Darwin was surprised to find a horse tooth in Argentina, and at first he thought it might be the remains of a domestic animal (Lister, 2018). After careful examination, however, he was left with no doubt that it was from a fossil horse, because he had collected it from a layer that also contained other native extinct mammals (Lister, 2018). This molar is believed to be the first fossil evidence of native horses in South America and is housed in the Natural History Museum in London (England). The fossils collected by the *Beagle* expedition were studied and first described by Richard Owen in 1838, and he considered the aforementioned horse molar to be essentially similar to those of living (domestic) horses, identifying it only as "a species of horse" (Lister, 2018; **Figure 2A**). Subsequently, Owen (1845) revisited the fossil molar and considered it to represent a new species, which was named *Equus curvidens*.

At the same time (between 1835 and 1845), the Danish explorer Peter W. Lund collected plants, animals and fossils in the region of Lagoa Santa in the State of Minas Gerais, southeastern Brazil. Lagoa Santa includes a very important Brazilian speleological province with hundreds of caves, from which numerous human and megafaunal fossils were recovered. Among these, a metacarpal fossil bone of a native horse was recognized as a previously unknown species by Lund (1840) and was named *E. neogeus* (**Figure 2B**). Although Lund misspelled its specific epithet (the correct orthography would have been "*neogaeus*," a Greek word meaning "new world"), the original spelling *Equus neogeus* must be maintained according to the International Code of Zoological Nomenclature. Later, Lund (1846) presented a list of species found in several caves at Lagoa Santa, in which the horse metacarpal appeared as *Equus* aff. *caballo* (probably a misspelling of *Equus caballus*). However, the use of this designation left open the interpretation that Lund might have been in doubt about the taxonomic validity of *Equus neogeus*. Additionally, this manuscript was among the first sources to mention the association of human and megafaunal fossils in South America, suggesting that both might have co-existed (Lund, 1846; Owen, 1869). Furthermore, Peter W. Lund left a manuscript indicating the existence of at least two more new species of *Equus* (*E. escrivanensis* and *E. soarensis*) from the Lagoa Santa caves, which were later described by Winge (1906). However, the specimens clearly represent the same species *Equus neogeus*, as noted in subsequent authors' revisions (Hoffstetter, 1950).

The French explorer Hugues A. Weddell collected and described several fossil mammals from the Tarija deposits of southern Bolivia (1845–1846; Weddel, 1851). Among those, he named an indigenous horse *Equus macrognathus*, diagnosed by a large-sized mandible. It should be noted that this author also pointed out the great resemblance of *E. macrognathus*, especially with regard to its large size, to the lowland Pampean fossil horse *E. curvidens* described by Owen (1845). Although most authors have indicated that *Equus* from the lowlands of South America (Argentina, Uruguay, and Brazil, including the Pampean region) are larger than those from Tarija (Hoffstetter, 1950; MacFadden and Azzaroli, 1987; Alberdi and Prado, 1992; Prado and Alberdi, 2017), direct comparisons of a large sample of specimens do not uphold this argument, and Machado et al. (2018) found no statistical support for a size difference in an analysis of autopodial bones of South American *Equus* from several localities representing its paleo geographical range (from the lowlands to the highlands of the Andes).

One of the most important studies of South American *Equus* taxonomy is that of Gervais (1855). This author argued that *E. macrognathus* from Andean Bolivia and *E. americanus*, *E. curvidens*, and *E. neogeus* from the lowlands of Chile, Argentina and Brazil must all represent the same species and should be synonymized by priority under the name *E. neogeus*. This is the first time that South American highland and lowland *Equus* were considered to belong to a single species, an argument defended by Machado (2018).

The first taxonomic comparisons among South, Central and North American *Equus* species were made by Owen (1869). In contrast to his French colleague, the British scientist argued that most known fossils of *Equus* recognized at that time (*E. neogeus*, *E. curvidens*, *E. conversidens*, *E. tau*, *E. macrognathus*, and *E. devillei*) represented valid, distinct species. However, most of these *Equus* species had been described by Owen himself, and his taxonomic contributions are known to have been underpinned by a taxonomic splitter approach. Accordingly, it is clear that the author's only intention was to identify morphological attributes that could distinguish (Lund's, 1840) *E. neogeus* from his own *E. curvidens* (Owen, 1845), given that Lund's name would have taxonomic priority if the two proved synonymous. However, it took more than 100 years before *E. curvidens* was formally recognized as a junior synonym of *E. neogeus* (Souza Cunha, 1971).

The second half of the nineteenth century witnessed paleontological explorations in South America that extended to the highest altitudes of the Andes. Wagner (1860) was the first to publish on a native *Equus* found on the Antiplano around Quito, Ecuador, which he recognized as a new species, *Equus fossilis andium*. Later, Branco (1883) proposed the new combination *Equus andium* for the fossils studied by Wagner (1860) and described several other specimens of *Equus andium* from diverse fossiliferous deposits in the Ecuadorian Andes.

During the second half of the nineteenth century and the beginning of the twentieth, several other new species of *Equus* were named from South America (e.g., *E. lundii* Boas, 1881, *E. argentinus* Burmeister, 1875, *E. quitensis* Wolf, 1875 and *E. rectidens* Gervais and Ameghino, 1880, *E. muñizi* Ameghino, 1904, *E. gracilis*, Ameghino, 1904, *E. insulatus* Ameghino, 1904, and *E. haasei* Reche, 1905), but this may be explained by the fact that taxonomy all around the world was dominated by a splitter approach. However, those species were very often poorly diagnosed (and sometimes lacked any diagnosis at all) and defined based only on variations in tooth morphology. Furthermore, there was a tendency among natural historians of the time to consider all morphological variations as valid taxonomic diagnostic features, neglecting that such variations can also result from ontogeny, dimorphism, and individual/population differences. In the particular case of horse teeth, many variations can arise through masticatory wear (Gromova, 1949, 1952).

As a result, most subsequent taxonomic studies on South American *Equus* were revisions of dental diagnoses of the diverse nominal species recognized in previous papers (Sefve, 1912; Boule and Thevenin, 1920; Hoffstetter, 1950, 1952; Souza Cunha, 1971; MacFadden and Azzaroli, 1987; Alberdi and Prado, 1992; Prado and Alberdi, 2017; Machado, 2018). Boule and Thevenin (1920) started their revision paper by arguing that: "… molars of horses are quite variable; and, because we did not sufficiently take into account this variability, we have multiplied to excess the names of fossil horse species." Based on this argument, these authors conducted a detailed morphological analysis, mainly considering dental features, of a very abundant sample of *Equus* from Tarija (Bolivia), named *E. insulatus* after Ameghino (1904). Thus, they demonstrated that *E. insulatus* is part of an extensive but expected range of morphological variation seen in *E. andium* (i.e., they considered the *Equus* from Tarija to be *E. andium* Branco, race *insulatus* Ameghino). Further, these authors reinforced their previous argument by saying: "There is, between the *E. andium* of Bolivia and the one that lived at a higher altitude in Ecuador, a similar size difference as exists between the extant (domestic) horses of the plain and those living in the highlands of Bolivia." Again, it was demonstrated that size distinctions within South American *Equus* from different altitudes were expected morphological variations of a single species with a wide geographic range. However, and unfortunately, most subsequent authors did not pay attention to these important arguments.

Spillman (1938) took the opposite perspective in conducting his taxonomic revision of Ecuadorian *Equus*. First, he applied the genus name *Neohippus* to these specimens (Abel, 1913), instead of *Equus*, without any justification. According to Hoffstetter (1950), the genus *Neohippus* must be considered a *nomen nudum*, because its original description neither includes a diagnosis, nor designates a genotype. Furthermore, Hoffstetter (1950) argued that *Neohippus* was a synonym of *Equus*, with the latter having taxonomic priority. However, the species of Spillman (1938) will be cited below under their original names (i.e., using the genus *Neohippus*) for historical reasons. Spillman (1938) recognized a diversity of five species, four of which were previously unknown. He recognized and diagnosed each of the species using chronostratigraphy and/or endemism (localities and altitudes) together with dental and post-cranial morphology. In this scheme, the following fossil horses would be present in Ecuador, from earliest to the most recent: *Neohippus andium*, the horse of the ancient Ice Age of Ecuador; *N. martinei* n. sp., the interglacial horse from the highlands of Ecuador; *N. santaeelenae* n. sp., the interglacial horse from the coastal region of Ecuador; *N. rivadeneirae* n. sp., the horse of the second or last main Ice Age (Last Glacial Maximum, LGM); and *N. postremus* n. sp., the post-glacial horse of Ecuador from prehistoric deposits. However, it is clear that this author did not consider the stages of tooth wear, leading to excessive taxonomic splitting, even though most of the morphological diagnoses for his new species are based on differences in dental crown morphology. Furthermore, Spillman (1938) was the first taxonomist to diagnose species of South American *Equus* using proportions and sizes of bones, a tendency seen in taxonomic treatments of the group over the following 80 years (Porta, 1960; MacFadden and Azzaroli, 1987; Alberdi and Prado, 1992; Prado and Alberdi, 2017). However, morphological variations would be expected to occur among animal populations that inhabited different environments, and in particular might have been driven by an altitudinal gradient (Avilla et al., 2018; Machado et al., 2018).

One of the most well-known taxonomic reviews for South American *Equus* was that by Hoffstetter (1950), mainly because it initiated a period of taxonomic stability lasting more than 60 years. One of the goals of Hoffstetter (1950) was to establish the genus *Amerhippus*, diagnosed by a single feature: the lack of an infundibulum in the lower incisors. This proposed genus was the result of dental comparisons between the extant *E. caballus* and the species recorded in the Pleistocene of Ecuador, *E. andium* from the highlands and *E. santaeelenae* from the lowlands (Hoffstetter, 1950). On a later and admittedly brief trip to South America, specifically to Bolivia and Argentina, Hoffstetter (1950) also recognized the lack of an infundibulum in both *E. insulatus* from the highlands and *E. curvidens* from the lowlands. The remaining South American species were analyzed according to the literature available at that time, and the lack of an infundibulum in their lower incisors was also noticeable (Hoffstetter, 1950). Therefore, *Amerhippus* was considered to include all South American *Equus* valid at that time, namely *Amerhippus andium*, *A. insulatus*, *A. martinei*, *A. curvidens*, *A. santaeelenae*, and *A. neogeus*, in addition to the North American *Equus occidentalis* from the La Brea Tar Pits, California (USA) (Hoffstetter, 1950). However, Hoffstetter (1950) did not mention or justify the exclusion of *Neohippus* (=*Equus*) *rivadeneirae* and *N. postremus*, species named by Spillman (1938), and no other study after this revision made any mention of either species. Under the taxonomy proposed by Hoffstetter (1950), the first three *Amerhippus* species listed above are, small, medium-sized and large Andean native horses, respectively, whereas the last three are very large lowland ones. However, Hoffstetter (1950) did not explicitly use size differences to distinguish among these species or provide any additional characters to diagnose those species. All revisions or taxonomic propositions after Hoffstetter (1950) followed this size-based taxonomic framework, which is why this contribution is so important for South American native *Equus* taxonomy. Moreover, Hoffstetter (1950) considered *A. andium* to be the type genus of *Amerhippus* since it was the best-known species of the putative genus at the time and was easily identifiable due to its reduced size. However, this same author in a latter monograph (Hoffstetter, 1952) proposed that *Amerhippus* was a subgenus of *Equus*, and most succeeding contributions followed this taxonomic rearrangement (MacFadden and Azzaroli, 1987; Alberdi and Prado, 2004; Prado and Alberdi, 2017; Machado et al., 2018).

In 1960, Porta studied the fossil horses from Bogotá (Colombia) and produced the first detailed description of a cranium of *E. lasallei*, a species that had been briefly described and named by Daniel (1948). However, one of the most important pieces of information overlooked in revisions of South American *Equus* until the work of Porta (1960) was not the taxonomic validity of *E. lasallei*, but the presence of two large-sized *Equus* that inhabited the Andes during the Pleistocene (specimens referred to *E. lasallei* and *E martinei*). Thus, at that moment, four size-based native horse species were recognized in the Andes: the small *E. andium*, the medium-sized *E. insulatus* and the very large *E. lasallei* and *E. martinei*.

Souza Cunha (1971) analyzed the holotypes of *E. neogeus* and *E. curvidens*, as well as several specimens assigned to each of these species, which collectively represented the first fossil horses discovered in South America. Souza Cunha (1971) also described for the first time the fossils of *E. neogeus* collected by Lund in Lagoa Santa, Minas Gerais (Brazil), which until then had been mentioned only briefly in the literature. However, the greatest contribution of Souza Cunha (1971) was to propose *E. neogeus* as a senior synonym of *E. curvidens* by priority. For the first time, all Cis-Andean (the area east of Andes) lowland native *Equus* were grouped under a single name, *E. neogeus*, leaving *E. santaeelenae* as the only lowland Trans-Andean native horse.

MacFadden and Azzaroli (1987) described the first skull of *E. insulatus*, a species that until then was known mainly from isolated teeth, post-cranial bones, and some tooth-bearing maxillae and fragmented mandibles. The authors reviewed *E. insulatus* and suggested it represented a "morphological intermediate" between the large *E. lasallei* and the small *E. andium*. Once more, size was used to define Andean native horse species. However, neither this contribution nor any subsequent taxonomic revision (Alberdi and Prado, 1992; Prado and Alberdi, 2017) made any comments (in either opposition or defense) on the arguments offered by Gervais (1855) and Boule and Thevenin (1920) in their studies of the Tarija horses, which insightfully discussed the validity of *E. insulatus* and proposed that this taxon might fall within the range of morphological variation expected in *E. andium*. Furthermore, MacFadden and Azzaroli (1987) assumed the validity of *E. insulatus* based on the features of a single skull and a few other specimens, disregarding the range of morphological variation pointed out by Gervais (1855) and Boule and Thevenin (1920). The classification of South American *Equus* recognized by MacFadden and Azzaroli (1987) is very similar to that proposed by Hoffstetter (1950, 1952), except for the inclusion of *E. lasallei* (Porta, 1960). However, MacFadden and Azzaroli (1987) appeared to ignore the study of Souza Cunha (1971) published 16 years before and considered *E. curvidens* valid without offering reasons for this judgment.

The revision by Alberdi and Prado (1992) once more used size to distinguish between South American *Equus* species but differed from previous studies in that quantitative and statistical analyses were used to determine how informative size was for this purpose. Their results supported a similar taxonomy to that proposed by MacFadden and Azzaroli (1987), combined with the synonymy proposition of Souza Cunha (1971). Accordingly, the taxonomy of South American *Equus* proposed by Alberdi and Prado (1992) included the following five species: *E. neogeus*, *E. andium*, *E. santaeelenae*, *E. insulatus* and *E lasallei*. However, Alberdi and Prado (1992) did not explain the exclusion of *Equus martinei* from their study (Spillman, 1938). There is a large sample of autopodia of *Equus martinei* in the collection of the Museo de Historia Natural in Quito, Ecuador, and it would have been helpful to include this species, the only large native horse that inhabited the highest Andean areas, in the quantitative analyses. The other large Andean *Equus* species, *E. lasallei*, was excluded from Alberdi and Prado's (1992) analyses due to a lack of preserved autopodia. Accordingly, their study and taxonomic proposals were biased in that the only large native horse to be analyzed was the lowland *E. neogeus*. During the following 12 years the literature on South American *Equus*, mostly published by Alberdi and Prado (1992, 1995, 2004); Prado and Alberdi (1994), contained no new taxonomic proposals. However, these publications did produce some taxonomic stability and a degree of consensus in how South American *Equus* species could be differentiated by their size and proportions, as follows: (1) *Equus andium* is characterized by the shortest and more robust extremities, with autopodials slightly more pronounced in length and robustness than in *E. insulatus*; (2) *E. insulatus* has a bigger skull than *E. andium*, but the two species are morphologically similar, and post-cranial skeletal features indicate that *E. insulatus* is an intermediate form between *E. andium* and *E. neogeus*; (3) *E. santaeelenae* has a larger post-cranial skeleton than *E. andium,* phalanges that are similar in size to those of *E. neogeus* but slightly more robust than *E. neogeus*, and a metatarsus that more closely resembles that of *E. insulatus*; (4) *E. neogeus* has larger autopodials than the others, and a dental morphology distinct from that of *E. santaeelenae*; and (5) *E. lasallei* is also large, but is similar in dental morphology to *E. neogeus*. In most cases, however, these criteria could not be successfully applied, because when a great sample of specimens was analyzed, there was a clear pattern of overlap between the species (Alberdi and Frassineti, 2000; Machado et al., 2018). In a revision of Chilean native horse fossils by Alberdi and Frassineti (2000), for example, only two specimens of *Equus* could be identified at specific level, both

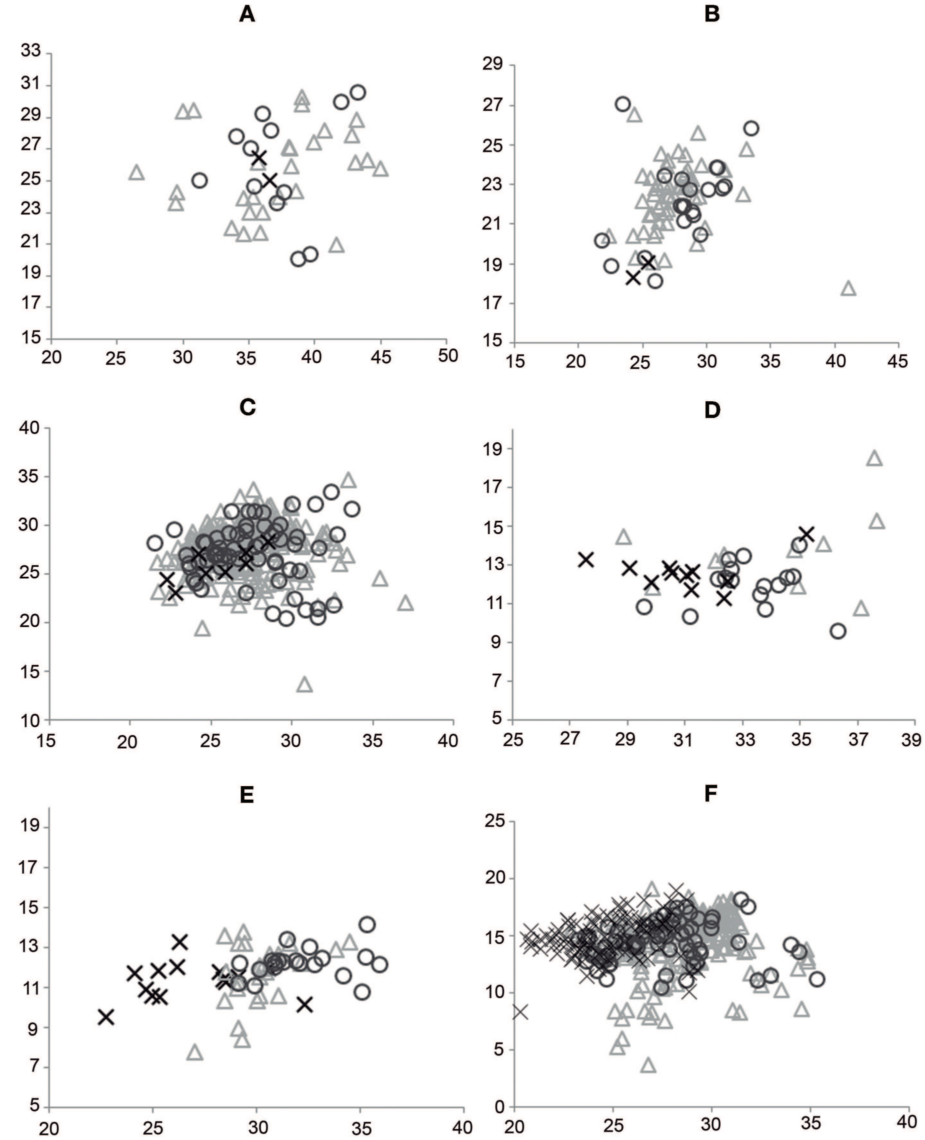

FIGURE 3 | Bivariate analysis of dimensions 2 vs. 4 of P2 **(A)**, M3 **(B)**, and P3, P4, M1, and M2 **(C)**, and dimensions 2 vs. 6 of p2 **(D)**, m3 **(E)**, and p3, p4, m1, and m2 **(F)** for *E. neogeus* (circle), *E. insulatus* (triangle), and *E. andium* (x).

proving to be *E. andium*. All other specimens were identified only as *Equus* sp. since their dimensions placed them in an area of overlap among the ranges of size variation seen in *E. santaeelenae*, *E. insulatus*, and *E. andium*.

However, one of Alberdi and Prado's collaborative published works did not follow the taxonomic arrangement of Alberdi and Prado (1992) and was also one of the first molecular (ancient DNA) studies to be carried out on South American native horses (Orlando et al., 2008). This study demonstrated that sequences from South American *Equus* fossils fell within the caballine horse cluster with maximum bootstrap support, and also cast doubt on the previously accepted taxonomic status of *Equus* (*Amerhippus*) as a distinct lineage of horses. Thus, this study left the taxonomy of South American native *Equus* open to at least two interpretations: (1) all American native horses belonged to a single species, possibly *Equus caballus*; or (2) South American native horses were a diverse paraphyletic lineage clustered within the total diversity of American species of *Equus*. The first hypothesis has been winning defenders among researchers of American native horses, and the 2010s have witnessed a change in the dominant taxonomic paradigm, in that even the most traditional authors have recognized that the diversity of South

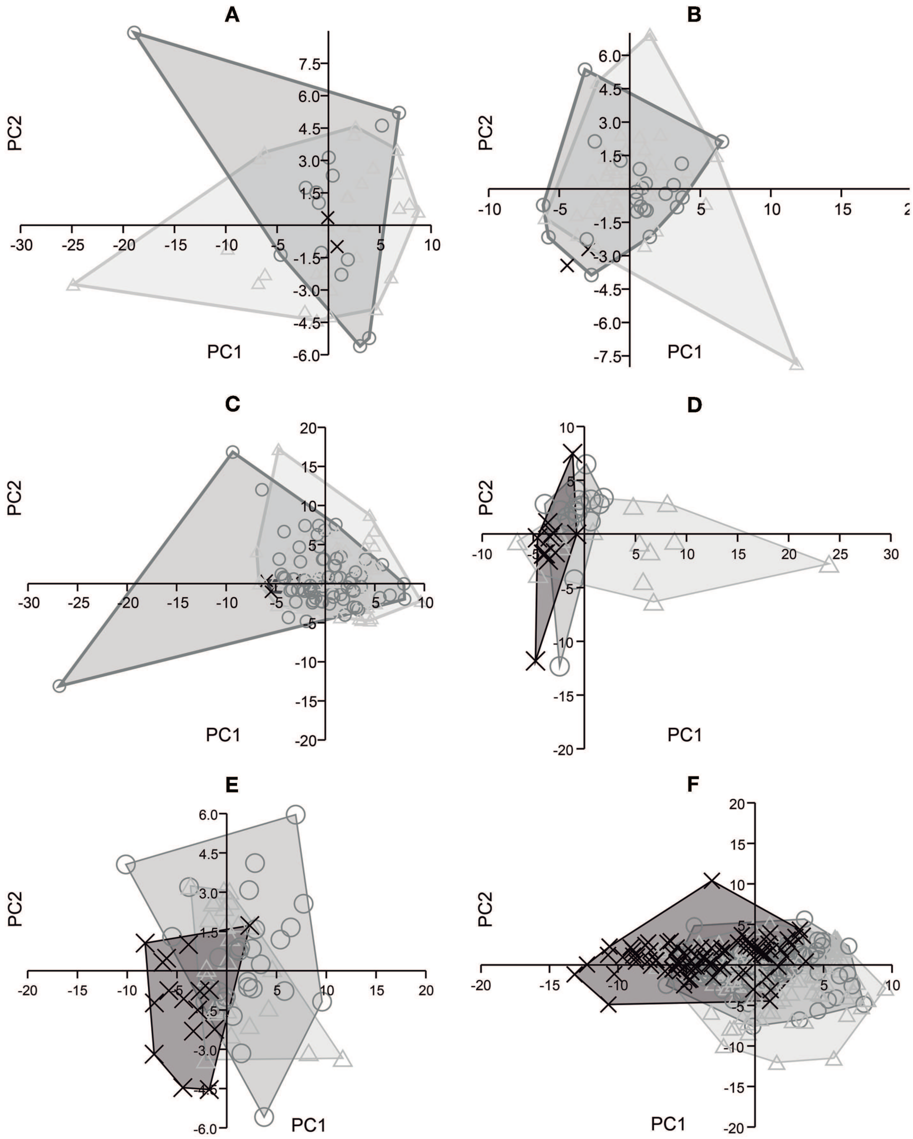

FIGURE 4 | Principal component analysis based on three dimensions of upper cheek teeth and five dimensions of lower cheek teeth of *E. neogeus* (circle), *E. insulatus* (triangle), and *E. andium* (x). Projected scores on: **(A)** Principal Components 1 (74%) and 2 (18%) from the analysis of P2; **(B)** Principal Components 1 (59%) and 2 (29%) from the analysis of M3; **(C)** Principal Components 1 (47%) and 2 (41%) from the analysis of P3, P4, M1, and M2; **(D)** Principal Components 1 (57%) and 2 (31%) from the analysis of p2; **(E)** Principal Components 1 (67%) and 2 (20%) from the analysis of m3; and **(F)** Principal Components 1 (61%) and 2 (25%) from the analysis of p3, p4, m1, and m2.

American native horses is smaller than previously proposed (Prado and Alberdi, 2017; Machado et al., 2018).

Consequently, Machado (2014) conducted a morphological comparative analysis of the distal appendicular skeleton of South American *Equus*, and two groups were recognized: an Andean one, composed of *E. andium* and *E. insulatus* and with shorter and more gracile metapodials; and another represented by the lowland species *E. neogeus* and *E. santaeelenae*, with longer and more robust metapodials.

Two taxonomic publications appeared in 2017, with contrasting proposals (Prado and Alberdi, 2017; Machado et al., 2018). The first is a reiteration of previous proposals, in which Prado and Alberdi (2017) questioned the validity of the subgenus *Equus* (*Amerhippus*) and considered the species *E. santaeelenae* and *E. lasallei* to be junior synonyms of *E. insulatus* and *E. neogeus*, respectively. Only three species of native South American *Equus* would then be valid: *E. andium*, *E. insulatus* and *E. neogeus*. However, the diagnoses offered for those species were still the same as in Alberdi and Prado (1992), which established that *E. insulatus* is an intermediate-sized species between the large *E. neogeus* and the small *E. andium*. The Prado and Alberdi (2017) study thus upheld the *status quo* of the last eight decades, at least since Spillman (1938).

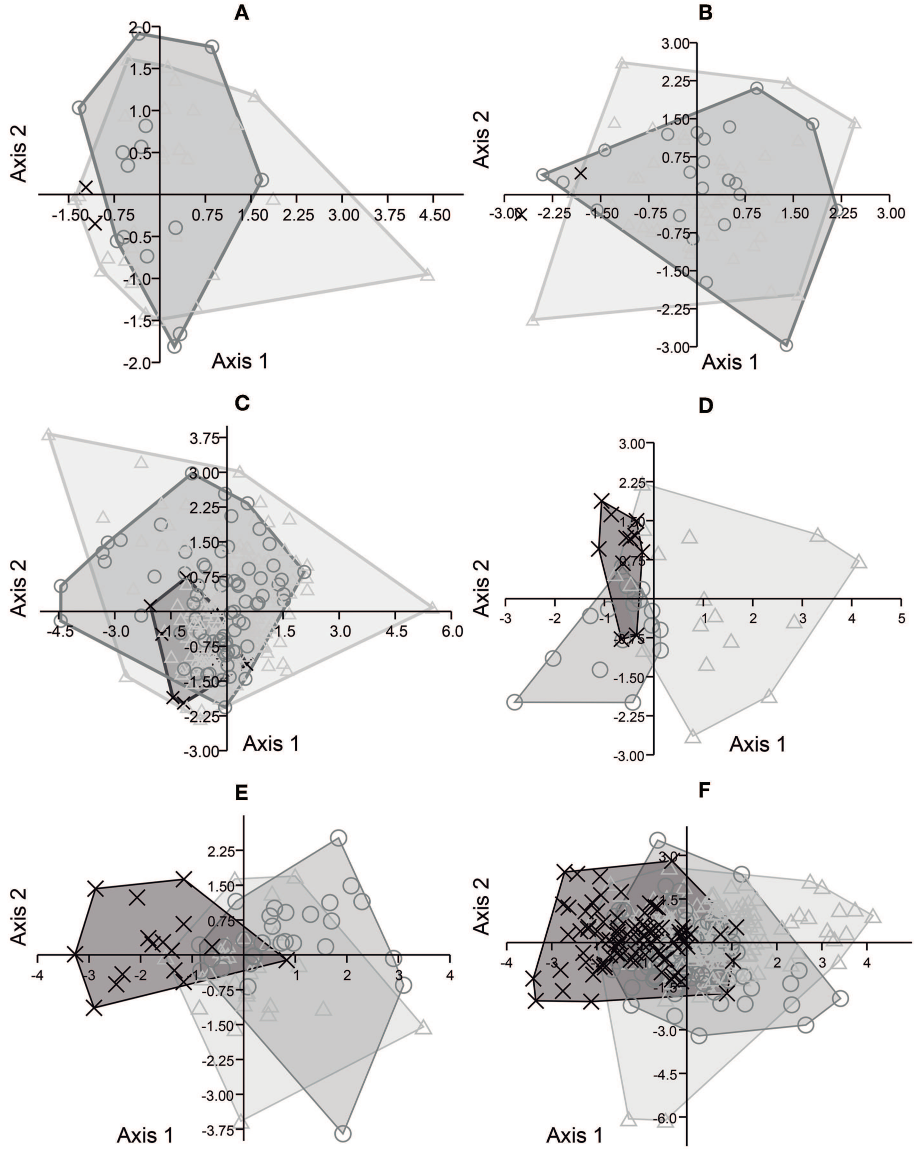

FIGURE 5 | Scatter plots from Canonical Variates Analysis based on three dimensions of upper cheek teeth of *E. neogeus* (circle), *E. insulatus* (triangle), and *E. andium* (x). Projected scores on: **(A)** axes 1 (93%) and 2 (7%) from the analysis of P2; **(B)** axes 1 (88%) and 2 (12%) from the analysis of M3; **(C)** axes 1 (71%) and 2 (29%) from the analysis of P3, P4, M1, and M2; **(D)** axes 1 (70%) and 2 (30%) from the analysis of p2; **(E)** axes 1 (90%) and 2 (10%) from the analysis of m3; and **(F)** axes 1 (86%) and 2 (14%) from the analysis of p3, p4, m1, and m2.

On the other hand, Machado et al. (2018) put forward a novel proposal and evaluated the taxonomic importance of the autopodials of South American native *Equus*, which traditionally were often used to diagnose species within this group as noted above. The results revealed that autopodial features previously used were inadequate for taxonomic purposes, since they failed to distinguish among any of the species of South American native *Equus*. In fact, the pattern recognized for all autopodial dimensions was a clear, overlapping continuum, revealing a linear variation gradient. The authors proposed that South American *Equus* might display a clinal variation in which *E. andium* and *E. neogeus* would represent the phenotypic extremes of a spectrum from small to large size, while the other species would represent intermediates. Accordingly, size (at least in the way it was traditionally used, described above) cannot distinguish between putative species within South American native *Equus*. This group might comprise a single species, *E. neogeus*, characterized by a wide spectrum of clinal morphological variation.

Teeth Analysis

Bivariate analysis (**Figure 3**) of dimensions 2 and 4 of the upper cheek teeth, and dimensions 2 and 6 of the lower cheek teeth, showed a complete overlap and superimposition of all specimens of *Equus* included here.

The PCA analyses (**Figure 4**) were unable to distinguish between the traditionally recognized five (Alberdi and Prado, 1992), or even the more recently posited three (Prado and Alberdi, 2017), species of South American *Equus*. Among the upper dentition analyses, that for P2 (**Figure 4A**) indicated

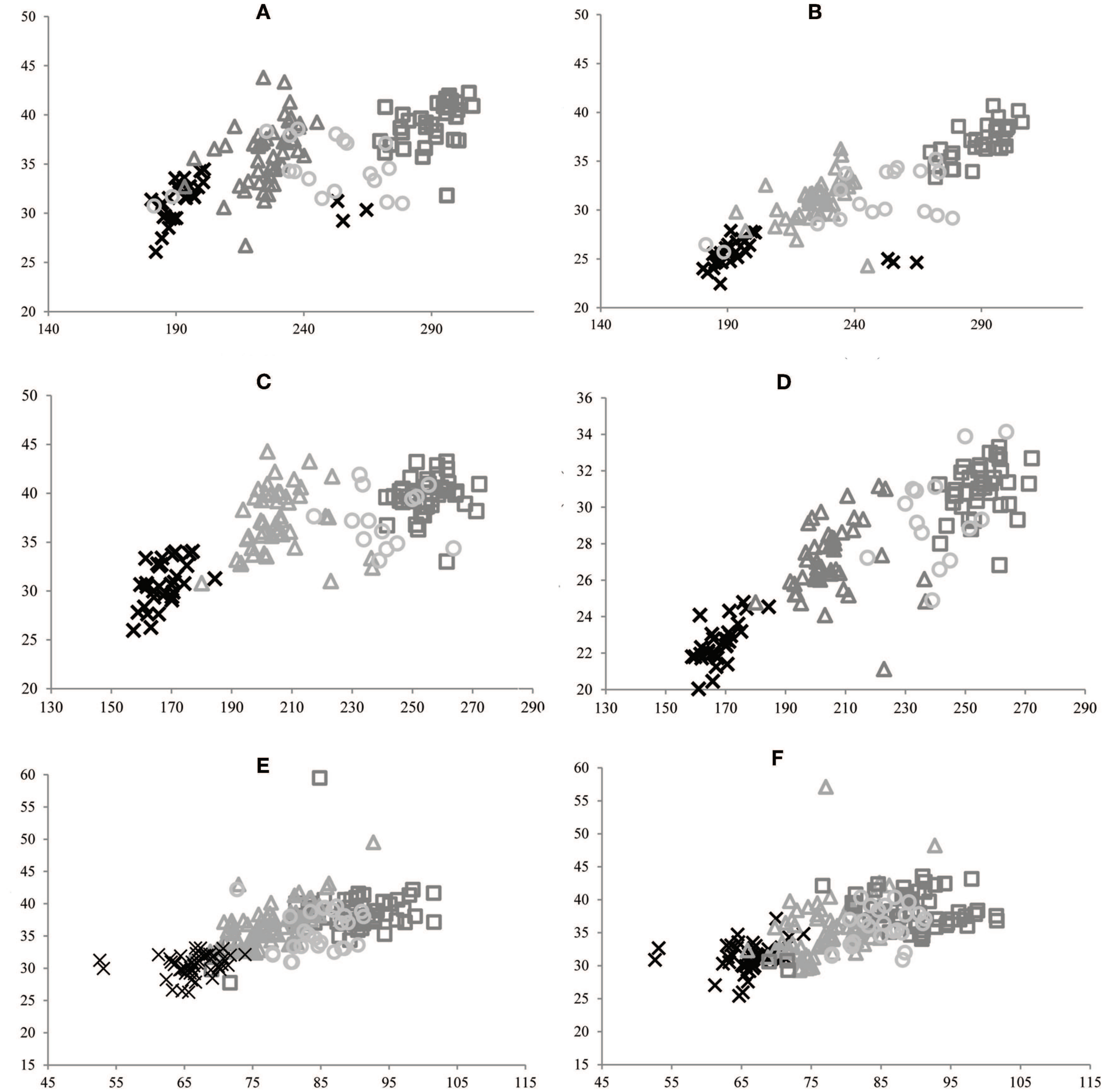

FIGURE 6 | Bivariate analysis of dimensions 1 vs. 3 **(A)** and 1 vs. 4 **(B)** of MTIII, dimensions 1 vs. 3 **(C)** and 1 vs. 4 **(D)** of MCIII, and dimensions 1 vs. 3 **(E)** and 1 vs. 5 **(F)** of IPHIII for *E. andium* (x), *E. insulatus* (triangle), *E. neogeus* (circle), and *E. occidentalis* (box).

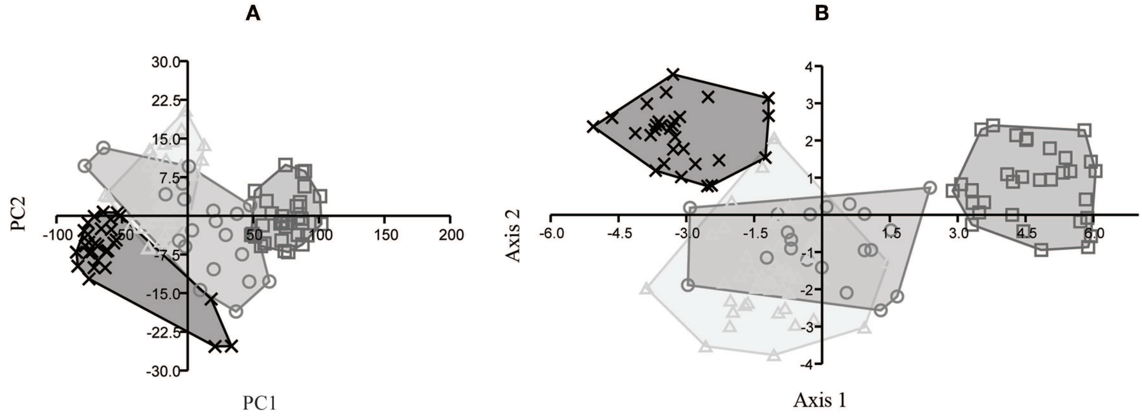

FIGURE 7 | MTIII analysis for *E. andium* (x), *E. insulatus* (triangle), *E. neogeus* (circle), and *E. occidentalis* (box): **(A)** projected scores from PCA, PC1 (96%) and PC2 (2%); **(B)** dispersal graph from CVA, axis 1 (77%) and axis 2 (20%).

that PC1 was responsible for 74%, and PC2 for 18%, of the variation. Dimensions 2 and 4 had the most significant effects on PC1 and PC2, respectively. In the analysis of M3 (**Figure 4B**), PC1 was responsible for 59% of the variation, and PC2 for 29%. Dimensions 1 and 4 had the most significant effects on PC1 and PC2, respectively. In the analysis of P3, P4, M1, and M2 (**Figure 4C**), PC1 was responsible for 47% of the variation and PC2 for 41%, and dimensions 2 and 4 had the most significant effects on both PC1 and PC2.

Among the lower dentition analyses, that for p2 (**Figure 4D**) indicated that PC1 was responsible for 57% of the variation and PC2 for 31%. Dimensions 2 and 3 had the most significant effects on PC1, while dimensions 4 and 5 had the most significant effects on PC2. In the analysis of m3 (**Figure 4E**), PC1 was responsible for 67% of the variation, and PC2 for 20%. Dimension 2 and dimension 5 had the most significant effects on PC1 and PC2, respectively. In the analysis of p3, p4, m1 and m2 (**Figure 4F**), PC1 was responsible for 61% of the variation and PC2 for 25%. Dimensions 2 and 5 had the most significant effects on PC1, and dimension 6 had the most significant effect on PC2.

The CVA of P2 (**Figure 5A**) revealed that axis 1 was responsible for 93% of the variation, and axis 2 for 7%. For M3 (**Figure 5B**), axis 1 was responsible for 88% of the variation, and axis 2 for 12%. In the analysis of P3, P4, M1, and M2 (**Figure 5C**), axis 1 was responsible for 71% of the variation. Among the lower dentition analyses, CVA for p2 (**Figure 5D**) revealed that axis 1 was responsible for 70%, and axis 2 for 30%, of the variation. For m3 (**Figure 5E**), axis 1 was responsible for 90% of the variation, and axis 2 for 10%. The analysis of p3, p4, m1, and m2 (**Figure 5F**) revealed that axis 1 was responsible for 86% of the variation and axis 2 for 14%.

All the CVA analyses (**Figure 5**) revealed an overlap among all putative species of South American *Equus*, especially regarding axis 1, and recognized only a single group.

Autopodia Analysis

The bivariate analysis took into consideration the relationships between dimensions 1 and 3 and between dimensions 1 and 4 of MTIII and MCIII, and the relationships between dimensions 1 and 3 and between dimensions 1 and 5 of IPHIII, in the putative species *E. andium*, *E. insulatus*, *E. neogeus*, and *E. occidentalis*. The results obtained do not allow the species to be distinguished from one another: there is clear overlap among the clusters of points representing the various species, revealing a continuum of gradual linear variation (**Figure 6**).

In the PCA portion of the MTIII analysis (**Figure 7A**), PC1 was responsible for 96% of the variation, with dimensions 1 and 2 as the most significant ones, while PC2 was responsible for 2% of the variation with dimensions 5, 6, and 10 as the most significant variables. In the CVA portion (**Figure 7B**), axis 1 was responsible for 77% of the variation and axis 2 for 20%.

The Kruskal-Wallis analyses performed on MTIII (**Table 1**) presented significant values in comparisons of all dimensions between *E. andium* and *E. insulatus*; between *E. andium* and *E. neogeus*; between *E. andium* and *E. occidentalis*; between *E. insulatus* and *E. occidentalis*; and between *E. neogeus* and *E. occidentalis*. All other comparisons resulted in non-significant values.

In the PCA portion of the MCIII analysis (**Figure 8A**), PC1 was responsible for 96% of the variation, with dimensions 1 and 2 as the most significant ones, and PC2 for 1%, with dimensions 3, 5, and 10 as most significant. In the CVA portion (**Figure 8B**), axis 1 was responsible for 91% of the variation and axis 2 for 5%.

The results of the Kruskal-Wallis analysis performed on MCIII (**Table 2**) revealed significant values in comparisons of all dimensions between *E. andium* and *E. insulatus*; between *E. andium* and *E. neogeus*; between *E. andium* and *E. occidentalis*; and between *E. insulatus* and *E. occidentalis*. In comparisons involving dimension 1 a significant difference was also found between *E. insulatus* and *E. neogeus*. All other comparisons resulted in non-significant values.

TABLE 1 | Kruskal-Wallis test results for comparative analysis of MTIII.

	1	3	4	5	10
E. andium vs. *E. insulatus*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
E. andium vs. *E. neogeus*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
E. andium vs. *E. occidentalis*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
E. insulatus vs. *E. neogeus*	ns	ns	ns	ns	ns
E. insulatus vs. *E. occidentalis*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
E. neogeus vs. *E. occidentalis*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$

Significant values ($p < 0.05$) were obtained in the analyses of dimensions 1, 3, 4, 5, and 10 of E. andium vs. E. insulatus, E. andium vs. E. neogeus, E. andium vs. E. occidentalis, E. insulatus vs. E. occidentalis, and E. neogeus vs. E. occidentalis; non-significant values were found for all other analyses.

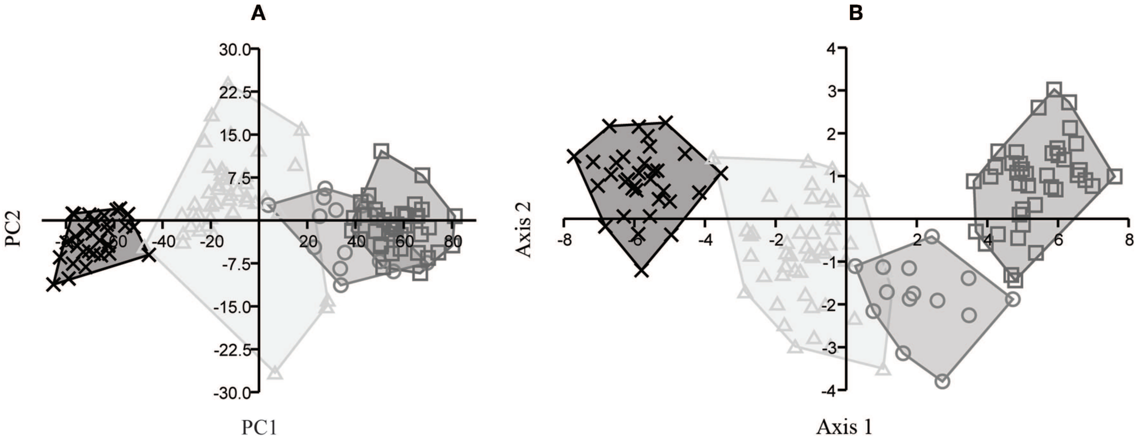

FIGURE 8 | MCIII analysis for *E. andium* (x), *E. insulatus* (triangle), *E. neogeus* (circle), and *E. occidentalis* (box): **(A)** projected scores from PCA, PC1 (96%) and PC2 (1%); **(B)** dispersal graph from CVA, axis 1 (91%) and axis 2 (5%).

In the PCA portion of the IPHIII analysis (**Figure 9A**), PC1 was responsible for 82% of the variation, with dimensions 1 and 2 as the most significant ones, while PC2 was responsible for 7% of the variation with dimensions 2 and 4 as most significant. The CVA (**Figure 9B**) revealed axis 1 to be responsible for 90% of the variation, and axis 2 to be responsible for 5%.

The results of the Kruskal-Wallis analysis of IPHIII (**Table 3**) revealed significant values in comparisons of all dimensions between *E. andium* and *E. insulatus*; between *E. andium* and *E. occidentalis*; and between *E. insulatus* and *E. occidentalis*. Significant values were also found with respect to comparisons of dimensions 1, 3, 5, and 7 between *E. andium* and *E. neogeus*; with respect to comparisons of dimension 1 between *E. insulatus* and *E. neogeus*; and with respect to comparisons of dimension 7 between *E. neogeus* and *E. occidentalis.* All other comparisons resulted in non-significant values.

Fossil Record Update

In updating the known distribution of *Equus* fossil sites in South America, 152 localities were found (**Table 4**), making it possible to observe the very widespread distribution of the genus throughout the continent (**Figure 10**; Alberdi and Prado, 1992, 2004; Prado and Alberdi, 1994; Faure et al., 1999; MacFadden et al., 1999; Alberdi and Frassineti, 2000; Frassinetti and Alberdi, 2001; Alberdi et al., 2003; Porpino et al., 2004; Pujos and Salas, 2004; Dantas et al., 2005; Labarca and López, 2006; Rincón et al., 2006; Araújo-Junior and Porpino, 2007; Mendoza, 2007; Dias Neto et al., 2008; Hubbe, 2008; Kerber and Oliveira, 2008a; Kerber and Oliveria, 2008b; Ximenes, 2008; Borrero, 2009; Scheffler et al., 2010; Silva et al., 2010, 2012; França et al., 2011; Prado et al., 2011; Recabarren et al., 2011; Pereira et al., 2012; Román-Carrión, 2012; Nogueira and Barbosa, 2015; Suárez and Santos, 2015; Avilla et al., 2018).

The genus *Equus* spread through most of the South American continent, occupying highlands and lowlands (**Figure 11**). Although most records indicate altitudes of <500 m, there are several records over almost 3,000 m, and there are no records south of latitude 40°S.

DISCUSSION

The state of the art of South American native *Equus* taxonomy was dominated by a splitter tendency beginning in the second half of the nineteenth century, when several poorly diagnosed species were named. Most of these species were maintained until the second half of twentieth century, when a stable taxonomy of South American native *Equus* was finally achieved (Hoffstetter, 1950; Alberdi and Prado, 1992; Prado and Alberdi, 2017).

TABLE 2 | Kruskal-Wallis test results for comparative analysis of MCIII.

	1	3	4	5	10
E. andium vs. *E. insulatus*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
E. andium vs. *E. neogeus*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
E. andium vs. *E. occidentalis*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
E. insulatus vs. *E. neogeus*	$p < 0.05$	ns	ns	ns	ns
E. insulatus vs. *E. occidentalis*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
E. neogeus vs. *E. occidentalis*	ns	ns	ns	ns	ns

Significant values (p < 0.05) were obtained in the analyses of dimensions 1, 3, 4, 5, and 10 of E. andium vs. E. insulatus, E. andium vs. E. neogeus, E. andium vs. E. occidentalis, and E. insulatus vs. E. occidentalis, and in the analysis of dimension 1 of E. insulatus vs. E. neogeus; non-significant values were found for all other analyses.

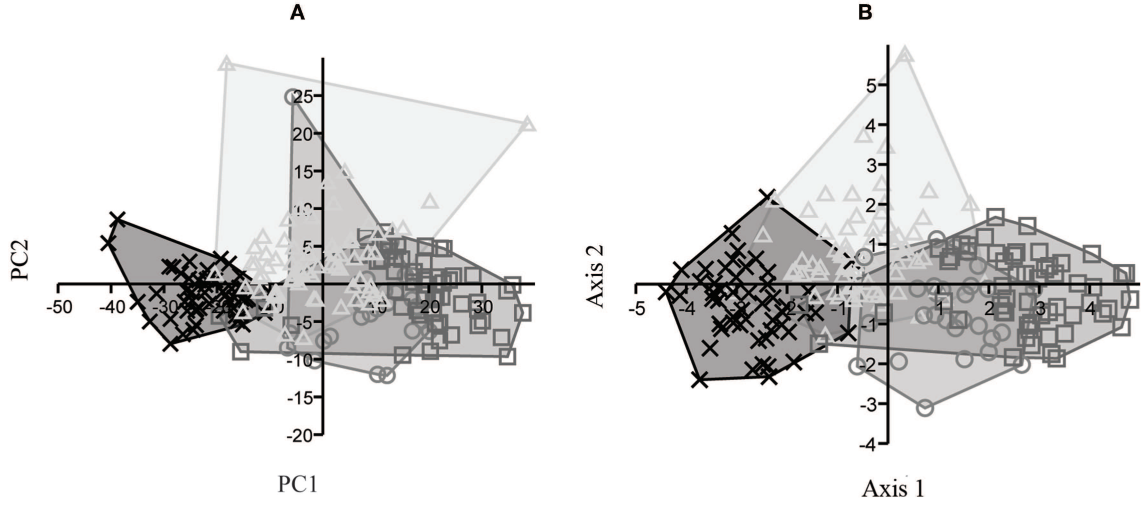

FIGURE 9 | IPHIII analysis for *E. andium* (x), *E. insulatus* (triangle), *E. neogeus* (circle), and *E. occidentalis* (box): **(A)** projected scores from PCA, PC1 (82%) and PC2 (7%); **(B)** dispersal graph from CVA, axis 1 (90%) and axis 2 (5%).

Size was assumed to be the best (and even only) basis for diagnosing South American *Equus* species within this group, and this consensus held until the end of the 2010s (Machado, 2018; Machado et al., 2018). The results obtained in the present study revealed that it is not possible to distinguish between South American *Equus* based on the morphological characters previously used: size, and the proportions of the autopodia and teeth.

Dental analyses revealed a clear overlap in tooth proportions among the species. The results demonstrated that dimensions 2 and 4 for the upper cheek teeth, and dimensions 2 and 6 for the lower cheek teeth, were the most important variables in the PCA. Even these variables, however, were not sufficient to differentiate among the species.

These results were in accordance with the autopodial analysis, which corroborated all the analyses performed by Machado et al. (2018). The bivariate analysis, PCA and CVA that were carried out on autopodial measurements revealed not only a clear overlap between all the species, but also a continuum of gradual linear variation. This continuum was already observed in Machado et al. (2018), and the superimposition of autopodial metric characters was even more clearly observed in the present study, which included more data.

PCA revealed that the most significant variables in the case of PC1 were measurements 1 and 2 of MTIII, MCIII and IPHIII. PC1 was responsible for over 90% of the variation in each case except that of the IPHIII analysis, in which it was responsible for 82%. Thus, length was the most significant character in the autopodial analyses but was still not sufficient to distinguish among the species. Instead length showed a continuum of gradual linear variation. These analyses were corroborated by the Kruskal-Wallis test, which found significant values only in the comparison of species on the extremities of the continuum. The only species found to be somewhat distinct from the others, both on axis 1 in the CVA of MTIII and MCIII and in the Kruskal-Wallis test, was the North American *E. occidentalis*. Furthermore, *E. occidentalis* can be distinguished from the South American species by diagnostic cranial characters according to MacFadden and Azzaroli (1987).

Considering the complete overlap seen in the autopodial and dental metric characters, it is inferred here, as proposed by Machado (2018) and Machado et al. (2018), that South America was probably inhabited by only a single species of *Equus*, *E.*

TABLE 3 | Kruskal-Wallis test results for comparative analysis of IPHIII.

	1	3	5	7	8
E. andium vs. *E. insulatus*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
E. andium vs. *E. neogeus*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	ns
E. andium vs. *E. occidentalis*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
E. insulatus vs. *E. neogeus*	$p < 0.05$	ns	ns	ns	ns
E. insulatus vs. *E. occidentalis*	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
E. neogeus vs. *E. occidentalis*	ns	ns	ns	$p < 0.05$	ns

Significant values ($p < 0.05$) were obtained in the analyses of dimensions 1, 3, 5, 7, and 8 of E. andium vs. E. insulatus, E. andium vs. E. occidentalis, and E. insulatus vs. E. occidentalis, of dimensions 1, 3, 5, and 7 of E. andium vs. E. neogeus, of dimension 1 of E. insulatus vs. E. neogeus, and of dimension 7 of E. neogeus vs. E. occidentalis; non-significant values were found for all other analyses.

neogeus. However, the continuum observed in the autopodial analyses indicates an intraspecific variation that allows the establishment of a phenotypic variation according to the species in the extremities, even though it cannot be used to distinguish any distinct groupings.

Morphological analyses allow the interpretation of a vast variety of biological processes that can result in morphological differences between individuals and populations, either through a long period of genetic divergence or by phenotypic plasticity oriented by the environment (Kangas et al., 2016). Morphological variations related to biotic and abiotic gradients in heterogeneous environments are commonly observed in species with wide geographic distributions (Salomon, 2001; Ennen et al., 2014). Intraspecific variation analyses are common in morphological studies of ungulates, and several groups display a relationship between morphological phenotypic variation and latitudinal variation (Kangas et al., 2016). Examples of this relationship usually conform to Bergmann's Rule (Bergmann, 1848 in Mayr, 1963a,b), which posits a correlation between larger bodies and higher altitudes or cold environments, often considered an adaptation to climatic variations (Ashton et al., 2000; Blackburn and Hawkins, 2004; Kangas et al., 2016). However, the phenotypic variation observed in South American *Equus* is different and does not fit the latitudinal variation pattern, so the possibility that it represents a case of Bergmann's Rule can be excluded. Allen's Rule is also commonly invoked when dealing with phenotypic and latitudinal variations and implies a correlation between shorter appendages, and therefore shorter limb bones, and colder environments in endothermic mammals (Nudds and Oswald, 2007; Symonds and Tattersall, 2010; Alho et al., 2011). This rule likewise does not seem to explain the variation observed in *Equus* in South America. There are records of long limb bone morphotypes in localities with colder environments, such as those at latitude 40°S, and also in areas characterized by a greater range of phenotypic variation. Ecuador, for example, was once believed to have three species distinguished by limb bone proportions. It was once postulated that the Gracility Index of South American *Equus* autopodia, and especially of IPHIII, was related to the environment, with slenderness linked to harder ground and robustness to softer ground (Prado and Alberdi, 1994; Alberdi and Prado, 2004). However, recent studies (Machado et al., 2018) have refuted this idea and revealed that the Gracility Index has a negatively allometric relationship with bone length.

The genus *Equus* has a continuous geographic distribution in South America, bypassing the Amazon region, and this pattern seems to be correlated with phenotypic variation in *E. neogeus*. The Amazon basin was the region of South America most strongly affected by Pleistocene climatic variations, with constant alternations between contraction and expansion of the tropical forest (Arruda et al., 2017). The Amazon forest constituted a relatively warm and wet habitat that probably remained isolated through much of the Pleistocene (Arruda et al., 2017). However, *Equus* usually favor open plain environments, like savannas (MacFadden, 1994; Alberdi and Prado, 2004; Costa, 2017; Prado and Alberdi, 2017), and the typical environmental instability of closed forest biomes might have worked as a geographic barrier to dispersion of the genus in the South American continent. Most records indicate altitudes as high as 500 meters, with several records approaching 3,000 m and this approximate altitude was probably a limit for the taxon. There are no records south of latitude 40°S, a pattern that is also observed in other Pleistocene mammals, such as *Notiomastodon platensis* (Mothé and Avilla, 2015). This distribution also differs importantly from that of *Hippidion*, the other South American equid, for which records are limited to southern Patagonia but surpassing latitude 50°S (Prado and Alberdi, 2017). According to Ray and Adams (2001), during the Last Glacial Maximum, the environment at latitudes exceeding 40°S corresponded to a temperate desert with permanent ice sheets at the southern area of the continent, which probably formed a barrier to the dispersal of *Equus* in South America. Furthermore, the geographic distribution of *Equus* in South America surrounds the Amazon. The possibility that the lack of Amazonian records of *Equus* is a result of taphonomic factors can be excluded, since Pleistocene records of other fossil mammals are known from the Amazon (Rancy, 1999).

As proposed by Machado et al. (2018) and Machado (2018), South American *Equus* appears to represent a case of clinal variation. Clines can be categorized as smooth or stepped, the former corresponding to gradual continua without marked intraspecific boundaries and the latter to continua with steeper slopes, abrupt changes and clear demarcations between possible subspecies (Salomon, 2001, 2002; Katzner and Collar, 2013). With increasing evolutionary differentiation, smooth clines

TABLE 4 | Locations and altitudes of *Equus* fossil occurrences in South America.

Localities	Country	Altitude	Latitude
Napostá Grande (Bahía Blanca)	Argentina	34 m	38°8′ S
Arroyo Camet (Buenos Aires)	Argentina	35 m	37°49′ S
Arroyo Claromecó (Buenos Aires)	Argentina	11 m	38°51′6.67″ S
Arroyo Tapalqué (Buenos Aires)	Argentina	160 m	36°58′15.71″ S
Ayacucho (Buenos Aires)	Argentina	79 m	37°07′00″ S
Ayacucho (Buenos Aires)	Argentina	47 m	31° 07′00″ S
Balcarce (Buenos Aires)	Argentina	121 m	37°8333 S
Bahía San Blas (Buenos Aires)	Argentina	5 m	40°33′08″ S
Barrancas (Buenos Aires)	Argentina	8 m	38°44′32.50″ S
Buenos Aires (Buenos Aires)	Argentina	29 m	34°35′08.8″ S
Campo Spósito (Buenos Aires)	Argentina	278 m	33°44′34″ S
Centinela del Mar (Buenos Aires)	Argentina	13 m	38°26′00″ S
Chacra del Brié (Buenos Aires)	Argentina	204 m	37°19′43.65″ S
Chascomús (Buenos Aires)	Argentina	19 m	35°36′ S
González Chaves (Buenos Aires)	Argentina	199 m	38°2′0″ S
Indio Rico (Buenos Aires)	Argentina	143 m	38°33′3″ S
La Chata (Buenos Aires)	Argentina	20 m	38°33′16.50″ S
Las Conchas (Buenos Aires)	Argentina	13 m	34°25′17.26″ S
La Plata (Buenos Aires)	Argentina	28 m	34°54′04.5″ S
Lobos (Buenos Aires)	Argentina	33 m	35°11′7″ S
Malacara (Buenos Aires)	Argentina	37 m	34°24′52.71″ S
Magdalena (Buenos Aires)	Argentina	11 m	35°4′35.40″ S
Mar del Plata (Buenos Aires)	Argentina	443 m	38°00′16.2″ S
Mercedes (Buenos Aires)	Argentina	44 m	34°39′16.57″ S
Miembro Guerrero (Buenos Aires)	Argentina	?	35° S
Miramar (Buenos Aires)	Argentina	20 m	38°16′13.25″ S
Monte Hermoso (Buenos Aires)	Argentina	8 m	38°59′15.5″ S
Necochea (Buenos Aires)	Argentina	18 m	38°12′08″ S
Olavarría (Buenos Aires)	Argentina	170 m	36°58′44″ S
Paso Otero (Buenos Aires)	Argentina	10 m	38°12″08″ S
Pehuen Có (Buenos Aires)	Argentina	7 m	39°0′0″ S
Playa del Barco (Buenos Aires)	Argentina	1 m	39°00′09″ S
Paso del Médano (Buenos Aires)	Argentina	8 m	38°44′32.50″ S
Punta Carballitos (Buenos Aires)	Argentina	107 m	38°53′33″ S
Punta Hermengo (Buenos Aires)	Argentina	20 m	38°16′13.25″ S
Quequén Grande (Buenos Aires)	Argentina	107 m	38°16′58.9″ S
Rio Luján (Buenos Aires)	Argentina	21 m	34°33′58.9″ S
Río de La Plata (Buenos Aires)	Argentina	22 m	34°30′37.99″ S
Rio Sauce Grande (Buenos Aires)	Argentina	11 m	38°49′51.2″ S
Rio Quequén Salado (Buenos Aires)	Argentina	8 m	35°37′36.6″ S
Tandil (Buenos Aires)	Argentina	204 m	37°19′43.65″ S
Tapalqué (Buenos Aires)	Argentina	90 m	36°21′21.3″ S
Tres Arroyos (Buenos Aires)	Argentina	115 m	38°23′0″ S
Vicente López (Buenos Aires)	Argentina	26 m	34° S
Wilde (Buenos Aires)	Argentina	7 m	34°41′54″ S
Mar Chiquita (Córdoba)	Argentina	2 m	37°40′S
San Francisco (Córdoba)	Argentina	422 m	31°26′ S
Sitio El Silencio (Córdoba)	Argentina	18 m	30°53′20″ S
Arroyo Alcaráz (Entre Ríos)	Argentina	47 m	31°5′27.6″ S
Arroyo Ensenada (Entre Ríos)	Argentina	6 m	31°85′ S
El Boyero (Entre Ríos)	Argentina	27 m	31°25′ S
Espinillo (Entre Ríos)	Argentina	88 m	24°58′0″ S
Zanjón Seco (Jujuy)	Argentina	1,034 m	38°10′7″ S
Laguna Meum	Argentina	23 m	34.64352 S
El Carriza (Mendoza)	Argentina	786 m	32°20′20″ S
Gruta del Indio (Mendoza)	Argentina	114 m	34°45′ S
Malargüe (Mendoza)	Argentina	1,198 m	35°28′32″ S
Cañada Honda (San Luis)	Argentina	611 m	31°58′49.5″ S
Inti Huasi (San Luis)	Argentina	17 m	37.25193 S
Río Seco de Chical (San Luis)	Argentina	696 m	32°75′ S
Alvear (Santa Fe)	Argentina	63 m	33° S
Arroyo Frías (Santa Fe)	Argentina	30 m	33°9′0″ S
Arroyo Seco (Santa Fe)	Argentina	30 m	33°9′0″ S
Cercanías (Santa Fe)	Argentina	42 m	31°27′0″ S
Chaco Santafesino (Santa Fe)	Argentina	56 m	27°27′05″ S
Esperanza (Santa Fe)	Argentina	42 m	31°27′0″ S
Laguna Setubal (Santa Fe)	Argentina	11 m	31°33′37.5″ S
Puerto San Martín (Santa Fe)	Argentina	663 m	33° S
Puerto San Martín (Santa Fe)	Argentina	26 m	32°44′29″ S
Río Dulce (Santiago del Estero)	Argentina	153 m	27°47′0.14″ S
Rio Carcarañá (Santa Fe)	Argentina	84 m	32°51′06.3″ S
Rio Paraná (Santa Fe)	Argentina	34 m	33°2′29.60″ S
Río Salado (Santa Fe)	Argentina	22 m	31°37′45.4″ S
Rosario (Santa Fe)	Argentina	84 m	33°5′32.85″ S
Tacural (Santa Fe)	Argentina	98 m	30°83′3″ S
La Banda (Santiago del Estero)	Argentina	193 m	27°44′9.02″ S
Nuapa (Chuquisaca)	Bolivia	1,856 m	20°00′0.00″ S
Tarija (Tarija)	Bolivia	1,603 m	21°31′56″ S
Lagoa de Pedra (Alagoas)	Brazil	309 m	9°32′13″ S
Chique-Chique (Bahia)	Brazil	408 m	10°49′23″ S
Curaçá (Bahia)	Brazil	364 m	08°59′31″ S
Itaguaçu (Bahia)	Brazil	422 m	11°01′46.6″ S
Ourolândia (Bahia)	Brazil	597 m	10°55′52″ S
Toca dos Ossos (Bahia)	Brazil	597 m	10°55′52″ S
Waterwhole deposit (Bahia)	Brazil	775 m	10.46667 S
Itapipoca (Ceará)	Brazil	106 m	3°29′59.32″ S
Corumbá (Mato Grosso do Sul)	Brazil	153 m	18°58′48″ S
Águas do Araxá (Minas Gerais)	Brazil	976 m	19°50′09″ S
Francisco Sá (Minas Gerais)	Brazil	670 m	16°29′ S
Lagoa Santa (Minas Gerais)	Brazil	772 m	19°38′ S
Curimatã (Paraíba)	Brazil	357 m	7°43′36″ S
Taperoá (Paraíba)	Brazil	537 m	7°12′2.86″ S
Mangueirinhia (Paraná)	Brazil	912 m	25°47′30″ S
Alagoinha (Pernambuco)	Brazil	310 m	8°24′ S
Afrânio (Pernambuco)	Brazil	477 m	8°30′54″ S
Pesqueira (Pernambuco)	Brazil	714 m	8°24′ S
São Raimundo Nonato (Piauí)	Brazil	346 m	9°00′55″ S
Toca do Serrote do Artur (Piauí)	Brazil	371 m	8°49′35″ S
Ponte Velha II (Rio Grande do Sul)	Brazil	156 m	29°39′45.46″ S
Quaraí (Rio Grande do Sul)	Brazil	107 m	30°10′ S

(Continued)

TABLE 4 | Continued

Localities	Country	Altitude	Latitude
Santa Vitória do Palmar (Rio Grande do Sul)	Brazil	14 m	33°44′11.4″ S
Lajedo de Soledade (Rio Grande do Norte)	Brazil	121 m	5°35′20″ S
São Rafael (Rio Grande do Norte)	Brazil	83 m	5°50′ S
Gararu (Sergipe)	Brazil	161 m	37°05′33″ S
Poço Redondo (Sergipe)	Brazil	193 m	9°55′37″ S
Aurora do Tocantins (Tocantins)	Brazil	468 m	12°35′0.08″ S
Tuina (Atacama)	Chile	2,642 m	22°35′ S
San Vicente de Tagua (Cachapoal)	Chile	208 m	34°28′18″ S
Cerro Caracol (Concepción)	Chile	60 m	36°50′03″ S
Los Vilos (Coquimbo)	Chile	18 m	31°51′ S
Valle de Elqui (Elqui)	Chile	123 m	29°50′ S
Estero de Coyanco (La Laja)	Chile	2,134 m	33°40′59″ S
Tierra Blancas (La Lingua)	Chile	701 m	32°27′00″ S
Calera (Lo Aguirre)	Chile	211 m	32°47′00″ S
Pilauco Site (Osorno)	Chile	63 m	40°34′11″ S
Cachabuco (Santiago)	Chile	642 m	33°12′ S
Chacabuco (Santiago)	Chile	544 m	33°01′40″ S
Colina (Santiago)	Chile	597 m	33°12′00″ S
Conchalí (Santiago)	Chile	1,356 m	31°53′ S
Punta de Rieles (Santiago)	Chile	574 m	33.48101 S
San Bernardo (Santiago)	Chile	571 m	33°12′ S
Huimpil (Temuco)	Chile	257 m	38°45′0″ S
Sabana de Bogotá (Bogotá)	Colombia	2,796 m	5°11′46.54″ N
Tibitó (Cundinamarca)	Colombia	2,559 m	4°10′20″ N
Zanjón Seco (Ginebra)	Colombia	1,034 m	3°75′52.8″ S
Cerro Gordo (Guamo)	Colombia	392 m	4°10′20″ N
Fm. Villavieja (Huila)	Colombia	387 m	3°13′08″ N
La Venta (Huila)	Colombia	2,139 m	3°18′ N
Chalán (Sucre)	Colombia	294 m	9°32′38″ N
Punín (Chimborazo)	Ecuador	2,801 m	1°46′00″ S
La Carolina (Pichincha)	Ecuador	2,768 m	0°11′07.1″ S
Alangasí (Quito)	Ecuador	2,552 m	0°18′25.19″ S
El Colegio (Quito)	Ecuador	2,850 m	0°15′01.8″ S
La Magdalena (Quito)	Ecuador	2,802 m	0°15′ S
La Ronda (Quito)	Ecuador	2,801 m	0°15′ S
Otón (Quito)	Ecuador	2,779 m	0°01′37.6″ S
Quebrada Colarada (Quito)	Ecuador	2,595 m	1°46′45.9″ S
Quebrada Grande (Quito)	Ecuador	2,595 m	0°09′58.5″ S
Rio Chiche (Quito)	Ecuador	2,398 m	0°12′28.79″ S
Península de Santa Elena (Santa Elena)	Ecuador	2 m	2°13′ S
Sacaco (Arequipa)	Peru	2,321 m	15°30′36.3″ S
Pampa de los Fósiles (Paijan)	Peru	94 m	7°43′ S
Talata Tar Pit (Talara)	Peru	86 m	4°33′ S
Pikimachay Cave (Valle del Ayacucho)	Peru	2,718 m	13°2′26.88″ S
Rio Cuareim (Artigas)	Uruguay	57 m	30°16′08.29″ S
Arroyo Sopas (Salto)	Uruguay	90 m	31°15′ S
Taima (Falcón)	Venezuela	39 m	11°29′54″ N
Inciarte (Zulia)	Venezuela	94 m	10°47′00″ N

FIGURE 10 | Updated map of South American *Equus* fossil occurrences.

could gradually change into steeper ones. If the distinctions between adjacent populations within the cline become relatively large, the slopes occurring along the cline may turn into steps and potentially even "break" the cline, indicating some kind of speciation (Salomon, 2001, 2002). Considering the geographic distribution of *Equus* in South America along with the continuum of gradual linear variation observed in the autopodial analyses, which does not allow identification of marked intraspecific entities, it seems that South American *Equus* can be regarded as a smooth cline.

The lengths of the bones in the locomotor apparatus are usually related to cursoriality. In horse evolution this relationship is particularly evident in the distal bones, which tend to be longer in species inhabiting open and plains environments (Hildebrand, 1987; MacFadden, 1994; Christiansen, 2002; Alberdi and Prado, 2004). Still, maneuverability is related to mobility and to the ability to make rapid changes in speed and direction and is favored by a small body size (Hildebrand, 1987). The relation between body size and maneuverability is fundamentally based on Newton's First Law, the law of inertia (Newton, 1687). A larger body has more resistance to any change in its state of motion, and a smaller body is conversely characterized by lower resistance and consequently more maneuverability. Yet stability is related to the position of an individual's center of mass. For greater stability, the center of mass should be low and/or positioned over a large area

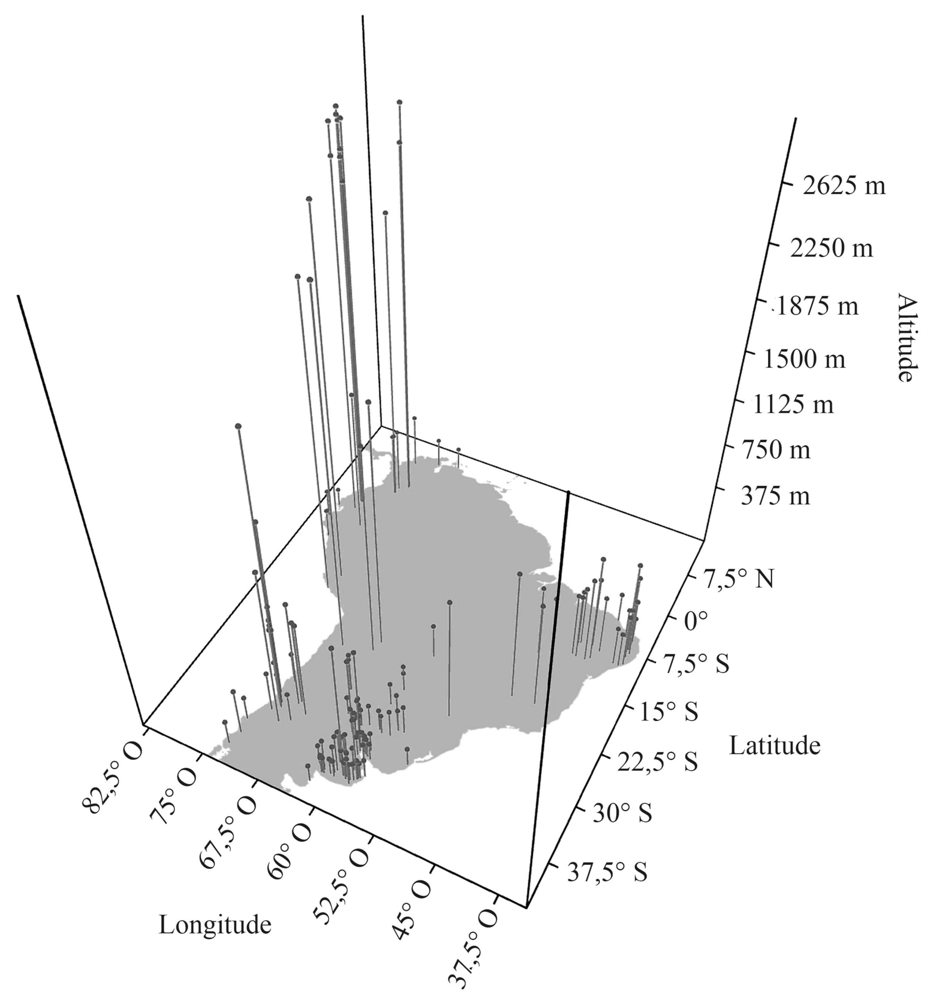

FIGURE 11 | Dispersal graph of the geographic coordinates and altitudes of South American *Equus* fossil occurrences.

delimited by the supporting feet, which is favored by short legs and large feet (Hildebrand, 1987).

Moreover, locomotion on sloping ground is different from locomotion on the plains, because in the former case postural readjustments are essential to propel the body and elevate the leg (Higgins and Ruff, 2011). These readjustments lead animals with shorter autopodials to have relatively higher step length on steep slopes, opposite to the pattern observed in plain environments (Higgins and Ruff, 2011). This tendency for species with shorter autopodials to occur in higher-altitude environments is observed in Perissodactyla: it applies to African zebras (Equidae, also of the genus *Equus*) from the mountains and the plains and, in Tapiridae, to Andean and plains tapirs (Machado, 2014). Within the Equidae, however, Asian asses present a distinct pattern, in which the higher altitude *Equus* species has longer limb bones than the ones from lower altitudes (Machado, 2014). Nonetheless, the Altiplano of Tibet differs from the African and Andean ones in being a plateau, consisting of a wide-open plain at high altitude (Moehlman, 2002). Thus, it seems that the observed variation in the limb proportions of South American *Equus* might have been driven by local topographic relief rather than altitude alone.

The taxonomy of South American *Equus* has always relied on dental and autopodial dimensions. Over almost two centuries, numerous species were identified based on unclear and biased diagnoses that were based primarily on size differences, ignoring the possibility that the observed morphological variations might not in fact be taxonomically diagnostic. Most review publications perpetuated this same idea, and for too long the taxonomy remained confusing and unclear. This contribution has analyzed a broader range of specimens from all over the continent, and from this greater picture it is possible to conclude that the dimensions of the teeth and autopodia are not diagnostic and therefore should not be used in the taxonomy of South American native *Equus*. Dental proportions showed clear superimposition among previously recognized species, and no marked species boundaries could be identified on this basis. Furthermore, autopodial analyses revealed clear superimposition with gradual linear variation, also without any marked intraspecific distinctions. It is inferred here that South America was inhabited by a single species of *Equus*, namely *E. neogeus*, and that its phenotypic variation represents a smooth cline probably driven by the type of topographic relief.

CONCLUSIONS

The results obtained here support the conclusions of Machado et al. (2018), and it is proposed here that *Equus* in South America comprised a single species, *Equus neogeus*. The use of dimensions of teeth and autopodials in South American *Equus* as diagnostic features, as was done previously, is erroneous. Knowledge of the geographic distribution of *Equus* has been increased, showing that this genus was present in the majority of the continent, with the exceptions of the Amazon forest and latitudes south of 40°S. The updated distributional map of South American *Equus* fossils, along with the autopodial analyses, allowed identification of a pattern that may represent a smooth cline of phenotypic variation correlating with topographic relief.

DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

HM and LA were involved in all processes pertaining to the manuscript, from the collection's visits to the analyses and writing.

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Mammal Biochronology (Land Mammal Ages) Around the World From Late Miocene to Middle Pleistocene and Major Events in Horse Evolutionary History

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Biochronology is important to vertebrate chronology because the primary temporal units developed and applied by vertebrate paleontologists for correlation of terrestrial deposits (Land Mammal Ages, LMA) are all biochronologic units. Specific mammal biochronologic scales have been developed for Europe (MN units or ELMA), Asia (ALMA), North America (NALMA), and South America (SALMA). Each timescale is based on land mammal first appearances and characteristic associations on different continental landmasses. Herein, we summarize and review the bases for recognizing mammalian biochronologic units with the most recent update of the Land Mammal Ages. We correlate these ages with the global magnetochronostratigraphic and geochronologic time scales including the major equid evolutionary events of the last 8 million years.

Keywords: ***Equus*** **evolutionary history, biochronology, land mammal ages, Late Neogene, dispersal events**

INTRODUCTION

Vertebrate paleontologists have a long tradition of correlating vertebrate occurrences and evolutionary events into stratigraphic and biochronologic contexts. Both have been utilized for the last 50 years together with an increased usage of radioisotopic and magnetostratigraphic correlations. However, the term biochronology was rarely used prior to 1970's when the application of radiometric dating became widespread and the distinction was made between radiochronology and biochronology as different aspects of geochronology (re: Berggren and Van Couvering, 1974; Gradstein et al., 2004)

According to the original definition (Williams, 1901) a biochron is "*a time unit whose measure is the endurance of an organic character.*" Based on this definition, Berggren and Van Couvering (1974) suggested the application of the term biochron for units of geologic time that are based on paleontologic data without reference to lithostratigraphy or rock units. Thus, the emphasis of mammal occurrences *in time rather than in rocks* distinguishes biochronology from other chronologic systems (Lindsay and Tedford, 1990). The need for a heuristic method for temporal ordering of the fossil vertebrate record without reference to rock units (biostratigraphy) is crucial for the vertebrate record due to the discontinuous nature of terrestrial stratigraphic sequences (e.g., the case of fissure fillings in karstic systems).

Biochronology is an important concept for geochronology, but it has been compromised by a history of loose definitions and diverse usages. In addition, biochronology has never been discussed in any stratigraphic code because of that "loose and ambiguous" application. Furthermore, biochronology is important to vertebrate chronology because the primary temporal units developed and applied by vertebrate paleontologists for correlation in terrestrial deposits are all biochronologic units.

Specific mammal biochronologic scales (LMA = Land Mammal Ages) have been developed for Europe (ELMA), Asia (ALMA), North America (NALMA) and South America (SALMA) based on the succession of evolutionary stage of faunal assemblages and dispersal events (first occurrence of evolving lineages; Mein, 1975, 1979; Lindsay, 1990, 2003; Lindsay and Tedford, 1990; Berggren et al., 1995; Walsh, 1998). These timescales are variously expressed in terms of conventional mammal biochronologic units (sometime termed "zones") or land mammal ages, defined by Lindsay (2003: p. 222) as "*relatively short interval[s] of geological time that can be recognized and distinguished from earlier and later such units (in a given region or province) by a characterizing assemblage of mammals.*" Each timescale is based on land mammals in different continental landmasses and has its own history of development reflecting the uniqueness of the records and the extent to which faunal succession has been resolved. When stratigraphic fortune occurs, these biochronologic units can be tied to biostratigraphic sequences such as the Potwar Plateau, Pakistan (Barry et al., 1982, 2013).

Berggren and Van Couvering developed the concept of a FAD, First Appearance Datum, to identify mammalian lineages that made "a geochronologically instantaneous prochoresis" across intercontinental expanses. Examples of FADs were the "Hipparion" Datum, Proboscidean Datum and later, as exemplified by Lindsay et al. (1980) the *Equus* Datum. Mein (1975, 1979) defined European MN units based in part on migratory events (FADs) and characteristic associations of faunas that he aggregated into MN "zones" (=units).

The "Datum" concept has been challenged by the dearth of independent ages associated with demonstrably primitive species of invading lineages. Bernor (1983, 1984) recognized that Eurasia and Africa were highly provincial throughout the Neogene and proposed provincial mammal biochronologies that led to age realignment for many Old World localities. Steininger et al. (1996) imposed a set of rules that tied MN unit chronology to independently calibrated faunas whenever possible. Resolution of the taxonomic content of a genuinely primitive species of "Hipparion" with dated rocks led to the refinement of the "Hipparion" Datum demonstrating that the first occurring "Hipparion" in Europe was a species of North American *Cormohipparion* circa 11.2 Ma (Woodburne, 2007, 2009; Bernor et al., 2017). The "Hipparion" Datum, as such was renamed the *Cormohipparion* Datum by Bernor et al. (2017) in recognition of the ancestral North American lineage reported from Pakistan, Turkey and North Africa at 10.8 Ma. The original Berggren and Van Couvering (1974) mammalian lineage "Datum Event" has given way to a realization that what FADs are actually accomplishing is demonstrating local earliest occurrences of immigrating taxa. In the case of Old World "Hipparion", first occurrence discrepancy has narrowed: 11.2 in Central Europe and Spain, 10.8 Ma in Pakistan, Turkey and North Africa (Bernor et al., 2017). Diachroneity in local FADs can be due to physical barriers and/or ecological filters, or to the lack of appropriate sedimentary rocks. Proposed mammalian FADs represent testable hypotheses about invading lineages and their extension over great geographic extent during a short interval of time.

We summarize and review herein a comparative biochronologic framework that provides the most recent update of the Land Mammal Ages characterized, defined and calibrated across different continents (either in Old or New World). We correlate these with magnetochronostratigraphic and geochronologic time scales (**Figure 1**) and summarize the major equid evolutionary events for the last 8 million years. This contribution is intended to compliment contributions to the Frontiers in Ecology and Evolution work on "Examining Evolutionary Trends in *Equus* and its Close Relatives from Five Continents," and has been written with the aim of offering an overview of the chronology of *Equus* and its close relatives across the geographic/chronologic range where they occur: North and South America, Eurasia and Africa. It is not intended to integrate molecular and DNA interpretations of divergence times in *Equus*; it addresses only the paleontological data reviewed and revealed in this Frontiers collection of works.

A TIMESCALE FOR HORSE EVOLUTION IN NORTH AMERICA

The Hemphillian LMA ranges from approximately 8 Ma up to about 4 Ma, with four faunal stages (Hh1-Hh4), and therefore is late Miocene to early Pliocene in age (**Figure 1**). It is marked by a continuous loss of autochthonous taxa and by a rising immigration rate including from South America and diverse small mammals and carnivores and some ungulates from Eurasia including the hipparionine *Plesiohipparion* from China (Hulbert and Harington, 1999). There is a 7–6 Ma turnover event (Hh2/Hh3) with the extinction of *Protohippus, Calippus,* and *"Hipparion"* as well as species level turnover in most surviving genera. Equid species richness at many North American late Clarendonian or early Hemphillian sites often ranged between 8 and 11; after this event it was never >6 and most often 3 or 4; monodactyl equids (mostly *Dinohippus* and *Astrohippus*) became abundant at this time (Hulbert, personal communication). Hh4 extends across the Mio-Pliocene boundary (5.33 Ma) calibrated as being 5.3–4.9 to 4.6 Ma (Bell et al., 2004; Tedford et al., 2004). Equids recorded from this interval include *Dinohippus mexicanus, Neohipparion* cf. *eurystyle* and *Astrohippus stocki* and with more limited distributions *Cormohipparion emsliei, Nannippus aztecus,* and *Pseudhipparion simpsoni;* these last taxa can be considered relictual from the late Miocene.

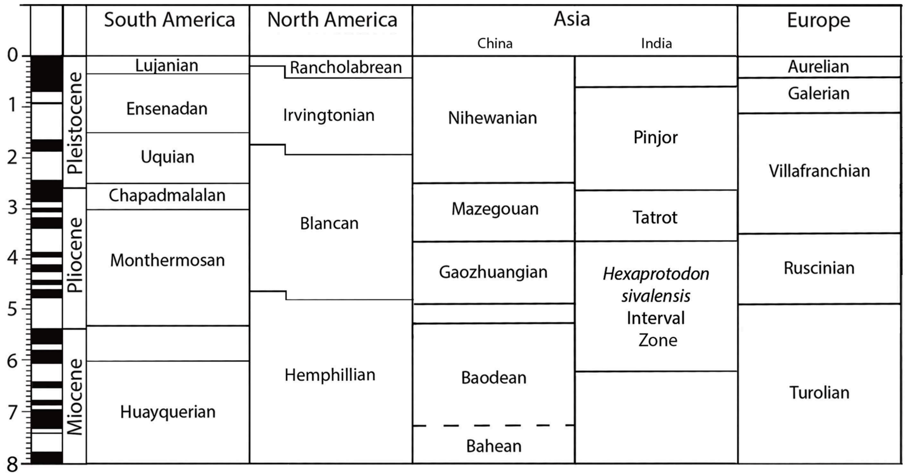

FIGURE 1 | Land Mammal Ages in South America, North America, Asia (China and India) and Europe from 8 Ma with magnetochronostratigraphic and geochronologic time scales.

As cited above, the Hemphillian LMA ranges from the latest Miocene into the early Pliocene, 4.6 Ma (Hh4), but a range of 5.2–4.6 Ma for the earliest Blancan has been proposed (Repenning, 1988; Bell et al., 2004). The succeeding Blancan LMA has been defined by the first appearance In North America of arvicoline rodents, circa 4.8 Ma (Repenning, 2003). Repenning (1988) divided the Blancan into 5 intervals: Blancan I (4.9–4.62 Ma.), Blancan II (4.62–4.1 Ma.), Blancan III (4.1–3.0 Ma.), Blancan IV (3.0–2.5 Ma.), Blancan V (2.5–1.9 or 1.72 Ma.). Subdivision of the Blancan is based largely on small mammal faunas (Repenning, 1988). Bell et al. (2004) reviewed the data suggesting a 5-part subdivision of the Blancan and concluded that Blancan II and IV cannot be distinguished, but accepted Blancan I, III, and V. Blancan II is essentially a continuation (and further characterization) of Blancan I, while Blancan IV is a continuation and further characterization of Blancan III. Revised Blancan chronologic ranges are: Blancan I (∼4.9–4.1 Ma), Blancan III (∼4.1–2.5 Ma), and Blancan V (∼2.5–1.9 or 1.72 Ma) (Bell, personal communication).

Dinohippus is known to occur in the Blancan I interval, while *Equus* (*Plesippus*) *simplicidens*, *E. (P.) idahoensis*, and *E. cumminsii* are reported from the Blancan III and later Blancan assemblages. The diminutive hipparionine horse *Nannippus peninsulatus* is reported from the Blancan V interval but does not survive into the Irvingtonian. The base of Blancan V corresponds closely to the initiation of the Quaternary, i.e., the beginning of the Pleistocene.

The Irvingtonian is divided into three units, Irvingtonian I (1.9–1.7 Ma), Irvingtonian II (0.85–0.4 Ma), and Irvingtonian III (0.4–0.195 Ma) (Bell et al., 2004). Early Irvingtonian *Equus* includes *E. scotti, E. conversidens* (sensu Scott, 2004), and *Haringtonhippus francisci* (possibly including *E. calobatus*). The Rancholabrean NALMA extends from 0.195 to about 0.011 Ma with the onset of the Holocene. Common Rancholabrean equid species include *Equus scotti*, *E. conversidens*, and *Haringtonhippus francisci*. *Equus occidentalis* is also abundant in the American southwest during this period. Fossils resembling *Equus ferus* have also been documented from Rancholabrean faunas.

The Blancan NALMA is defined by the first appearance in North America south of 55 degrees N Latitude of the arvicoline rodents *Mimomys* and *Ophiomys* (5.2–4.6 Ma) (Repenning, 1988; Bell et al., 2004). The Irvingtonian NALMA is defined by the first appearance of *Mammuthus* south of 55 degrees N Latitude. The Rancholabrean NALMA is defined by the first appearance of the bovid *Bison* in North America.

A TIMESCALE FOR HORSE EVOLUTION IN ASIA

Pleistocene fossils of *Equus* are abundant in Asia and overlap those of hipparionine horses. The vast central Asian steppe provided an ideal habitat for these horses adapted to open landscapes. These rich fossil records enabled a long history of studies on the equids (Qiu et al., 1987; Deng and Xue, 1999; Bernor et al., 2018b), but chronological control for a precise timing and sequence of horse evolution, particularly that of *Equus*, has been neglected until recently (Deng and Sun, in press). The Late Neogene faunal record in East Asia is now based on a greatly improved chronological framework given intense interest in Pleistocene climate oscillations and in the multiple dispersions of hominids (cfr. Li et al., 2019; Zanolli et al., 2019).

East Asian paleoenvironments were intensely influenced by monsoons during the Ice Age and cyclical development of windblown sediments left a paleosol sequence in the Chinese Loess Plateau that archives a high-resolution chronologic record. These fine-grained deposits are ideally suited for paleomagnetic analysis, the dating of which can be further refined by astronomical tuning to the Milankovitch cycles. The resulting chronological framework helps to establish the sequence of several classical *Equus*-producing localities as well as recently discovered records. From old to young, the following early Pleistocene chronology for *Equus* represents the current state of knowledge.

Equus eisenmannae (Qiu et al., 2004) is a large primitive stenonine horse from the Longdan loessic section in Linxia Basin, Gansu Province. The Longdan area (35.5°N, 103.5°E) is located in the central part of the Linxia Basin. The locality has been correlated biochronologically with the early Nihewanian (Qiu et al., 2004; Wang and Deng, 2011). Wang and Deng (2011) reported 13 levels in the entire Longdan section and the base of this section is considered about 3.5 Ma (Qiu et al., 2004). The fossils referred to *Equus eisenmannae* occur in the 5th, 9th, and 11th levels correlating to 2.55, 2.16, and 1.86 Ma, respectively (Wang and Deng, 2011). Wang and Deng combine the 9th and 11th levels into an "upper level" recognizing level 5 as the "lower level," as was originally proposed by Qiu et al. (2004). Wang and Deng (2011) found no statistical differences among fossils from the upper and lower levels and referred them all to *Equus eisenmannae. Equus eisenmannae* is one of the largest Old World stenonine horses close in its size to first-occurring European *Equus, E. livenzovensis* (Bernor et al., 2018a).

Although represented by poorly preserved fossils, *Equus* sp. from Zanda Basin in southern Tibet (Wang et al., 2013) was correlated to 2.48 Ma, suggesting fast dispersion of *Equus* even in higher elevations, where modern Tibetan ass, *E. kiang*, currently lives. *Equus sanmeniensis*, another large species of *Equus,* is reported from the Shangshazui stone artifact site in the classical Nihewan Basin (1.7–1.66 Ma) and nearby Majuangou III (1.66 Ma) hominin tool site (Ao et al., 2013). This species was also recorded from the *Homo erectus* site at Gongwangling, Lantian Area, Shaanxi Province, and magnetically considered slightly younger ∼1.54–1.65 Ma (Zhu et al., 2015). *E. yunnanensis* from the *Homo erectus* site at Niujianbao in Yuanmou Basin was magnetically correlated as slightly younger than chron C2n, ∼1.7 Ma (Zhu et al., 2008).

In South Asia, equids are represented by hipparionines in the Miocene and Pliocene. The diverse *Sivalhippus* lineage, common in the late Miocene, disappears from the record after 6.0 Ma (Wolf et al., 2013). Within the *Hexaprotodon sivalensis* Interval Zone in the Siwalik Group (6.2 Ma to 3.6 Ma; Flynn et al., 2013), equid remains are rare. Hipparionines represented by *Plesiohipparion huangheense*, and *Eurygnathohippus* sp. appear in the record between 3.6 and 2.6 Ma (Jukar et al., 2018, in press), in an interval of time (correlative to the Gauss chron) commonly called the Tatrot Faunal Zone (**Figure 1**), or sometimes the *Elephas planifrons* Interval Zone in the Indian Siwaliks (Nanda, 2002). The youngest indeterminate hipparionine records are correlated paleomagnetically to ∼2.6–2.5 Ma, around the same time the first *Equus* occurs in South Asia (Opdyke et al., 1979; Patnaik, 2013). *Equus* makes its appearance just above the Gauss-Matuyama chron boundary, which coincides with the Plio-Pleistocene transition (Patnaik, 2013). In the Siwaliks, remains of *Equus* have been found in sediments ranging from 2.6 to 0.6 Ma, a faunal unit termed the Pinjor Faunal Zone (reviewed by Patnaik, 2013). The Pinjor Faunal Zone is named after the Pinjor Formation near the town of Chandigarh, Northern India (Kumaravel et al., 2005). Temporally equivalent sections are known from the Pabbi Hills and Mirpur areas in Pakistan (Hussain et al., 1992; Dennell et al., 2006). As noted in Bernor et al. (2019), two morphotypes of *Equus* have been recorded—a large taxon called *Equus sivalensis*, and a smaller taxon sometimes called *Equus sivalensis minor* for specimens from the Upper Pinjor Formation near the town of Mirzapur (Gaur and Chopra, 1984), *Equus* cf. *sivalensis* from the Pabbi Hills (Dennell et al., 2006), and Equus sp. A (small) for specimens from the Mangla-Samwal anticline (Hussain et al., 1992). *Equus sivalensis* has been recorded from the entire temporal range of the Pinjor Faunal Zone (Patnaik, 2013), however, the temporal range of the smaller horse appears to be restricted to ∼2.2–1.2 Ma (Hussain et al., 1992; Dennell et al., 2006). In the late Pleistocene, *Equus namadicus* and *Equus hemionus* are known from the Indian peninsula (Chauhan, 2008).

A TIMESCALE FOR HORSE EVOLUTION IN EUROPE

Equus is not recorded in the Miocene—Pliocene fossil record of Europe: Vallesian, Turolian, Ruscinian, and early Villafranchian in the European Land Mammal Age scheme (**Figure 1**). European Land Mammal Ages are also referable to the MN (=Mammal Neogene) "zone" or unit, a system used to correlate European mammal-bearing fossil localities: it consists of 16 consecutive zones (numbered MN 1 through MN 17; MN 7 and 8 have been joined into MN 7/8) defined through reference faunas, well-known sites that other localities can be correlated with (Mein, 1975, 1990; Bruijn et al., 1992). These times are characterized by different hipparionine horse evolutionary lineages (Bernor et al., 1996, 2010, 2017). The European Plio-Pleistocene interval is mostly included in the Villafranchian Land Mammal Age (Rook and Martínez-Navarro, 2010). The early Villafranchian correlates with the Late Pliocene, ca. 3.5 to 2.6 Ma, the middle Villafranchian ca. 2.6 to 2.0 Ma (most of the "former" Late Pliocene), and the late Villafranchian is correlative with the remaining Early Pleistocene (Matuyama from Olduvai to Jaramillo subchrons), a time span of ca. 2.0 to 1.0 (that includes the latest part of the former Late Pliocene to most of the former Early Pleistocene). The first appearance of *Equus* in Europe corresponds to the base of the Middle Villafranchian, ca. 2.6 Ma.

Montopoli was identified by Azzaroli (1970, 1977) as representing an early Middle Villafranchian locality and Lindsay et al. (1980) recognized the Montopoli *Equus* as representing the local *Equus* Datum, ca. 2.6 Ma. Bernor et al. (2018a) identified the large horse at Montopoli as being referable to *Equus* cf. *livenzovensis.* Earlier, Rook et al. (2017) identified a small hipparion co-occurring at Montopoli as one of the last surviving members of these tridactyl horses. The arrival of *Equus* in Europe (the so called "elephant-*Equus* event") has been classically indicated by Azzaroli (1983) as "a turning point in the history of Eurasia." *Equus livenzovensis* appears to be at the base of the radiation of the later lineage of fossils horses, the European Pleistocene *Equus stenonis* group (= stenonine horses). The European stenonine horses have been revised by Alberdi and Palombo (2013). In addition to *Equus livenzovensis*, the

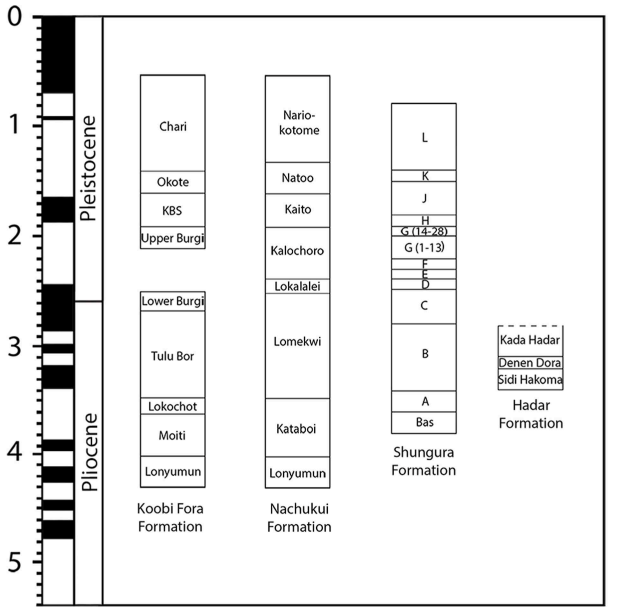

FIGURE 2 | Correlation of the Koobi Fora, Nachukui, Shungura and Hadar Formation with magnetochronostratigraphic and geochronologic time scales. Modified from Werdelin (2010).

species (and their chronological ranges) included in this group are *Equus stenonis* (end of middle Villafranchian to early late Villafranchian; Early Pleistocene, 2.4–1.7 Ma), *Equus stehlini* (late Villafranchian; Early Pleistocene, 1.8–1.6 Ma), *Equus altidens*, and *Equus suessenbornensis* (end of late Villafranchian to early Galerian, Early Pleistocene to early Middle Pleistocene, 1.6–0.6 Ma). Most of these taxa are discussed at greater length by Bernor et al. (2019).

A TIMESCALE FOR HORSE EVOLUTION IN AFRICA

The Miocene to Pleistocene mammal record of Africa is overall less complete than the fossil record on other continents and there is no established land mammal age scheme for Africa at a continental scale (Werdelin, 2010). The completeness of the mammal fossil record across the continent is extremely variable with regions in which the Neogene record is totally missing and others (such as Kenya or Ethiopia) with a relatively densely documented record. Without an established continental-scale biochronology, Africa's "biochronology" is based on the stratigraphic ordering of mammal-bearing localities in different sedimentary basins and is largely dependent on radiochronology with limited use of magnetostratigraphy (**Figure 2**). Pickford (1981) divided Miocene faunas from Kenyan sites into Faunal Sets I to VII. Pickford (1981) suggested age spans for his late Miocene sets to be 12.0–10.5 Ma (V), 10.5–7.5 (VI), and 7.5–5.5 (VII)

The Late Miocene-Early Pliocene boundary is poorly represented in Africa. Hipparionine horses are first found in North and East Africa circa 10.5 Ma (Bernor and White, 2009) the richest sites being the Algerian locality of Bou Hanifia and the Ethiopian locality of Chorora (Bernor et al., 2010). At the end of the Late Miocene, diversification of the hipparionine genus *Eurygnathohippus* (exhibiting evolutionary relationships to Siwalik hipparionines; Jukar et al., in press) was well under way, as was significant evolution among endemic elephants and marked successes by new bovid tribes and suines arriving from Eurasia.

Again, also for the Plio-Pleistocene of Africa there are no established land mammal ages. This time period has been rigorously studied biochronologically by temporal distributions of elephants (particularly subspecies or stages of *Elephas recki*) and suids, often in conjunction with the dating of hominin finds (re: Sanders et al., 2010). *Equus* first occurs in Africa during the early Pleistocene, in lower Member G of the Omo Shungura Formation (2.33 Ma) (Bernor et al., 2010). This age in Africa is delayed relative to Eurasia, where it is 2.6 Ma. First occurring African *Equus* is apparently related to European *E. stenonis* and Chinese *E. eisenmannae* (a detailed morphological comparison is necessary to resolve their relationships; Bernor et al., 2019). Eisenman (1983) named a new species of *Equus* from Koobi Fora, *E. koobiforensis* (circa 1.9 Ma) and recognized a smaller horse also from Koobi Fora, *E.* cf. *tabeti*. Bernor et al. (2019) distinguished *Equus oldowayensis* from Member 1, Olorgesailie (0.99 Ma) from *E. koobiforensis* and *E.* cf. *tabeti*. Azzaroli (1982, 2003) suggested that *E. koobiforensis* was referable to *E. grevyi* and recent study by Bernor at the Kenya National Museum, Nairobi suggests that *E. koobiforensis* is morphologically similar to *E. grevyi. Equus oldowayensis* from Olorgesailie however is derived in its robustly built premaxilla and symphysial region and great cheek tooth crown height (Bernor and Potts, personal observation). Representatives of the genus *Equus* dominate *Eurygnathohippus* by a ratio of 2:1 in the Ethiopian locality of Daka (Gilbert and Bernor, 2008) as well as Member 1 of Olorgesailie (Bernor and Potts, personal observation) with *Eurygnathohippus* sharply declining in its numbers in East and South Africa after 1 Ma. Our current understanding of extant African zebra and ass morphology, combined with our investigations of East African Pleistocene *Equus* evolution, thus far does not permit us to identify genuine representatives of *Equus quagga, Equus grevyi, Equus zebra* or *Equus africanus* in the African Pleistocene record.

A TIMESCALE FOR HORSE EVOLUTION IN SOUTH AMERICA

Two lineages of Equidae occurred in South America during the Pleistocene, *Hippidion* and *Equus*. Although there is no fossil record of *Hippidion* in Central or North America, most evidence suggests that both taxa originated and diversified in North or Central America and then migrated independently to South America during the important biogeographical events known as the Great American Biotic Interchange (GABI, ca. 3.0 Ma; Woodburne, 2010; MacFadden, 2013; Avilla et al., 2015). However, there is no record for Equidae in South America until the beginning of Pleistocene, well after the Pliocene formation of the Isthmus of Panama (around 3 Ma; Woodburne, 2010;

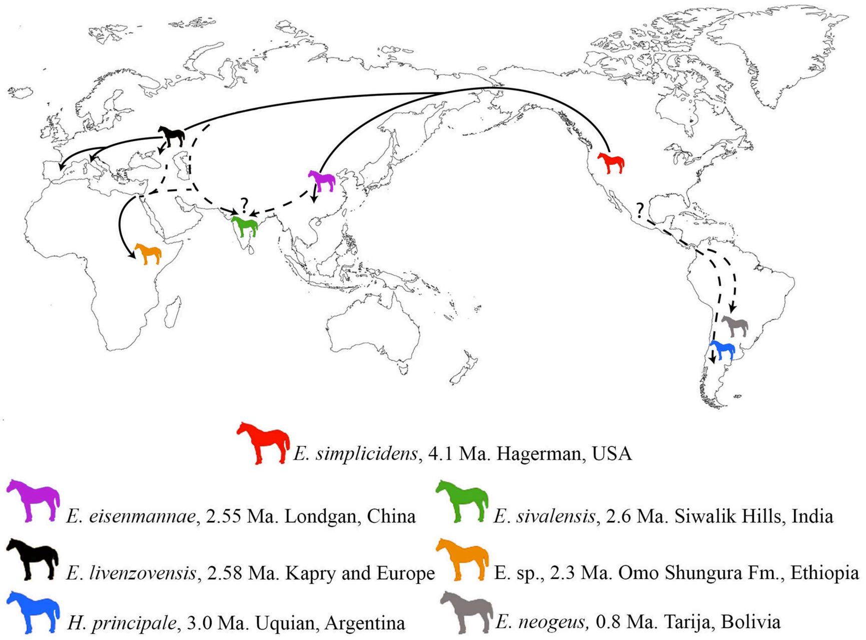

FIGURE 3 | Biogeographic extension of early *Equus* species across the five continents, with timing of early record of each species.

MacFadden, 2013). The first known occurrence of Equidae in South America is *Hippidion principale* from Early Pleistocene deposits (Uquian) of Argentina (Woodburne, 2010; Avilla et al., 2015). However, the age of the first record of *Equus* in South America is controversial. Traditionally, its earliest record is considered middle Pleistocene (Ensenadan SALMA) for Tarija outcrops in Southern Bolivia, with a biostratigraphic sequence at Tolomosa Formation independently calibrated to between ∼0.99 to <0.76 Ma (MacFadden, 2013). Nevertheless, there is no consensus about the age of those deposits and some researchers consider the deposition in Tarija to have occurred only during the Late Pleistocene (Coltorti et al., 2007 and references there in). Recently, it was proposed that only one species of *Equus* lived in South America during the Pleistocene, *E. neogeus* (Machado et al., 2017). This species is considered an index-fossil for deposits of Lujanian SALMA (late Pleistocene-earliest Holocene; 0.8 to 0.011 Ma; **Figure 1**). Although *E. neogeus* was widely distributed in South America, only a few localities are calibrated by independent chronostratigraphic data, indicating a Lujanian SALMA (Prado and Alberdi, 2017). Therefore, the dispersal of *Equus* into South America occurred during the GABI (from 3.0 Ma on), but if the *Equus* earliest record is truly Late Pleistocene, then it falls in the fourth and latest phase of the GABI (SALMA Lujanian, from 0.8 to 0.011 Ma) or possibly *Equus* migrated to South America during GABI 3 (SALMAs Ensenadan and Bonaerian, from 1.2 to 0.8 Ma), considering its early record in the middle Pleistocene (between ∼0.99 and <0.76 Ma; MacFadden, 2013). All equids that occurred in South America during the Pleistocene (*Hippidion* and *Equus*) became extinct in the early Holocene (10,710 ± 100 cal ka BP, from Southern Chile; Avilla et al., 2015; Villavicencio et al., 2016; Machado et al., 2017).

CONCLUSION

Unlike high-resolution biostratigraphic and geochronologic tools available in the marine realm, mammalian biochronology is not permissive of recognizing strictly synchronous events at global scale. The *Equus* "Datum" event was heralded by Lindsay et al. (1980) as being a synchronous dispersion of *Equus* from North America to Eurasia and Africa at 2.5 (now 2.6) Ma. We have shown that this extension can be recognized at the genus, not species level, in Europe and rather closely in East and South Asia but was apparently later in Africa (**Figure 3**). The "*Equus* Datum" really reflects a first regional-intercontinental scale event with an approximate chronology: 2.6 Ma in Europe (Alberdi and Palombo, 2013) and 2.55 Ma in the Linxia Basin, China (Qiu et al., 2004; Wang and Deng, 2011) and 2.33 Ma in Ethiopia, East Africa (Bernor et al., 2010 and herein). Nevertheless, our review of the currently available evidence of the Land Mammal Ages, defined and calibrated across different continents (both Old and New World), allows us to recognize major faunal change. These changes in some cases correspond the limit between successive Land Mammal Ages, and can be dated by combining biochronologic, radioisotopic and magnetostratigraphic data.

AUTHOR CONTRIBUTIONS

LR and RB conceived the paper. LA provided data on South America. RB and ES provided data on North America. AJ, LF, and XW provided data on Asia. LR and OC provided data on Europe. WS, RB, and LR provided data on Africa. LR wrote the paper with input from all authors. All authors contributed to the final version of the manuscript.

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Evolutionary Significance of Equinae From the Mexican Neogene

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North American Equinae integrates a monophyletic clade that consists of about 20 genera and 80 species. This group includes horses with hypsodont cheek teeth belonging to the merychippines and the tribes Hipparionini, Protohippini, and Equini. The primary adaptive radiation and diversification of Equinae occurred in the Neogene period (23.03–2.53 Ma). In Mexico, 11 genera and 20 species of Neogene Equinae have been reported, which correspond to 55 and 28% of the generic and specific diversity in North America, respectively. The Mexican record exhibited their major diversity during the late Miocene (10 species) and evidences part of the evolutionary history of North American Equinae, as it is stated in the following considerations: (1) The presence of merychippine species from the late Hemingfordian—early Barstovian (18–15 Ma) of southern Mexico ("*Merychippus*" cf. *primus* and "*M.*" cf. *sejunctus*) that are related with earliest representatives of Equinae in North America. (2) The occurrence of populations referable to *Cormohipparion* aff. *quinni*, *Calippus* sp., and *Pliohippus* sp. from the early—late Barstovian (15–14 Ma) of southern Mexico, which are synchronous with the first known appearances of those genera from the Great Plains and Gulf Coastal Plain in the United States. (3) The equine horse *Dinohippus mexicanus* from the late Hemphillian (4.8 Ma) of central and northern Mexico that is considered the closest sister species of primitive *Equus*. These records suggest that early differentiation of some hipparionines, protohippines, and equines may have had occurred also in areas of southern tropical North America during the middle Miocene; furthermore, the origin of primitive *Equus* could be traced from the Mexican record.

Keywords: species diversity, taxonomic evolution, adaptive radiation, horses, Neogene, Mexico

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INTRODUCTION

Horses were one of the most common components of the Cenozoic faunas of North America (MacFadden, 1992, 1998). Because of their significant occurrence in the fossil record, they have been considered as a suitable model to explain rates and patterns of evolution (MacFadden, 1988, 1992; MacFadden and Hulbert, 1988; Carroll, 1998). These perissodactyls experienced one of their major adaptive radiations during the Miocene (18–15 Ma), resulting in the differentiation of members that comprise the subfamily Equinae (Hulbert and MacFadden, 1991).

The subfamily Equinae is defined as a group of subhypsodont to hypsodont horses (unworn molar crown height $\geq$25 mm), consisting of a set of paraphyletic species traditionally referred as the merychippines, as well as the monophyletic hipparionines (Hipparionini), protohippines

(Protohippini) and equines (Equini) (Hulbert and MacFadden, 1991; Hulbert, 1993; Kelly, 1995, 1998).

In North America, the Equinae spanned from the early Miocene to the late Pleistocene, having a geochronological duration of about 18 million years. They became extinct at about 11 ka and survived in the Old World, although Europeans brought them back to the Americas in the sixteenth century (MacFadden, 1992). Extant members belong to the genus *Equus*, and include horses, asses, and zebras (MacFadden, 1992; Franzen, 2010).

Most of the evolutionary history of North American Equinae occurred during the Neogene (23–2.6 Ma). This group of horses experienced important changes in their species diversity related to speciation and extinction processes (Hulbert, 1993). Most of what is known regarding the evolution of North American Equinae derives from the study of fossil samples recovered from numerous localities in the United States (MacFadden, 1984a, 1992; Hulbert, 1989; Hulbert and MacFadden, 1991; Kelly, 1995, 1998; Maguire and Stigall, 2008). A small number of studies have considered Mexican samples in order to understand evolutionary aspects of some members of Equinae (e.g., MacFadden, 1984b; MacFadden and Carranza-Castañeda, 2002; Ferrusquía-Villafranca et al., 2014).

The North American record of Neogene Equinae consists of 20 genera and at least 70 species (Maguire and Stigall, 2008). The Mexican record includes 11 genera and 20 species, evidencing 55 and 28% of the generic and specific diversity respectively, from North America (Priego-Vargas et al., 2016).

Given the significant representation of members of Equinae throughout the Mexican Neogene the aims of this study are to present an overview of the known record of this group of horses and to provide some assumptions on their taxonomic evolution. Furthermore, comments on the significance of the Mexican record in relation to the adaptive radiation of North American Equinae and the origin of *Equus* are also provided.

MATERIALS AND METHODS

Taxonomic information and geographic distribution of Equinae from the Mexican Neogene were collected from the comprehensive review of the Cenozoic horses from Mexico by Priego-Vargas et al. (2016) (**Table 1**). The Mexican horse record is described in a biochronological sequence from the Hemingfordian to the Blancan North American Land Mammal Ages (NALMAs). NALMAs are from Tedford et al. (2004) and Bell et al. (2004).

The pattern of species richness of the Mexican Equinae was described using a bar graph of the number of species reported throughout the Neogene. The change in the number of species has been related to the geology and climate of the Mexican Neogene. Geologic history is for the most part from Ortega-Gutiérrez et al. (1992) and Ferrusquía-Villafranca (1993), whereas climatic history is from González-Medrano (1998).

An approach of the taxonomic evolution of Equinae from the Mexican Neogene is described in terms of the chronological range of selected taxa (Hulbert, 1993; Carroll, 1998). The chronological range is defined by the first and last appearances of a particular horse species in the Mexican fossil record, considering its occurrence in all localities where it has been reported. It should be stated that species reported from a single locality were removed from this approach because cannot provide a suitable estimation of its temporal range (Robinson et al., 2018). The species *"Merychippus"* sp. from the Hemingfordian of Oaxaca and the majority of the protohippines have been not considered given that are known from single localities. It is noted that *Calippus hondurensis* is the well-known and documented protohippine from the late Miocene of central Mexico (Carranza-Castañeda, 2006; Carranza-Castañeda et al., 2013).

Temporal ranges of the selected species are derived from the dating of some of the rock bearing-units and the biochronology of Mexican mammalian faunas that contain Neogene horses (Lindsay et al., 1984; Ferrusquía-Villafranca, 1992, 1996, 2001; Kowallis et al., 1999; Carranza-Castañeda, 2006; Carranza-Castañeda et al., 2013). The species considered comprise 70% of the known record of the Mexican Neogene horses (**Table 2**).

We compared the temporal range of selected Mexican hipparionines and equines with that from the North American record. The comparison with the other groups of horses (merychippines and protohippines) is restricted given their information available from the Mexican Neogene. The temporal duration of the North American species is derived from the temporally calibrated cladogram of the Equinae of Maguire and Stigall (2008; **Figure 1**, p. 176) (**Supplementary Data**). A Mann-Whitney *U*-test was used to compare the temporal range of the Mexican and North American Equinae. This test was selected because the normality of the data is unwarranted. It should be stated that the results derived from the analysis represent a rough interpretation of the taxonomic evolution of the Equinae from the Mexican Neogene.

The interpretation of the species diversity and the taxonomic evolution of the Mexican Neogene horses is derived from the available information of this group of horses. It should be stated that the known record shows taxonomical, chronological, and geographical limitations. Taxonomically, there are an important number of taxa whose species identity is uncertain, such as the merychippines and the majority of the protohippines. Chronologically and geographically, there is a biased to the Hemphillian and Blancan faunas of central Mexico. Hence, considerations regarding these topics are susceptible to be modified and/or corroborated, as new evidence of Mexican Neogene horses is available. Nevertheless, this report represents the first attempt to provide information on the evolutionary significance of the Mexican Neogene horses.

The following terms have been used to refer to the groups of horses considered in the study:

> Equinae.-A group of hypsodont horses consisting of merychippines, hipparionines, protohippines, and equines.
> Merychippine.-A paraphyletic group of species referred as to *"Merychippus,"* including *"Merychippus" gunteri*, *"M." primus*, *"M." sejunctus*, *"M." intermontanus*, *"M." coloradensis*, *"M." republicanus*, and *"M." goorisi*.

TABLE 1 | List of localities that bear fossil material belonging to Equinae from the Mexican Neogene.

Taxon	**Northern Mexico**		**Central Mexico**																	**Southern Mexico**			
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**
MERYCHIPPINES																							
"Merychippus" sp.																				X			
"M." cf. primus																					X	X	
"M." cf. sejunctus																					X	X	
HIPPARIONINI																							
Merychippus cf. *californicus*																						X	
Cormohipparion aff. *quinni*																						X	X
Hipparion sp.									X														
Neohipparion eurystyle		X	X			X	X	X			X		X			X							
Nannipus aztecus				X			X				X	X											
Nannipus peninsulatus		X		X				X			X		X	X	X	X							
PROTOHIPPINI																							
Calippus sp.																						X	
C. martini										X													
C. hondurensis					X	X	X				X	X				X							
Protohippus sp.									X														
EQUINI																							
Pliohippus sp.																					X	X	
P. potosinus																		X					
Astrohippus ansae						X																	
A. stockii		X		X	X		X				X		X										
"Dinohippus" interpolatus							X	X			X					X							
"D." mexicanus		X	X		X	X					X		X										
Equus simplicidens	X			X				X			X			X	X				X				

***Localities**: 1, El Golfo (BCN); 2, Yepómera (CHIH); 3, Los Gigantes (NAY); 4, Tecolotlán (JAL); 5, Teocaltiche (JAL); 6, Juchipila (JAL—ZAC); 7, Colotlán—Tlatenango (JAL—ZAC); 8, Charo (MICH); 9, Escobedo (GTO); 10, Neutla (GTO); 11, San Miguel de Allende (GTO); 12, Landa de Matamoros (QRO); 13, Tula—Tepeji (HGO); 14, Actopan—Ixmiquilpan (HGO); 15, Santa María Amajac (HGO); 16, Zietla (HGO); 17, Tehuichila (HGO); 18, Paso del Águila (SLP); 19, Las Tunas (BCS); 20, Suchilquitongo (OAX); 21, Matatlán (OAX); 22, Nejapa (OAX); 23, Ixtapa (CHIS). BCN, Baja California Norte; BCS, Baja California Sur; CHIH, Chihuahua; GTO, Guanajuato; HGO, Hidalgo; JAL, Jalisco; MICH, Michoacán; OAX, Oaxaca; QRO, Querétaro; SLP, San Luis Potosí; ZAC, Zacatecas. Data source: Priego-Vargas et al. (2016).*

Hipparionine.-A monophyletic group of species in the tribe Hipparionini, including *Merychippus insignis*, *M. brevidontus*, *M. californicus*, *Neohipparion*, *Pseudhipparion*, *Hipparion*, *Nannipus*, and *Cormohipparion*.

Protohippine.-A monophyletic group of species in the tribe Protohippini, including the genera *Protohippus* and *Calippus*.

Equine.-A monophyletic group of species in the Tribe Equini, including *Acritohippus*, *Parapliohippus*, *Pliohippus*, *"Pliohippus*,*"* *Astrohippus*, *Dinohippus*, *"Dinohippus*,*"* *Equus*, *Onohippidion*, and *Boreohippidion*.

OVERVIEW OF EQUINAE FROM THE MEXICAN NEOGENE

The record of Equinae from the Mexican Neogene consists of 20 species in 11 genera, including representatives of the merychippines, hipparionines, protohippines, and equines. The fossil sample that integrates this record includes skulls, mandibles, as well as numerous teeth and postcranial bones. The material has been recovered from about 23 areas unevenly distributed across the Mexican territory. Most of the sites are late Miocene to Pliocene in age and are distributed in central Mexico, except El Golfo (Baja California Norte) and Yepómera (Chihuahua) localities, northern Mexico. There are one early Miocene site and three middle Miocene sites in southern Mexico (**Figure 1**, **Table 1**).

Hemingfordian and Barstovian Mexican Horses

The horses of these faunal stages come from the Suchilquitongo, Matatlán, and Nejapa localities in Oaxaca, as well as the Ixtapa locality in Chiapas, all in southern Mexico. The record consists of seven species that comprise 35% of the Mexican Equinae, including the oldest members of this group of horses from the Neogene of Mexico and the southernmost occurrences of fossil populations referable to merychippines, hipparionines, protohippines, and equines from North America during the middle Miocene (Bravo-Cuevas, 2000; Bravo-Cuevas and Ferrusquía-Villafranca, 2006, 2008, 2010). The fossil bearing-units are part of the Suchilquitongo Formation (K-Ar and paleomagnetic dated in 18.2–19.6 Ma) (Ferrusquía-Villafranca, 1992; Urrutia-Fucugauchi and Ferrusquía-Villafranca, 2001), the Matatlán and El Camarón formations (both K-Ar dated 15.15 ± 0.8–16.35 ± 0.75 Ma), Oaxaca (Ferrusquía-Villafranca, 1992, 2001); as well as the Ixtapa Formation (K-Ar dated 15.02 ± 0.35–16.02 ± 0.53 Ma), Chiapas (Ferrusquía-Villafranca, 1996).

The Hemingfordian record consists of a single occurrence referable to *"Merychippus"* sp. from Suchilquitongo (Ferrusquía-Villafranca, 1990), which is (as far as we know) the oldest member of the Mexican Equinae. The sample includes a tooth fragment whose crown height and fossette plication degree are comparable to those observed in some Hemingfordian and Barstovian equines (e.g., *Acritohippus tertius*) and hipparionines (e.g., *Merychippus californicus*) (Ferrusquía-Villafranca, 1990).

Six Mexican species of Equinae are known during the Barstovian. The merychippines have been referred to *"Merychippus"* cf. *primus* and *"Merychippus"* cf. *sejunctus* from the Matatlán and Nejapa localities. The sample belonging to these species includes a mandibular fragment, a maxillary fragment, and several isolated teeth (Bravo-Cuevas and Ferrusquía-Villafranca, 2006).

TABLE 2 | Observed geochronological range and temporal duration of the selected species of Equinae from the Mexican Neogene.

Taxon	Geochronological range (Ma)	Temporal duration (m. y.)
MERYCHIPPINES		
"M." cf. primus	16.2–15.0	1.2
"M." cf. sejunctus	16.2–15.0	1.2
HIPPARIONINES		
Cormohipparion aff. quinni	16.2–15.0	1.2
Hipparion sp.	12.2–10.6	1.6
Neohipparion eurystyle	7.5–4.8	2.7
Nannipus aztecus	6.8–4.8	2.0
N. peninsulatus	4.8–3.3	1.5
PROTOHIPPINES		
C. hondurensis	7.5–5.7	1.8
EQUINES		
Pliohippus sp.	16.2–15.0	1.2
Astrohippus ansae	7.5–5.7	1.8
A. stockii	6.8–4.8	2.0
"Dinohippus" interpolatus	7.5–5.7	1.8
"D." mexicanus	7.5–4.8	2.7
Equus simplicidens	4.8–2.6	2.2

The information is derived from data in Carranza-Castañeda (2006), Carranza-Castañeda et al. (2013), Ferrusquía-Villafranca (1992, 1996, 2001), Kowallis et al. (1999), Lindsay et al. (1984). Ma, million years ago; m. y. million years.

"Merychippus" primus is known from the late Hemingfordian of Nebraska and Florida (Hulbert and MacFadden, 1991) and the early Barstovian of Florida (Bryant, 1991); it is one of the basal species of the North American Equinae (Hulbert, 1989; Hulbert and MacFadden, 1991). *"Merychippus" sejunctus* has been reported from the Barstovian of Colorado and Texas and it is a species that exhibits a combination of cranial and dental features related to the equines and hipparionines (Hulbert, 1989; Hulbert and MacFadden, 1991); however, recent phylogenetic information on the North American Equinae, places this merychippine as ancestral to the Protohippini—Hipparionini clade (Maguire and Stigall, 2008). The coexistence of related species of ancestral Equinae in the middle Miocene of Oaxaca, suggests that part of the differentiation of the advanced hypsodont horses also took place in southern areas of tropical North America.

The Barstovian record of hipparionines includes *Merychippus* cf. *californicus* from Nejapa and *Cormohipparion* aff. *quinni* from Nejapa and Ixtapa. Sets of isolated teeth and several postcranial remains have been referred to these species (Bravo-Cuevas, 2000; Bravo-Cuevas and Ferrusquía-Villafranca, 2008).

Merychippus insignis [Barstovian of Nebraska, Texas, Colorado, and California (Hulbert and MacFadden, 1991)],

FIGURE 1 | Geographic distribution of Mexican Equinae throughout the Neogene. The list of localities as in **Table 1**.

M. brevidontus [Barstovian of California (Kelly and Stewart, 2008)], and *M. californicus* [Barstovian of California (Downs, 1961; Kelly and Stewart, 2008)] are among the basal species of the Hipparionini (Maguire and Stigall, 2008). Therefore, *Merychippus* cf. *californicus* from the Barstovian of Oaxaca should be considered as one of the earliest hipparionines in North America.

Cormohipparion quinni is one of the oldest members of the genus and it is known from the late Barstovian (14–13 Ma) of Nebraska and Colorado (MacFadden, 1984a; Hulbert, 1987; Woodburne, 1996), together with *C. sphenodus* from the early late Barstovian (15–14 Ma) of northeastern Colorado (MacFadden, 1984a). *Cormohipparion* aff. *quinni* would extend the temporal range of *C. quinni*, its probable closest species, to the early late Barstovian (Bravo-Cuevas and Ferrusquía-Villafranca, 2008).

By the Barstovian, protohippines include *Calippus* sp. from Nejapa, which is characterized by having a crown height similar to that of the small-sized *Calippus* [= *C.* (*Calippus*) sensu (Hulbert, 1988a)], but with an occlusal pattern comparable to that of the medium-sized *Calippus* (= *C.* (*Gramohippus*) sensu Hulbert, 1988a; Bravo-Cuevas, 2000). The genus *Calippus* is recognized from the early late Barstovian to the late early Hemphillian (ca. 14.5–6 Ma) (Hulbert, 1988a). *Calippus* sp. is relatively synchronous to *C. circulus* from the middle late Barstovian (13.5–12.5 Ma) of Texas (Hulbert, 1988a), which is one of the most primitive species of the genus (Maguire and Stigall, 2008).

Barstovian equines include several isolated teeth assigned to *Pliohippus* sp. from Matatlán and Nejapa (Bravo-Cuevas and Ferrusquía-Villafranca, 2010). The occlusal pattern of this species resembles that of *P. mirabilis* from the late early Barstovian–late Barstovian (ca. 12–15 Ma) of Nebraska, Colorado, and Florida (Hulbert and MacFadden, 1991; Kelly, 1998), which is considered as the oldest and most plesiomorphic species of the genus (Kelly, 1998).

Cormohipparion aff. *quinn*i, *Calippus* sp., and *Pliohippus* sp. had a biochronological range and geographic distribution that place these records among the most primitive populations of each genus, extending their geographic distribution from the Great Plains and the Gulf Coast to southern Mexico during the middle Miocene.

Clarendonian Mexican Horses

Clarendonian horses have been recently discovered from Escobedo, Guanajuato and Paso del Águila, San Luis Potosí, central Mexico (Robles-Rivera and Carranza-Castañeda, 2012; Ferrusquía-Villafranca et al., 2014; Robles-Rivera, 2015). The record includes three species that comprise 15% of the Mexican Equinae. The fossil horse sample from Escobedo comes from a fossil-bearing unit that underlies a sequence of andesitic lava flows Ar^{40}/Ar^{39} dated 12.2 ± 04–10.6 ± 0.3 (Robles-Rivera, 2015). The fossil-bearing strata of El Paso de Águila are part of the San Nicolas Formation, whose age is bracketed between 12.33 and 7.41 Ma by the Ar^{40}/Ar^{39} dating of volcanic ashes above and below the fossiliferous strata (Ferrusquía-Villafranca et al., 2014).

Isolated teeth have been referred to *Protohippus* sp. and *Hipparion* sp. from Escobedo, Guanajuato (Robles-Rivera and Carranza-Castañeda, 2012; Robles-Rivera, 2015). To extent of our knowledge, these are the only mentions of these genera from the Mexican Neogene. Members of *Protohippus* and *Hipparion* were more common in the United States, spanning from the late Barstovian to the early Hemphillian, whose records are known from different sites in the Great Plains, the Great Basin, the Gulf Coast, and the Coast of California (MacFadden, 1984a; Hulbert, 1988a,b). The protohippines and hipparionines from the Clarendonian of central Mexico evidence that representatives of *Protohippus* and *Hipparion* reached areas of southern temperate North America by the early late Miocene.

A rostral fragment has been assigned to a new species named as *Pliohippus potosinus* from El Paso del Águila, San Luis Potosí (Ferrusquía-Villafranca et al., 2014). This species is only known from the Mexican territory, exhibiting a cranial and dental configuration similar to that of *Pliohippus fossulatus* from the Clarendonian of Texas (Kelly, 1998). *Pliohippus potosinus* together with *Pliohippus* sp. from the Barstovian of Oaxaca are the only known representatives of the genus from the Mexican Neogene, spanning from the late early Barstovian to the earliest Hemphillian; a similar biochronological range for *Pliohippus* is reported from the United States (Kelly, 1998).

Hemphillian and Blancan Mexican Horses

The greatest number of fossil horses from the Mexican Neogene is from Hemphillian and/or Blancan localities. The record encompasses 50% of the known Mexican Equinae, including three hipparionines, two protohippines, and five equines. An important number of fossil-bearing localities in central Mexico have been dated by fission track, $^{40}Ar/^{39}Ar$, and/or U/Pb radiometric techniques. Several localities in the San Miguel de Allende Basin, Guanajuato, have yielded ages ranging from about 4.8 to 3.9 Ma (Kowallis et al., 1999), whereas some localities in the states of Jalisco and Nayarit yield ages of 4.89 ± 0.16 Ma and 5.50 ± 0.05 Ma respectively (Carranza-Castañeda, 2006; Carranza-Castañeda et al., 2013). Recently, the dating of localities at the Juchipila Basin in Zacatecas indicates dates from 6.95 ± 0.27 to 5.59 ± 0.11 Ma (Carranza-Castañeda et al., 2013). The age of other localities in the states of Baja California, Hidalgo, Michoacán, and Querétaro is established by means of biochronology, indicating Hemphillian and Blancan faunas (Carranza-Castañeda, 2006). Particularly, the Yepómera locality in Chihuahua is placed between the magnetic chrons C3n2r and C3n2n (Gilbert Time), thus evidencing an age of about 4.6 Ma (Lindsay et al., 1984).

The species *Neohipparion eurystyle* and *Nannipus aztecus* were the typical hipparionines in the Hemphillian of Mexico, whereas *N. peninsulatus* was Blancan. These horses are represented by an important sample of cranial, dental, and/or postcranial remains (Priego-Vargas et al., 2016).

Neohipparion eurystyle is the best-known and well-documented Mexican hipparionine, which has been recorded through a major part of the Hemphillian (7.5–4.8 Ma) and had a wide distribution across the country (Stirton, 1955; Carranza-Castañeda, 2006; Carranza-Castañeda et al., 2013). This species exhibited the greatest temporal range (of about 2.7 million years) of all hipparionines from the Miocene and Pliocene of Mexico.

The genus *Nannipus* includes the late Hemphillian *N. aztecus* and the Blancan *N. peninsulatus*. Their record mainly comes from localities in central Mexico (Carranza-Castañeda, 2006; Carranza-Castañeda et al., 2013); however, there is evidence of both species from the Yepómera locality, Chihuahua, northern Mexico (Lance, 1950; MacFadden, 2006). The type localities of these hipparionines are in Mexico, including Rancho El Ocote in Guanajuato for *N. aztecus* (Mooser, 1968) and Tehuichila in Hidalgo for *N. peninsulatus* (Osborn, 1918). *Nannipus aztecus* has been considered as the putative ancestral species of the Blancan *N. beckensis* and *N. peninsulatus* of North America (MacFadden, 1984a; Hulbert, 1993). *N. aztecus* and *N. peninsulatus* are chronologically successive at several localities in the Tecolotlán Basin, Jalisco and San Miguel de Allende Basin, Guanajuato (Carranza-Castañeda, 2006). It seems that differentiation, probably by anagenesis, of some populations of Blancan *Nannipus* could have had occurred in areas of central Mexico. It is noted that anagenetic differentiation of Blancan *Nannipus* through *N. aztecus* has been previously suggested (MacFadden, 2006).

Protohippines include members of *Calippus* belonging to *C. martini* and *C. hondurensis*; both species are mainly known from dental material. Of these two species, *C. hondurensis* is better known and has been reported from several late early Hemphillian to early late Hemphillian (7.5–5.7 Ma) localities across central Mexico (Carranza-Castañeda, 2006; Carranza-Castañeda et al., 2013). In contrast, *C. martini* is represented by a single occurrence from the late early Hemphillian (7.5–6.8 Ma) of Guanajuato (Robles-Rivera, 2015). In the United States, *C. martini* is known from the early to middle Clarendonian (about 12.0 to 10.0 Ma) of the Great Plains and Gulf Coast, whereas *C. hondurensis* from the early Hemphillian (about 7.0–9.0 Ma) of Florida (Hulbert, 1988a). Hence, the Hemphillian records of these species in Mexico extend its biochronological range by about 3 million years, representing the youngest populations of North America.

Fossil material of equines includes skulls, mandibles, numerous teeth, and/or postcranial bones belonging to *Astrohippus*, *Dinohippus*, and *Equus*. The two species of *Astrohippus* from North America, namely *A. ansae* and *A. stockii*, have been reported in Mexico. The record of *A. ansae* consists of a single occurrence from the early Hemphillian of Zacatecas, central Mexico (Carranza-Castañeda et al., 2013). *A. stockii* is the most common species of the genus and it is known from several late Hemphillian localities in Chihuahua, Jalisco, Guanajuato, and Hidalgo (Lance, 1950; MacFadden, 1984b; Carranza-Castañeda, 2006).

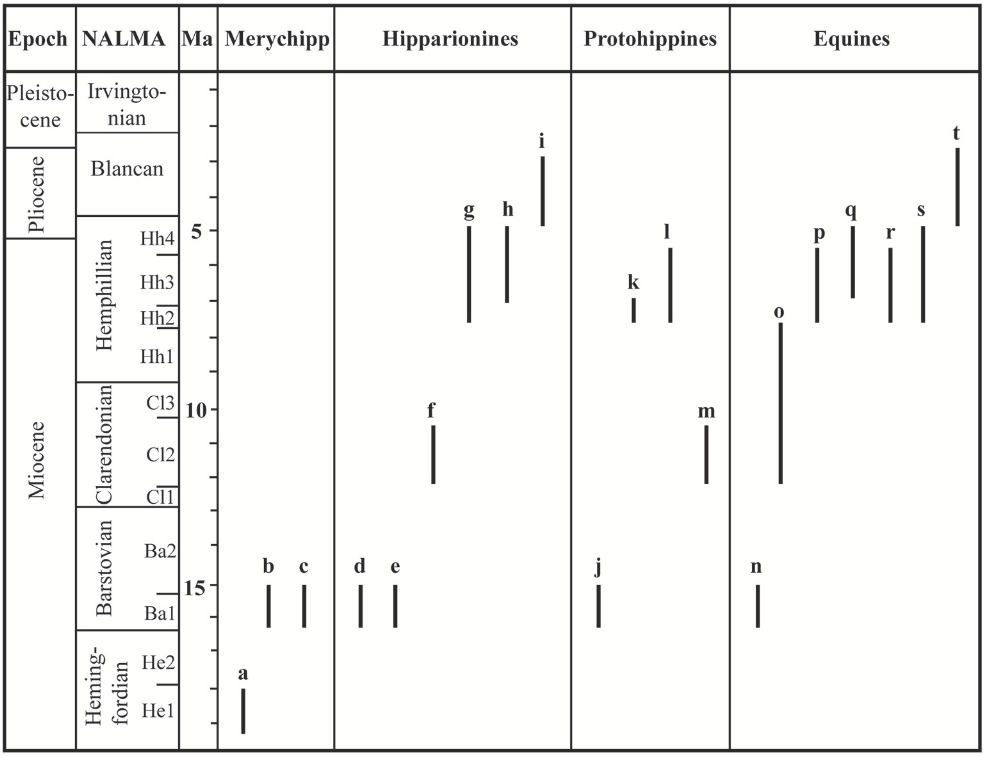

FIGURE 2 | Temporally calibrated record of Equinae from the Mexican Neogene. Merychippines (Merychipp): a, *"Merychippus"* sp.; b, *"M."* cf. *primus*; c, *"M."* cf. *sejunctus*. Hipparionines: d, *Merychippus californicus*; e, *Cormohipparion* aff. *quinni*; f, *Hipparion* sp.; g, *Neohipparion eurystyle*; h, *Nannipus aztecus*; i, *N. peninsulatus*. Protohippines: j, *Calippus* sp.; k, *C. martini*; l, *C. hondurensis*; m, *Protohippus* sp. Equines: n, *Pliohippus* sp.; o, *P. potosinus*; p, *Astrohippus ansae*; q, *A. stockii*; r, *"Dinohippus" interpolatus*; s, *"D." mexicanus*; t, *Equus simplicidens*. The first and last appearance datums are derived from Lindsay et al. (1984), Ferrusquía-Villafranca (1992, 1996, 2001), Kowallis et al. (1999), Urrutia-Fucugauchi and Ferrusquía-Villafranca (2001), Carranza-Castañeda (2006), Carranza-Castañeda et al. (2013), Ferrusquía-Villafranca et al. (2014), Robles-Rivera (2015). North American Land Mammal Ages (NALMAs) from Tedford et al. (2004).

Two species of *"Dinohippus"* are known from the Mexican Neogene, including *"D." interpolatus* and *"D." mexicanus*. The sample belonging to *"D." interpolatus* comes from the early Hemphillian of Guanajuato, Hidalgo, and Jalisco (Carranza-Castañeda, 2006). The taxonomic status of this species is controversial, and it has been reported from the late early Hemphillian and early late Hemphillian (ca. 6.8 Ma) of Texas and California (Kelly, 1998 and references therein); other alleged records are from Colorado, Kansas, Oklahoma, Arizona, South Dakota, and New Mexico (MacFadden and Carranza-Castañeda, 2002). The Mexican record testifies that members of *"D." interpolatus* reached areas of southern temperate North America during the late Miocene.

"Dinohippus" mexicanus is present in all the late Hemphillian faunas known from Mexico (Carranza-Castañeda et al., 2013). This species was originally described trough fossil material recovered from Yepómera, Chihuahua in northern Mexico (Lance, 1950). It has been shown that *"D." mexicanus* gave rise to primitive species of *Equus*, such as *E. simplicidens* (Hulbert, 1989, 1993; MacFadden, 1992; MacFadden and Carranza-Castañeda, 2002).

Equus simplicidens is the youngest equine known from the Mexican Neogene. It is reported from several Blancan localities in Baja California, Guanajuato, Hidalgo, Michoacán, and Jalisco (Miller, 1980; Carranza-Castañeda and Miller, 1999; Carranza-Castañeda, 2006). This species is the oldest and most plesiomorphic of *Equus* and it is well-known from the early Blancan of Hagerman, Idaho and Broadwater, Nebraska (Azzaroli, 1992).

DIVERSITY CHANGES IN THE MEXICAN NEOGENE HORSES

The known Mexican horse record evidences a diversity that varied from one to eight contemporaneous species (**Figure 2**). Based on the available information, it appears that the greatest species diversity occurred during the early middle Miocene (16–14 Ma) and the latest Miocene (7–5 Ma) (**Figure 3**). The 70% of the total diversity of the Mexican Equinae is represented in these geochronological intervals. Hipparionines and equines were the most diverse with six and seven species respectively, whereas merychippines and protohippines were less diverse with three species in each group throughout the Neogene. Hipparionines and equines showed the greatest temporal range of about 13 million years followed by the protohippines with 8 million years and in a lesser extent the merychippines with 5 million years (**Figure 2**).

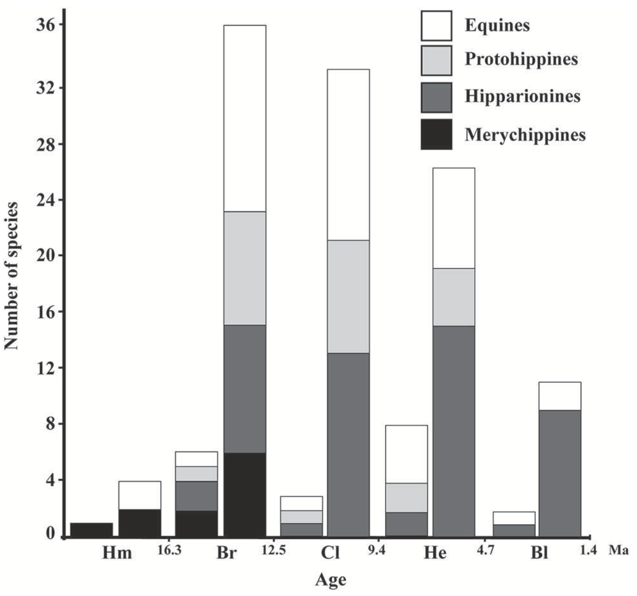

FIGURE 3 | Pattern of species richness of Neogene Equinae from Mexico (left column) and North America (right column). Hm, Hemingfordian; Br, Barstovian; Cl, Clarendonian; He, Hemphillian; Bl, Blancan.

It seems that the species diversity of Mexican Equinae increased significantly from one species in the late Hemingfordian to six species in the late early Barstovian. In the late early Barstovian, merychippines and hipparionines were most diverse in comparison to the protohippines and equines. Then in the Clarendonian, merychippines are unknown and the other groups of Equinae included one species each.

In the late early Hemphillian it is observed the maximum species diversity known (so far) from the Mexican Neogene, including eight contemporaneous species. In this faunal stage, the equines were the most diverse with four species, whereas the protohippines are unknown. It is observed a significant reduction of species at the end of the Hemphillian, implying the loss of the 75% of the recorded species in this faunal stage. In the Blancan, one hipparionine and one equine species are observed.

The change in species diversity observed from the known record of the Mexican Neogene horses indicates two intervals of major diversity, the first at about 15 Ma (six species) and the second at about 7 Ma (eight species); later at about 5 Ma the group experienced an important reduction of species (two species). A similar pattern in species diversity is recovered from the record of the United States, showing a maximum of contemporary species at least twice during the Miocene (at 13.5 Ma and at 6.5 Ma) and a decline in species diversity by about 4.5 Ma (**Figure 3**). Hipparionines, protohippines, and most of the equines became extinct at about 2 Ma (Hulbert, 1993).

Diversity of Mexican Equinae in the Miocene

It has long been recognized that the evolution of North American Equinae was driven by environmental fluctuations during the Neogene (see Hulbert, 1993; Webb et al., 1995; Maguire and Stigall, 2008). The geological evolution of Mexico in the Cenozoic was very complex, resulting in its rugged geomorphology and diverse climatic conditions (Ortega-Gutiérrez et al., 1992; Ferrusquía-Villafranca, 1993). Evolution of the Trans-Mexican Volcanic Belt started from the early to the middle Miocene (20–10 Ma) (Ferrari et al., 2012), while that of the Sierra Madre del Sur started during the Oligocene and still was active during the early Miocene (Mastretta-Yanes et al., 2015). The development of these volcanic arcs promoted an intense volcanic activity that had important effects in the orography (e.g., transformation of continental basins), hydrology (e.g., alteration of fluvial currents), and climate (e.g., modification in plant communities) of the Mexican Neogene (Cevallos-Ferriz and González-Torres, 2006).

The horse record (reported so far) indicates that the first members of Equinae occurred in areas of southern Mexico during the first half of the Miocene. The climate of southern Mexico varied from temperate to humid tropical at the beginning of the Miocene (González-Medrano, 1998). The palynoflora of Simojovel from the late Oligocene—early Miocene of Chiapas evidence this climatic variation, consisting of oak-pine woodland associated with mangrove forest (*Rhizophora*) (Graham, 1994, 1999) (**Figure 4**). The warmest temperatures recorded in the Neogene were reached during the middle Miocene (ca. 15 Ma); this episode has been called the "Mid-Miocene climatic optimum" (Zachos et al., 2001). In this regard, the palynological data recovered from the Ixtapa Formation, middle Miocene of Chiapas indicates the presence of tropical plant communities (mangrove forest of *Rhizophora* and *Pelliceria*) with some grasses (*Monoporites*) and gymnosperms (*Pinus*) (Martínez-Hernández, 1992). A progressive decrease in temperature occurred at the end of the middle Miocene and continued until the Pliocene (González-Medrano, 1998; Graham, 1999).

The volcanoclastic deposits that preserved the Miocene horse communities of southern Mexico evidence at least two events of silicic explosive eruptions, at about 20 Ma (Suchilquitongo Formation) and at about 15 Ma (Matatlán, El Camarón, and Ixtapa formations). The volcanic activity spread from the Oaxaca Valley, the Tehuantepec Isthmian Region, and areas of central-western Chiapas, during the middle Miocene (Jiménez-Hidalgo et al., 2002). The volcanism has been associated with extensional tectonics that produced a complex basin and range topography, making up valleys (graben) flanked by highlands (horsts) (Ortega-Gutiérrez et al., 1992).

Climate conditions, plant communities, and geological features of southern Mexico in the first half of the Miocene (20–15 Ma) suggest that horses inhabited tropical lowland areas covered by heterogeneous vegetation. It is noted that mammalian composition of faunas from the middle Miocene of Oaxaca and Chiapas are related to savanna-like ecosystems, including browsers (e.g., gomphotheres, leptomerycids, and oreodonts), mixed-feeders (e.g., camelids and protoceratids), and grazers (e.g., rhinocerotids and antilocaprids) (Jiménez-Hidalgo et al., 2002).

The first peak of diversity in Equinae coincides with the warmest and humid conditions of the Mexican Neogene

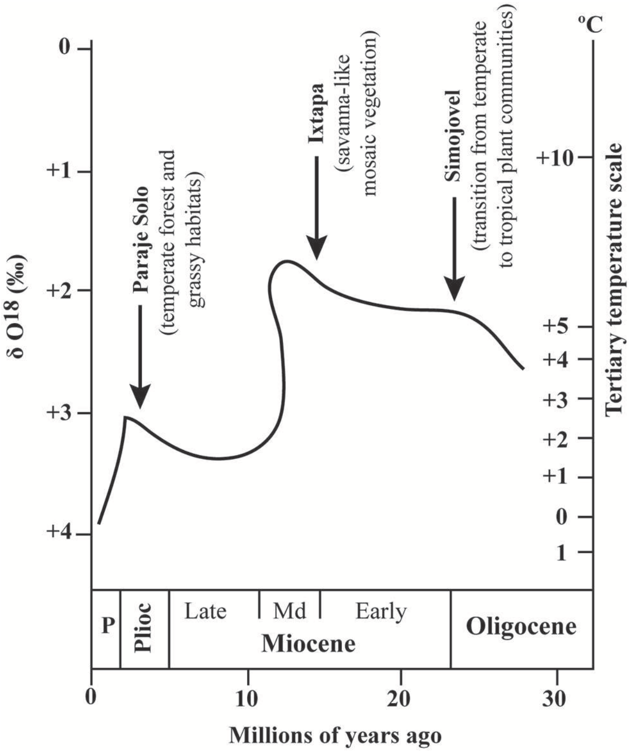

FIGURE 4 | Neogene temperature change based on marine benthic δ O^{18} record. The arrows indicate representative palynofloras and related plant communities from the Mexican Neogene (modified from Graham, 1994; **Figure 3**).

(**Figure 4**). The horse communities of the middle Miocene of southern Mexico include subhypsodont (mean molar crown height between 25 and 30 mm) species such as *"Merychippus"* cf. *primus*, *"M."* cf. *sejunctus*, *Merychippus* cf. *californicus*, and *Calippus* sp. (Bravo-Cuevas, 2000; Bravo-Cuevas and Ferrusquía-Villafranca, 2006), as well as hypsodont (mean molar crown height >30 mm) species like *Cormohipparion* aff. *quinni* and *Pliohippus* sp. (Bravo-Cuevas, 2000; Bravo-Cuevas and Ferrusquía-Villafranca, 2008, 2010). This high species diversity is comparable to that reported from several Barstovian faunas in the United States, such as Norden Bridge of north-central Nebraska (Tedford et al., 2004), Eubanks of northeastern Colorado (Galbreath, 1953), and Cold Spring of Texas (Quinn, 1955).

Traditionally, the evolution of hypsodont molars in horses (and in other herbivore mammals) has been explained as a coevolutionary process in response to the expansion of grassland habitats during the middle Miocene (Webb, 1977, 1983). Nevertheless, isotopic evidence and mesowear data in North American fossil horses indicate that there is not a definitive correlation between the increase of the crown height with the shifting from browsing to grazing (Wang et al., 1994; Mihlbachler et al., 2011). Tooth enamel carbonate $\delta^{13}C$ values in samples of *"Merychippus"* cf. *sejunctus*, *Cormohipparion* aff. *quinni*, and *Pliohippus* sp. from the middle Miocene of Oaxaca are characteristically <-9 ‰ (Pérez-Crespo et al., 2016). This carbon isotopic evidence suggests that C3 plants were an important component of the terrestrial ecosystems of southern Mexico at about 15 Ma. Paleobotanical evidence and fossil horse communities have shown that C3 biomes were common in the United States during the radiation phase of the Equinae (from 18 to 15 Ma) (Hulbert, 1993). The information presented here indicates that comparable biomes also occurred in areas of southern tropical North America.

Given the above, the complicated physiography and the presence of savanna-like mosaic vegetation in a humid and tropical climate of southern Mexico would be an appropriate scenario for sustaining a diverse horse community (four to six sympatric species), allowing for suitable resource partitioning. By the same token, this high diversity coincides with the adaptive radiation of Miocene Equinae, suggesting that part of this evolutionary process could also have had occurred in areas of southern Mexico.

The first horses of the Mexican Neogene to become extinct were the merychippines. It seems that this group of horses preferred humid and forested environments and their disappearance probably was in response to the progressive cooling and aridification which occurred across North America from the late Miocene to the Pliocene (Thomasson and Voorhies, 1990; Potts and Behrensmeyer, 1992). Merychippines were eventually replaced by more hypsodont hipparionines, protohippines, and equines, as evidenced by the horse record from the Clarendonian of central Mexico, including members of the genera *Hipparion*, *Protohippus*, and *Pliohippus* (**Figures 2**, **3**).

By the early late Miocene (ca. 9 Ma) a sudden temperature decrease in the Mexican territory occurred (González-Medrano, 1998) (**Figure 4**). This change in temperature is evidenced by the reduction of tropical plant communities and the arrival of boreal elements like the spruce (*Picea*) to areas of central Mexico at 18°N Lat. Furthermore, the presence of flora from temperate regions [e.g., pine (*Podocarpus* and *Pinus*), oak (*Quercus*), and sweetgum (*Liquidambar*)] in lowland areas (150–250 m.a.s.l.) of the Gulf Coastal Plain and southern Mexico was common (González-Medrano, 1998). The diversity dropped from six to three species together with the disappearance of the merychippines from the Barstovian to the Clarendonian (**Figure 3**). This decrease in diversity could have resulted from the climatic and vegetational changes at the beginning of the late Miocene, being the merychippines drastically affected. It should be stated that merychippines became extinct in temperate North America by the end of the Barstovian (Hulbert and MacFadden, 1991).

The aridification and cooling trend that occurred throughout the late Miocene certainly resulted in a progressive increase of open habitats in the Mexican territory, such as grasslands and prairies (Graham, 1993, 1994, 1999). In this regard, the mammalian communities from the Hemphillian of central Mexico were characterized by having hypsodont horses (e.g., *Neohipparion eurystyle*, *Calippus hondurensis*, and *"Dinohippus" mexicanus*). The presence of high crowned teeth in the Hemphillian Mexican horses allowed them to exploit abrasive food resources typical of grassy habitats.

In the Trans-Mexican Volcanic Belt of central Mexico, a mafic volcanic pulse gradually migrated eastwards from western

Mexico, from the late Miocene to the early Pliocene (11–3 Ma), creating large plateaus and gradually increasing the elevation ranges due to isostatic movements (Ferrari et al., 2000; Orozco-Esquivel et al., 2003; Ferrari, 2004). From the latest Miocene to the early Pliocene (≈7.5–3.0 Ma), calderas and ignimbrites covered large areas, and domes complexes were formed in central-western Mexico (Ferrari et al., 2012).

The Trans-Mexican Volcanic Belt was affected by NW–SE trans-tensive regime during the Miocene and Pliocene, generating grabens and semigrabens in western Mexico; these depressions were filled with water, creating extensive lakes (Israde-Alcántara et al., 2010). Additionally, the formation of the Trans-Mexican Volcanic Belt isolated the Mexican Central Plateau, preventing the entry of humid air from the Pacific Ocean, thus promoting aridification of this area (Ferrari, 2017).

The species diversity of Mexican horses during the Clarendonian partially coincides with the early development of the Trans-Mexican Volcanic Belt during the early to the late Miocene (19–8 Ma) (Ferrari et al., 2012). During the late Miocene, a tropical climate with forested habitats, with a mean annual temperature above 20°C and a high mean annual precipitation were evidenced in some areas of central Mexico (Castañeda-Posadas et al., 2009); these favorable conditions could support a large amount of herbivore mammals, including horses. As it has been stated, the record of Clarendonian horses is poorly known, although it is probable that the true nature of the mammalian faunas that inhabited the Mexican territory during this faunal stage is biased, considering the dynamics of the Trans-Mexican Volcanic Belt. In this regard, the accretion of mafic lava across central Mexico, could have had promoted the uplift of sedimentary sequences deposited during the late Miocene, which have been eventually eroded.

The known record of Mexican Equinae indicates that reached their major diversity of five genera and eight contemporaneous species during the Hemphillian (at about 7 Ma). In this faunal stage, all groups of advanced hypsodont horses displayed their greatest species diversity, being the equines the most diverse. By the late early Hemphillian (≈7.0 Ma) humid conditions allowed the basins of the Trans-Mexican Volcanic Belt to begin filling with water, creating several lakes (Israde-Alcántara et al., 2010). The mammalian associations recovered from the localities of central Mexico of this age and microfossil proxies suggest a woodland landscape under warm conditions (Israde-Alcántara et al., 2010; Carranza-Castañeda et al., 2013). The available resources during this age allowed for a great diversity of horses, showing its second diversity peak in Mexico (**Figure 3**).

Diversity of Mexican Equinae in the Pliocene

Between 5.2 and 3.6 Ma there was an increase in oceanic levels and warm temperatures at the marine surface, which promoted a high precipitation levels on land; the climate was warm and there was a maximum north-south tectonic extension in several areas along the Trans-Mexican Volcanic Belt (Israde-Alcántara et al., 2010).

By the latest Hemphillian -around 4.8 Ma- there was a large mammalian extinction event in North America (Webb, 1984), which is also observed in several local faunas of central Mexico (Jimenez-Hidalgo, 2005), including horses (**Figure 3**). This extinction event could be related to a cooler and drier climate, and to the emergence of more open vegetation in temperate North America (Prothero, 2006). It seems that this extinction could be correlated with volcanic activity, which disrupted plant communities, and the further uplift of the Trans-Mexican Volcanic Belt, which resulted in further aridification and the spreading of more open vegetation compared to the Miocene.

In the Blancan, only two horse species are recorded after the disappearance of the majority of the Hemphillian hipparionines and equines (**Figure 3**). Between 3.3 and 2.0 Ma, the oceans became cooler, with stronger cycles by 2 Ma, and there were more arid conditions in central and northern Mexico. The lakes from central Mexico became shallower and some disappeared (Israde-Alcántara et al., 2010). In central Mexico, mammalian assemblages of Blancan age indicate more open vegetation when compared to Hemphillian ones (Carranza-Castañeda, 2006). In east-central Mexico, within the Trans-Mexican Volcanic Belt, some floral assemblages indicate mesothermal woodland with a temperate climate (Velasco-de León et al., 2010). Furthermore, the floristic composition of the Paraje Solo Formation from the Pliocene of Veracruz, east-central Mexico, evidences an increase in diversity and abundance of temperate to cold elements, including pine-oak forest (*Abies*, *Picea*, and *Pinus*), deciduous forest (*Psilotum*, *Lycopodium*, and *Sphaeropteris*), and perennial forest (*Podocarpus* and *Alchornea*) (Graham, 1993, 1994; González-Medrano, 1998) (**Figure 4**).

TAXONOMIC EVOLUTION OF MEXICAN NEOGENE HORSES

The overall mean species duration of selected Mexican Neogene horses is 1.79 m.y., ranging from 1.2 m.y. (*"Merychippus"* cf. *primus*, *"M."* cf. *sejunctus*, and *Cormohipparion aff. quinni*) to 2.7 m. y. (*Neohipparion eurystyle* and *"Dinohippus" mexicanus*) (**Table 2**). The equines showed the highest average species duration with 1.95 m.y., whereas the hipparionines have average species duration of 1.85 m.y. The considered merychippines have species durations of 1.2 m.y. (**Table 2**). The Mexican record of *Calippus hondurensis* extends the biochronological range of this species of about 2 million years, similar to that observed in other calippines, such as *C. elachistus* from the late Clarendonian—early Hemphillian of central Florida, as well as *C. regulus* from the late Barstovian—Clarendonian of the Great Plains and early Clarendonian of the Texas Gulf Coastal Plain (Hulbert, 1988a).

A comparison of the temporal range of selected hipparionines and equines from Mexico with those from the United States indicates that these horses showed similar durations in North America during the Neogene (**Table 3**). The average temporal duration of the selected Mexican Equinae is near the lower limit of the range of the mean species duration of North American Cenozoic mammals of ∼2–3 million years and it is lower than

TABLE 3 | Results of the Mann-Whitney *U*-Tests ($p < 0.05$) of the temporal duration of the Mexican and North American hipparionines and equines.

Group of horses	*U*-value	*p*-value
Hipparionines	39.5	0.32
Equines	46.5	0.34

the average temporal duration of Equidae that is of 2.9 million years (Prothero, 2014).

The merychippines *"Merychippus"* cf. *primus* and *"M."* cf. *sejunctus* are characterized by having short temporal durations of 1.2 m.y., suggesting that they had a rapid evolution in the early to middle Miocene. The long temporal durations of the best documented hipparionines and equines of about 2.0 m.y., suggest that they could have evolved more slowly after their diversification in the middle to late Miocene and persisting until the end of the Neogene. It has been shown that horses have evolved rapidly during the Cenozoic (Simpson, 1984; MacFadden, 1992; Hulbert, 1993; Franzen, 2010). The data presented here provide additional information in this regard.

COMMENT ON THE ADAPTIVE RADIATION OF NORTH AMERICAN EQUINAE

It has been largely recognized that the adaptive radiation of North American Equinae started at about 18 Ma in particular areas of the United States (MacFadden and Hulbert, 1988; Hulbert and MacFadden, 1991; MacFadden, 1992; Hulbert, 1993; Maguire and Stigall, 2008). At least four species including primitive merychippines ("*Merychippus gunteri*" and "*M.*" *primus*) and equines (*Acritohippus tertius* and *Parapliohippus carrizoensis*) have been reported from the late Hemingfordian of the Coast of California, the Great Plains, and the Gulf Coast (Bryant, 1988, 1991; Hulbert and MacFadden, 1991; Kelly, 1995, 1998). The adaptive radiation continued in the same areas during the Barstovian at about 15 Ma, leading to the differentiation of earliest representatives of the advanced hypsodont genera *Pliohippus*, *Calippus*, *Protohippus*, and *Cormohipparion* (Hulbert, 1993).

In Mexico, there is a record referable to *"Merychippus"* sp. from the late Hemingfordian of Oaxaca (Ferrusquía-Villafranca, 1990). By the late early Barstovian, the Mexican horse communities were composed by basal merychippines ("*Merychippus*" cf. "*M.*" *primus* and "*M.*" cf. "*M.*" *sejunctus*) and primitive populations of hipparionines (*Cormohipparion* aff. *quinni*), protohippines (*Calippus* sp.), and equines (*Pliohippus* sp.), which inhabited humid and tropical areas that now are part of the states of Oaxaca and Chiapas, southern Mexico (Bravo-Cuevas, 2000; Bravo-Cuevas and Ferrusquía-Villafranca, 2006, 2008, 2010).

This information suggests that the adaptive radiation of Equinae would have occurred in areas of temperate and tropical North America. In this scenario, the evolutionary process occurred in separate areas at least 2, 000 km apart and in different biogeographic regions. Two hypotheses may explain this pattern as it is indicated in the following paragraphs.

(1) The differentiation occurred throughout North America, including tropical areas of southern Mexico. This scenario is less probable because it requires genetically continuous but geographically disperse populations. Furthermore, the known record of Equinae from the Hemingfordian—Barstovian of North America is unevenly distributed in different areas of the United States (Maguire and Stigall, 2008), and southern Mexico as well.
(2) The differentiation took place in areas of temperate and tropical North America, implying short temporal dispersals after a speciation event. This hypothesis appears more likely because the geographic distribution of Equinae shows some provinciality and speciation by dispersal was common in the evolution of the group at the base of their adaptive radiation during the middle Miocene (Maguire and Stigall, 2008).

It seems that the Mexican record evidences part of the radiation phase of the North American Equinae, which in turn indicates a somewhat synchronous appearance of primitive hipparionines, protohippines, and equines in temperate and tropical regions of North America during the early—middle Miocene. The proposed scenario implies regional dispersal events within the North American subcontinent, similarly to the *Hipparion* and *Equus* datum planes that involved dispersal events between North America and Eurasia during the late Neogene (Woodburne et al., 1981; Lindsay et al., 1984; Bernor et al., 1989).

COMMENT ON THE ORIGIN OF *EQUUS*

The species *"Dinohippus" mexicanus* and *Equus simplicidens* are closely related taxa (MacFadden, 1984b, 1986). Hulbert (1993) considered that, by anagenetic evolution, *Equus* descended from *"D." mexicanus*. Some years later, MacFadden and Carranza-Castañeda (2002) commented on the horse record from Anza-Borrego desert in California, where Downs and Miller (1994) described a cf. *Dinohippus* specimen of late Blancan age (≈2.7 Ma) associated with specimens of *Equus simplicidens*; they also reported some isolated teeth with a transitional morphology of equine horses pertaining to *Dinohippus* and/or *Equus* from the San Buenaventura Formation (late Blancan, 2.62 Ma) in the Tecolotlán area of Jalisco state, west-central Mexico (Kowallis et al., 2017); some of these teeth can be identified as *D. mexicanus*, while others can be referred to primitive *Equus* (*E.* cf. *simplicidens*). Both records indicate that primitive *Equus* originated from "*Dinohippus*" *mexicanus* by means of cladogenesis (MacFadden and Carranza-Castañeda, 2002). The geographic locations of both localities with these coetaneous taxa suggest that this cladogenetic event probably took place in western North America, including areas of central Mexico.

CONCLUSIONS

The record of Mexican Equinae provides additional support on their evolutionary history during the Neogene, characterized by having two peaks of diversity during the Miocene and a progressive decline by the Pliocene. The change in species diversity is largely related to the climatic and vegetational change occurred during the Neogene in areas of temperate and tropical North America.

The somewhat short temporal duration showed by some Mexican Equinae (ca. 1.6 m. y.) suggests that they evolved rapidly during the Miocene, although the hipparionines and equines probably evolved more slowly after their diversification in the middle to late Miocene, persisting to the end of the Pliocene.

The members of Equini and Hipparionini were dominant throughout much of the Mexican Neogene and, to a lesser extent, the Protohippini. The Mexican merychippines were restricted to the first half of the Miocene (from 18 to 15 Ma) at the base of the adaptive radiation of the North American Equinae.

The taxonomic composition of the diverse horse communities from the Barstovian of Oaxaca and Chiapas, southern Mexico, integrated by basal merychippines (*"Merychippus"* cf. *primus* and *"M."* cf. *sejunctus*) and primitive populations of advanced hypsodont hipparionines (*Cormohipparion* aff. *quinni*), protohippines (*Calippus* sp.), and equines (*Pliohippus* sp.), suggests that part of the radiation phase of Equinae could also have occurred in areas of tropical North America.

The species *"Dinohippus" mexicanus* was erected by Mexican fossil material, and it has been considered as the species that gave rise by cladogenesis to primitive *Equus*. The coexistence of *"D." mexicanus* and *E. simplicidens* in areas of central Mexico indicates that part of the differentiation of *Equus* took place in Mexican territory.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00287/full#supplementary-material

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Biostratigraphy and Palaeoecology of European *Equus*

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We present an inventory of the progress of recent research on the biostratigraphy and palaeoecology of the genus *Equus* sensu lato in Europe. Our discussion starts with the new hypotheses concerning the dispersal and evolution of non-caballine equids of the Early and the beginning of the Middle Pleistocene, focusing on recent discoveries, description of taxa, and revised diagnosis. In particular, we deal with the major debate surrounding the number of lineages, "stenonid horses," related species and the new subgenus "*Sussemionus.*" Possible phylogenetic scenarios and relationships with extant species are also taken into consideration. There is consensus that the lineage of true horses emerged in Europe at the beginning of the Middle Pleistocene. Their extensive skeletal plasticity enabled them to survive under a wide range of climatic conditions and environments, from interglacial forests to grass-steppes during glacial episodes. They exhibit homogeneous overall morphology but variability in terms of dental and skeletal proportions. Patterns of general body size, muzzle shape, macro- and microdonty, proportions of the limbs, robustness of the metapodials, and breadth of the third phalanx are influenced by global climate, the characteristics of the vegetation (in particular the degree of openness) and substrate, and are governed by Bergmann's and Allen's rules or other environmental pressures. In addition to palaeoecological information, these ecomorphological adaptations paradoxically provide real biochronological details in a given geographical province. Throughout the Upper Pleistocene, horses underwent a size diminution initiated at the end of the Middle Pleistocene. After the Last Glacial Maximum (LGM), investigation of body size in different regions of Europe demonstrates the existence of latitudinal and longitudinal clines, and the fragmentation of the horse population. The so-called European wild ass, *Equus hydruntinus*, has a wide geographical distribution but seems to be less ecologically flexible, or, alternatively, more specialized than true horses, with which it is often found in sympatry. The latest palaeogenetic studies place the species into phylogenetic context within the Asiatic wild asses, however, palaeontological evidence points to *E. hydruntinus* as a separate species. Its tooth morphology varies between biogeographical areas.

Keywords: ***Equus***, **Pleistocene, Europe, biochronology, ecomorphology, stenonid horses, caballoid horses,** ***Equus hydruntinus***

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INTRODUCTION

Over the past 15 years, the discovery of new fossils and the revision of reference collections, added to the increased precision of the dating of certain deposits, have led to a reconsideration of the biochronology of the equids of the Pleistocene (Alberdi et al., 1998; Forsten, 1999a; Eisenmann, 2004a, 2006a, 2010; Alberdi and Palombo, 2013; Palombo and Alberdi, 2017; Van der Made et al., 2017). In addition, the progress of palaeogenetics has made it possible to calibrate evolutionary models proposed by paleontology (Orlando et al., 2013; Jonsson et al., 2014; Bennett et al., 2017).

It is generally considered that the genus *Equus*, which most likely emerged some 4.0–4.5 Ma (Orlando et al., 2013), includes all monodactyl equids present in Europe, and the stenonid group (horses related to *Equus stenonis*) was the first to disperse at the Plio-Pleistocene boundary (*Equus*-Elephant event, Lindsay et al., 1980). *Equus livenzovenzis*, recorded during the Middle Villafranchian, is for some authors the first species recognized in Eurasia and considered as the phylogenetic root of all the European stenonoid species (Azzaroli, 1992; Alberdi et al., 1998; Palombo and Alberdi, 2017; Bernor et al., 2018; **Figure 1**). However, its definition remains disputed, in particular because of the heterogeneity of the material of the type locality (Livenzovka, near Rostov-Don, Russia), doubts about the chronology (Forsten, 1998a), and the disagreement about the taxonomy of contemporaneous fossils recorded in Western Europe and attributed to this taxa (i.e., at Montopoli in Italy, and Huélago, El Rincón in Spain; Forsten, 1999a; Eisenmann, 2004a).

According to Eisenmann and Baylac (2000) and Eisenmann (2006a, 2017), modern equids—genus *Equus*–can be differentiated from the earlier genera *Plesippus* and *Allohippus* (Stenonids) by their basicranial proportions. Following this outline, the first cranium of *Equus* described in Europe is that of Apollonia in Greek Macedonia (=*Equus apolloniensis*, Koufos et al., 1997; 1.2–0.9 Ma, Koufos and Kostopoulos, 2016) and the latest cranium of stenonids (*Allohippus* according to Eisenmann) could be that of Ceyssaguet with an age of 1.2 Ma (*Equus stenonis*, Aouadi and Bonifay, 2008). Beyond Europe, the crania from Nalaikha (0.9 Ma) in Mongolia [= *E. (Hemionus) nalaikhaensis*, Kuznetsova and Zhegallo (2009)] and from Kolyma in Siberia at the beginning of the Middle Pleistocene (=*E. coliemensis*) also belong to *Equus* (Eisenmann and Kuznetsova, 2004). According to Eisenmann (2006a, 2010, 2017), similarities in the morphology of the teeth suggest, even in the absence of the cranium, a common origin within the branch of ≪ *Equus* ≫ for certain equids, at least from 1.5 Ma and maybe soon before around 2.5 Ma just above the Gauss-Matuyama limit (Vatera Formation, Greece). These equids (*E. granatensis*, *E. altidens*, *E. hipparionoides*, *E. coliemensis*, *E. suessenbornensis*) are grouped together in the subgenus of *Equus* "*Sussemionus*" (Eisenmann, 2010). As a consequence, in this model, *Allohippus,* and *Equus* could have co-occurred in Europe for more than 1.0 Ma. These characters, however, are not constant, even within the same series. As a consequence, their presence is a good indicator but their absence is not and *Allohippus* "stenonine" patterns may occur in Sussemiones (Eisenmann and Boulbes, in preparation). During this period, this subgenus had great success from North America to Ethiopia, including both species adapted to relatively dry climatic conditions (*Equus granatensis*-like), and others adapted to more humid environments (*Equus coliemensis*-like). Recent molecular and osteological analyses indicate that this subgenus survived until 45,000 BP in Khakassia in southwestern Siberia (*Equus odovovi*, Eisenmann and Sergej, 2011).

According to Palombo and Alberdi (2017) this splitting of Pleistocene equids from Eurasia in different genus/subgenus names requires a great deal of caution, taking into account the homogeneity but also the large intra- and interspecific variation shown by fossil monodactyl horses. In this paper we will consider the genus *Equus* sensu lato, taking into account the different points of view of the specialists. The first part is dedicated to the non-caballoid equids from the Early Pleistocene and the start of the Middle Pleistocene. The second part deals with the true or caballoid horses, especially their ecology regarding the high level of plasticity of this group. The final part, about the European wild ass *Equus hydruntinus*, develops different aspects of its evolution.

METHODS

The nomenclature used for the morphological description of the teeth is illustrated in **Figure 2**. The occlusal measurements were taken from the outer edges of the enamel excluding the cement. Average occlusal size (occlusal surface) can be used to minimize the impact of deformation of the teeth by wear on the analysis. The Protoconal Index (PI) represents the ratio of protoconal length to total length i.e., mesio-distal diameter (IP = Lprot/DMD x 100). Increase in the length of protocone, dissymetry of the double knot and reduction of the vestibular groove (ectoflexid) are generally considered as progressive characters.

The measurement system for the postcranial skeleton is based on that established by Eisenmann (2019).

For the metacarpal several indices are calculated: slenderness index 1 (SI 1): breadth at the middle of the diaphysis (3)/maximal length (1) (Alberdi et al., 1998); slenderness index 2 (SI 2): breadth at the distal articular end (11)/maximal length (1) (Koufos, 1992); diaphysis flatness (DF): depth of the diaphysis (4)/breadth of the diaphysis (3) (Eisenmann, 2002); caballine index (CI): distal supra-articular breadth at tuberosities (10)/distal articular breadth (11) (Prat, 1980); proximal flatness (PF): proximal articular breadth (5)/proximal articular depth (6). The development of the sagittal crest is expressed by the Keel Index (KI) (Gromova, 1949) which is the distal maximal antero-posterior diameter of the medial condyle (14) expressed as a percentage of the distal maximal antero-posterior diameter of the keel (12). Gracility, flatness of proximal end, low development of distal tuberosities and protrusion of the keel are usually considered as advanced features (Eisenmann, 1979).

Simpson's ratio diagrams (Simpson, 1941) are used for comparisons of the general conformation i.e., proportion of the limbs (lengths of long bones) and metacarpals. The standard is chosen according to the species to be compared. *Equus hemionus onager* is most commonly used as a reference for log ratio diagrams; Przewalski's horse for caballoid or true horses; *Equus africanus* for *Equus hydruntinus*.

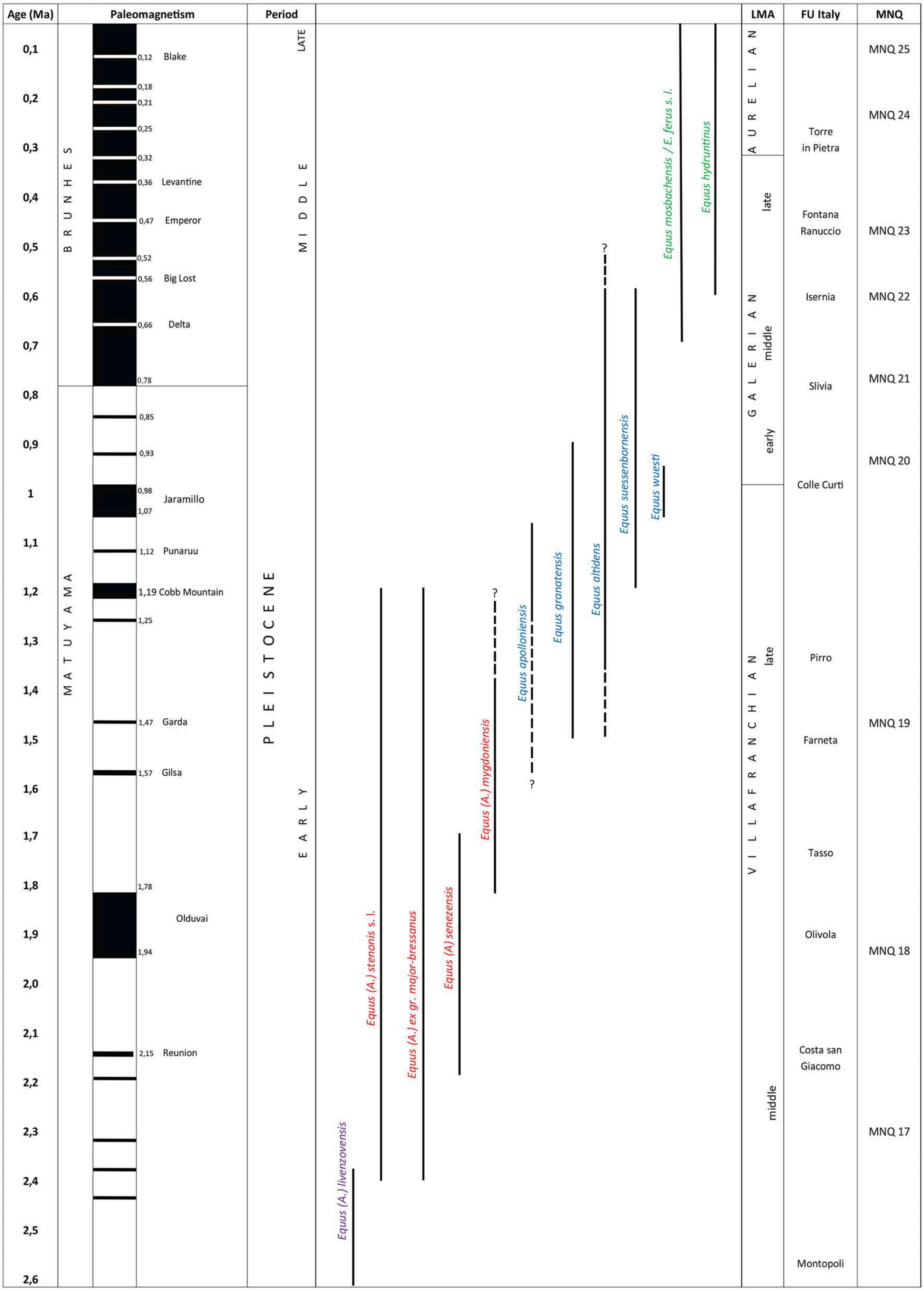


FIGURE 1 | Biochronological overview of the genus *Equus* s. l. from Europe.

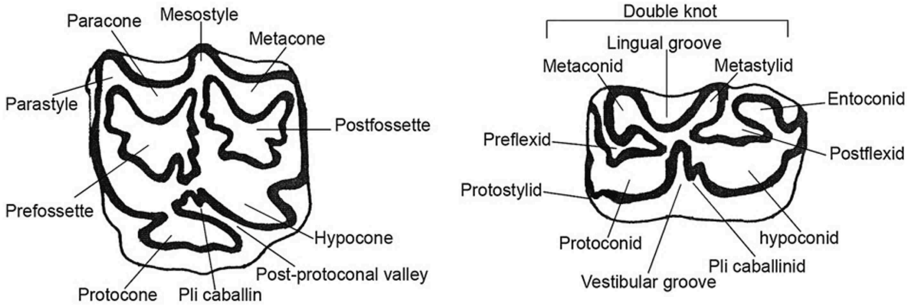


FIGURE 2 | Nomenclature used for upper and lower cheek teeth. Occlusal view.

EQUIDS OF THE EARLY PLEISTOCENE AND THE START OF THE MIDDLE PLEISTOCENE

Equus stenonis and Relatives

The typical stenonid horses (genus ≪ *Allohippus* ≫ following Eisenmann) are recorded in Europe from the end of the Pliocene and disappeared at the latest at the end of the Early Pleistocene. Based on an estimate of their body weight, their morphology, and their skeletal proportions, these fossils correspond to multiple species which are unequally documented. According to Eisenmann (2004a) these species formed a monophyletic group characterized by a deep nasal incision (apomorphy) and other characteristics recurring within this group, such as a weakly developed protocone, a rounded double knot, pointed linguaflexid, and a deep ectoflexid on the molars, cups on incisors, and ≪ flattened ≫ metapodials.

Equus stenonis Cocchi 1867

This species was described from material from an unregistered locality in the surroundings of Terranova in the Upper Valdarno Basin (Tuscany, Italy; De Giuli, 1972; Privat Defaus, 1986). According to Forsten (1999a) and Palombo and Alberdi (2017), the many forms of *E. stenonis* correspond to local variations depending on eco-geographic and maybe chronological factors, and they are little different from the hypodigm of the Upper Valdarno. The revised diagnosis after Alberdi et al. (1998) retains that *Equus stenonis* corresponds to a medium to large-sized horse with "heavy" proportions characterized by a long stylopod (humerus, femur; **Figure 4**); a skull with a deep nasal incision, elongated and narrow muzzle and very long diastema; the braincase is small in relation to the length of the face and strongly convex; the upper teeth have a short protocone (Protoconal Index lower than 40, Gromova, 1949; **Table 1**), the lower teeth have a typical double knot with a rounded metaconid and a slightly angular metastyloid and a deep lingual "V" groove; the vestibular groove is variable, deep or shallow on molars as in the type material (**Figure 3A**); metapodials are robust and "flattened" (low DF index and high PF index), the distal keel is well-developed with (low KI index; **Table 1**).

Several subspecies have been recorded (see Palombo and Alberdi, 2017), the samples from the sites in Valdarno and neighboring localities (Matassino, Olivola, about Olduvai event) are usually referred to the nominal subspecies (De Giuli, 1972). The best known are certainly the more robust form from Saint-Vallier (*E. stenonis vireti* Prat, 1964), descibed in detail with new collection by (Eisenmann, 2004a, "*Allohippus*" *s. vireti*), and the stenonid equid from Chilhac (*E. stenonis guthi* Bœuf, 1986), both dated to 2.5 and around 2.4 Ma (Nomade et al., 2014). The morphology and dimensions of *Equus stenonis olivolanus* (Caloi, 1997) (Olivola) mainly fall within the range of the nominal subspecies (Palombo and Alberdi, 2017). *Equus stenonis pueblensis* (Caloi, 1997) (Puebla de Valverde, located over the Reunion event and bellow the Olduvai chron (Sinusía et al., 2004) is considered as a synonym of the form of Chilhac (Alberdi et al., 1998) or a true species "*Allohippus*" *pueblensis* (Eisenmann, 2017). In eastern Mediterranean, *Equus stenonis* is abundant, especially during middle Villafranchian, and belong to one form similar to Saint-Vallier and La Puebla de Valverde (Koufos, 2001); one of the best described sample is that of Sésklo (Thessaly, Greece, MNQ 17; Athanassiou, 2001).

The temporal range of *Equus stenonis* sensu lato could be 2.5 Ma (Saint-Vallier, Chilhac) to 1.2 Ma (Ceyssaguet; **Figure 1**).

Small and/or Gracile Stenonids

Originally described as a subspecies of *Equus stenonis* (Prat, 1964), the small to medium-sized equid from Senèze (2.1–2.2 Ma, Pastre et al., 2015), *Equus senezensis*, was later elevated to the rank of species (Alberdi et al., 1998; Eisenmann, 2004a). Apart from its small size, *Equus senezensis* has a morphology (teeth and bones) and general proportions similar to *Equus stenonis* (**Figure 4**, **Table 1**). Alberdi et al. (1998) recognize two geographical subspecies, the nominotypical subspecies, recorded at Senèze, and the subspecies "*Equus senezensis stehlini*," including the younger fossils from *E. stehlini* described by Azzaroli (1965) in the late Villafranchian Upper Valdarno.

Equus senezensis stehlini, often considered as a different species, is smaller and characterized by proportionally shorter metapodials, recorded mainly in Italy (late Villafranchian from Casa Frata (1.7 Ma), Upper Valdarno, and Farneta, Val di Chiana; Azzaroli, 1965, 1984; Caloi and Palombo, 1982). During the second half of the Early Pleistocene, *E. stehlini* replaced *E. stenonis* in Italy (Azzaroli, 1965). Palombo et al. (2017) tentatively

TABLE 1 | Index on teeth and metacarpal for selected Early and Middle Pleistocene equids.

	P3/4	M1/2	Metacarpal III					
	PI	**PI**	**SI1(3/1)**	**SI2 (11/1)**	**DF (4/3)**	**PF (5/6)**	**CI (10/11)**	**KI (14/12)**
Equus stenonis vireti[a]	35,4	39,2	16,3	22,2	74,9	155,7	102,5	83,5
Equus stenonis guthi[b]	32,9	36,4	15,5	21,3		156,2	102,2	
Equus stenonis stenonis[c]			14,8	19,9	77,3	152,5	101,0	83,6
Equus senezensis senezensis[d]	30,0	37,3	15,2	20,8	79,2	154,9	102,4	83,9
Equus senezensis stehlini[c]			15,5	20,8	75,4	150,2	100,5	85,9
Equus mygdoniensis[e]	27,2	33,6	13,8	18,6	81,9	155,5	103,2	87,5
Equus bressanus[f]	33,1	39,0	15,6	21,2	78,4	149,9	101,4	86,0
Equus granatensis[g]	28,1	32,6	13,4	17,8	80,7	151,9	101,9	88,8
Equus apolloniensis[h]	35,4	44,0	14,4	20,6	81,5	154,9	100,5	86,3
Equus wuesti[i]	28,0	–	14,0	18,9	81,2	149,9	104,5	88,6
Equus altidens[j]	37,3	44,1	13,25	18,4	82,6	147,2	97,1	87,3
Equus suessenbomensis[j]	39,6	45,1	15,1	21,3	75,6	160,4	99,2	87,0

a, Saint-Vallier, (Eisenmann, 2004a); b, Chilhac (Bœuf, 1986); c, (Alberdi et al., 1998); d, Senèze, (Eisenmann, 2017); e, Mygdonia, (Koufos, 1992); f, Ceyssaguet, (Aouadi and Bonifay, 2008); g, Venta-Micena, Boulbes, pers. data; h, Apollonia P-1, (Koufos et al., 1997); i, Untermassfeld, (Eisenmann and Boulbes, in preparation); j, Süssenborn, (Eisenmann, 2008).

refer the equid from the middle Villafranchian site of Coste San Giacomo (Anagni, central Italy) dated around 2.2 Ma to *Equus* aff. *senezensis stehlini* (**Figure 1**). This recent discovery could roll back the appearance of this form much earlier than expected (Palombo and Alberdi, 2017).

E. mygdoniensis (Koufos, 1992) has been described in the locality of Gerakarou-1 (Mygdonia Basin) in Greek Macedonia (early Late Villafrancian, ∼1.8 Ma). It is a small equid with a short, wide muzzle, short dental rows, short protocones (IP index lower than other stenonids, **Table 1**), and elongated and slender metapodials (Koufos, 1992; low SI indices, **Table 1**) but with flat proximal end as E. stenonis and unlike *E. altidens/granatensis* group. According to Eisenmann (2004a), the equid from Gerakarou belongs to the stenonid group (*Allohippus*) but based on the differences with *Equus stenonis* (small size, cranial proportions, slender metapodials), the Gerakarou equid, originally described as a subspecies of *Equus stenonis* (Koufos, 1992), should be given a specific status (Eisenmann, 2004a). This species is likely to be present in other Greek localities of a similar age (e.g., Pyrgos, Krimni 1/2, Riza 1/2; Koufos, 1992) and may be at Tsiotra Vryssi also in the Gerakarou Formation, but with a younger age, intermediate between the localities Gerakarou-1 and Apollonia-1 (Konidaris et al., 2015). *E. mygdoniensis* is possibly present in Turkey (Denizli basin, Boulbes et al., 2014), Russia (Livenzovka and Psekups), and Valdarno in the wider sense (Eisenmann, 2004a). The stenonoid horses from Libakos and Polylakkos (Western Macedonia, Greece) are very close to *E. mygdoniensis* (including in *Equus altidens*, Gkeme et al., 2017). The taxonomic validity of this species is, however, questioned by other authors who consider that most of the fossils reported to it correspond to *Equus senezensis*/*Equus stehlini* and/or *Equus altidens* groups (Alberdi et al., 1998; Forsten, 1999a; Gkeme et al., 2017; Palombo and Alberdi, 2017).

Eisenmann (2017) also supports the close relationship of the Senèze equid with those of Gerakarou (*Allohippus mygdoniensis*) and Upper Valdarno (*Allohippus stehlini*), in particular with regard to certain common characteristics such as short-muzzled skulls, but keeps them at a species level.

Very Large Stenonids

There is consensus that during the Villafranchian, sometimes together with medium or small-sized forms, one or several species occurs with a very large size and characteristics that are similar to stenonids (Viret, 1954; Prat, 1980; Azzaroli, 1990; Alberdi et al., 1998; Forsten, 1999a; Eisenmann, 2003, 2004a, 2017; **Table 1**, **Figure 4**, "*Equus bressanus*" from Ceyssaguet"). This material is generally designated under the name *Equus major* Depéret in (Delafond and Depéret, 1893) ex Boule, poorly defined from the material of Chagny (revised by Viret, 1954; **Figure 3B**). The stratigraphic position of the fossils is not clearly known. Alternatively, Eisenmann (2017) distinguishes several groups of large (robust or gracile) to very large stenonids but tentatively refers the material from Chagny to the *E. suessenbornensis* group.

The sporadic presence of large stenonids s. l. is mentioned in several localities in France and in particular at Senèze (Prat, 1980; Eisenmann, 2017); in Germany in Schernfeld (Musil, 1992); in the Netherlands at Tegelen (Viret, 1954); in Great Britain at East Runton (Norfolk) and Italy at Upper Valdarno (Azzaroli, 1990). The equid described at Fonelas P-1 (Guadix-Baza depression, Spain), older than Olduvai episode (around 2 Ma, Arribas et al., 2009), has affinities with *Equus* cf. *major* (Garrido, 2008). In eastern Europe, *Equus athanasiui* described at Tetoiu-Valea Graunceanului (Romania) (Samson, 1975), a species possibly also presents at Oosterschelde, Forest Bed, El Rincón and Ceyssaguet according to Forsten (1999a). A large and gracile stenonian horse, under study, occurs in the lower Pleistocene layers (13 to 11b) of Kozarnika (Bulgaria) (Sirakov et al., 2010).

The small amount of material belonging to this group and the different points of view of specialists make it difficult to establish a biochronological framework and determine the

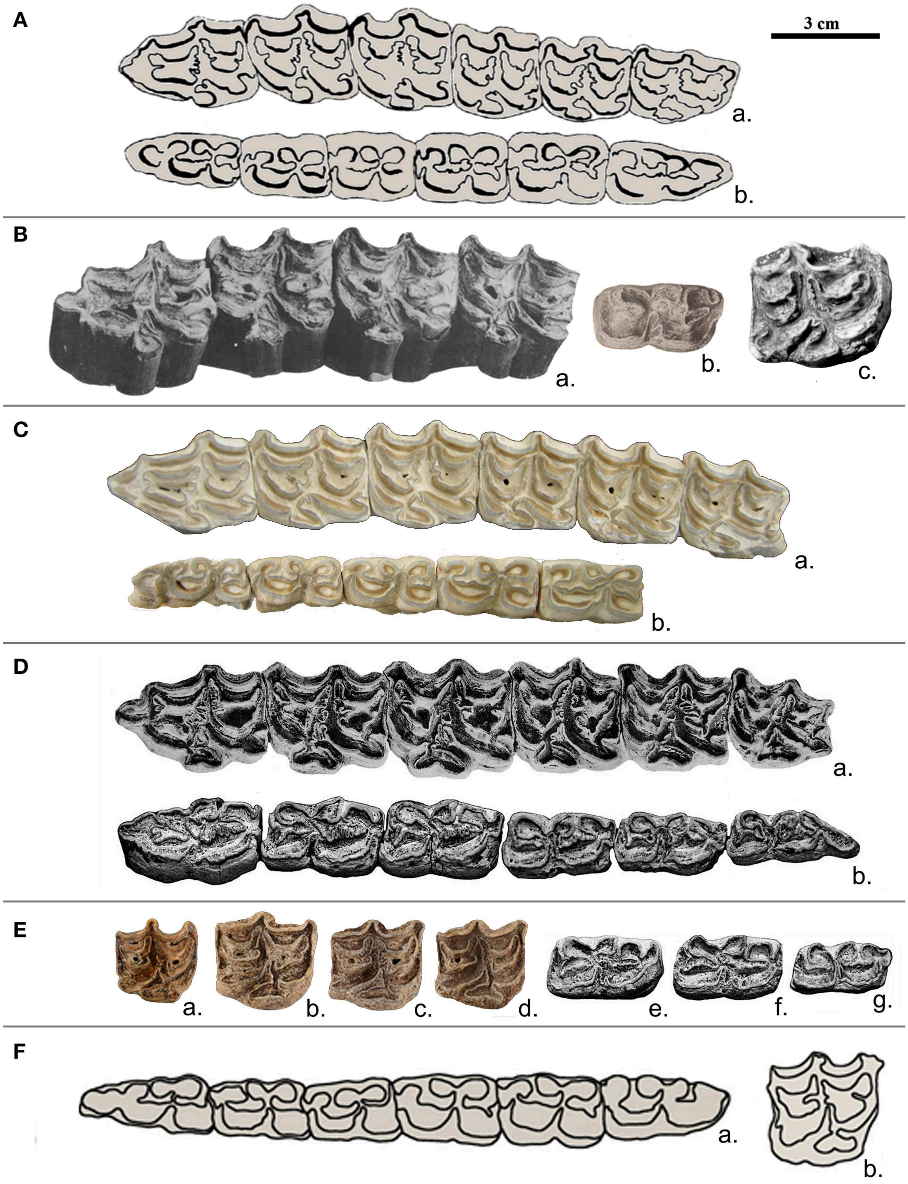


FIGURE 3 | Upper and lower cheek teeth from different Pleistocene equids. Occlusal view. **(A)** *Equus stenonis*, Upper Valdarno, a- left P2-M3, Type; b-right P2-M3 (after Azzaroli, 1965 *in* Caloi, 1997). **(B)** *Equus major*, Chagny, a-left P2-M1, b-left M2 (Delafond and Depéret, 1893); c-right P34, se 338, Senèze (Eisenmann, 2017). **(C)** *Equus granatensis*, Venta Micena, a-left P2-M3, Type, b-right P3-M3, VM 8297 (Boulbes, pers. photo). **(D)** *Equus suessenbornensis*, Süssenborn, a-left upper cheek teeth P2-M3, Type, b-left lower cheek teeth, P2-M3, S 6882 (Eisenmann, 2008). **(E)** *Equus altidens* (including *E. marxi*), Süssenborn, a-right P4, S 1365, M1, S 1366, M2, S 1367, b-left P3, S 1369, P4, S 1368, M2 (S 1370) (Eisenmann, 2019). **(F)** *Equus apolloniensis*, Apollonia P-1, a-right P2-M3, APL 147, b-right P4, APL 148 (after Koufos et al., 1997, in Eisenmann and Boulbes, in preparation).

morphometric and temporal range of the species (Alberdi et al., 1991). Musil (1992) considers that the chronological distribution of this Villafranchian species is between 2.2 and 1.7 Ma. However, "*E. bressanus*" (=*Equus major*) seems to be present later around 1.2 Ma (Ceyssaguet, Aouadi and Bonifay, 2008). According to Eisenmann (2017), very large "*Allohippus*" occurs from 2.5 Ma (Oasele, Romania, Samson, 1975) to around the Brunhes-Matuyama limit (Würzburg-Schalksberg, Germany; Mauser, 1987; **Figure 1**).

E. granatensis/E. altidens Group, *Equus wuesti*, and *Equus suessenbornensis*

Equus granatensis Alberdi and Ruiz Bustos (1985) refers to the slender equid of Venta Micena (Orce, Granada), situated above the Olduvai subchron, with an age around 1.5 Ma (Martínez-Navarro et al., 2011). On the upper teeth the protocone is very short (**Table 1**), often without an anterior part. The shape of the double knot varies from typically rounded stenonine, separated by a pointed and deep lingual groove, to a rather hemionine type

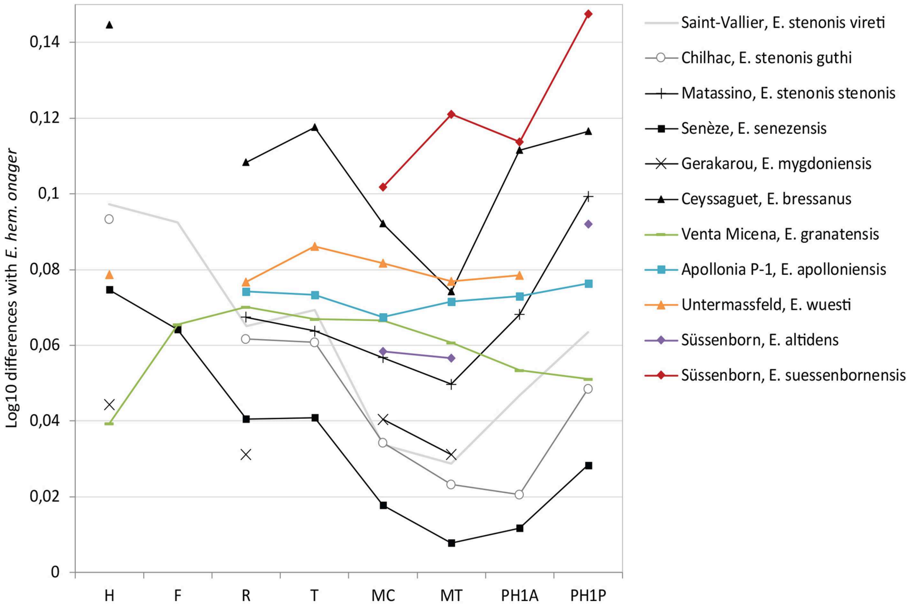


FIGURE 4 | Simpson's ratio diagram of bone lengths of European Early and Middle Pleistocene horses. Reference: *Equus hemionus onager* (Eisenmann, 1991a). H, Humerus; F, Femur; R, Radius; T, Tibia; MC, Metacarpal; MT, Metatarsal; PH1A, First Anterior Phalanx; PH1P, First Posterior Phalanx. Data: Saint-Vallier (Eisenmann, 2004a); Matassino (Eisenmann, 1999); Senèze (Eisenmann, 2017); Gerakarou (Koufos, 1992); Ceyssaguet (Aouadi, 2001); Apollonia P-1 (Koufos et al., 1997); Venta Micena (Boulbes, pers. data); Untermassfeld (Eisenmann and Boulbes, in preparation); Süssenborn (Eisenmann, 1999, 2008).

with an elongated metaconid and pointed metastylid, separated by a shallow lingual groove (Eisenmann, 1999). The vestibular groove is very deep and often touches the lingual one on molars; the ectoflexid may also be deep on P$_3$ and P$_4$; protostylids are frequent in premolars (**Figure 3C**). The general proportions of the limbs, different from *E. stenonis/E. senezensis*, show cursorial adaptations with elongated distal bones (**Figure 4**). The metapodials are slender (diaphysis and extremities) with a deeper diaphysis and proximal end (high DF index and low PF index), and a distal keel poorly developed in comparison to *E. stenonis* and *E. senezensis* (**Table 1**); as in hemiones the difference in length between the first anterior and posterior phalanges is important (Eisenmann, 1999). In our opinion and following Eisenmann (1999), the morphological differences of the teeth with both *E. stenonis* and *E. altidens* (including *E. marxi*) could justify a specific level. *E. granatensis* is mainly recorded in different localities in the south of Spain from 1.5 to 0.8 Ma (**Figure 1**), in particular in the Guadix-Baza basin (Venta Micena, Lachar, Fuensanta, Fuente Nueva 3, Barranco León 5, Marín, 1987; Alberdi and Ruiz Bustos, 1989; Alberdi et al., 1998; Alberdi, 2010) and according to Eisenmann in the site of Cueva Victoria (0.9–0.8 Ma, Gibert et al., 2016), although these fossils were identified as *Equus altidens altidens* by Alberdi and Piñero (2015). *Equus altidens* from epivillafrachian levels of Vallparadis (post Jaramillo, around 0.85 Ma, Duval et al., 2015) have short protocones (Aurell-Garrido et al., 2010) as in *E. granatensis*.

Equus altidens (Von Reichenau, 1915) was described (together with *E. suessenbornensis*) from the early Middle Pleistocene site of Süssenborn, most likely accumulated during marine oxygen isotope stage (MIS) 16, with an age of 0.65 Ma (Kahlke, 2014). There is disagreement about the number of species present in the site of Süssenborn due to the heterogeneity of the material and the long time sequence of the stratigraphy (Musil, 1969; Forsten, 1986; Eisenmann, 2008). *Equus altidens* is a medium-sized and slender species. Revised diagnoses (Forsten, 1986; Alberdi and Palombo, 2013) include the third species described at Süssenborn "*Equus marxi*" (Musil, 1969): the teeth have a small and narrow crown; the morphology of the protocone of the upper teeth is variable, often indented lingually with an elongated distal part, resulting high values of Protoconal Index in comparaison to *E. granatensis* (**Table 1**); the mesostyle sometimes divided into two; a deep post-protoconal valley; and a pli caballin moderately developed or even absent on worn molars. Lower teeth often show a pli protostylid fold including P$_2$; the ectostylid is sometimes present but rare; the double knot is asymmetric; the ectoflexid is deep on molars (**Figure 3E**). The skeleton is gracile and metapodials (similar to *E. granatensis*) are more slender than in all other stenonids forms; distal keel is less developped and distal tuberosies are not so strong (CI index < 100) than other species (**Table 1**). Following several authors (Alberdi et al., 1998; Forsten, 1999a; Alberdi and Palombo, 2013) *Equus altidens* also includes the fossils of the site of Venta Micena renamed *Equus altidens granatensis* (Alberdi et al., 1998) and those of the small equine of Akhalkalaki in Georgia (1.0 to 0.8 Ma) (=*Equus hipparionoides*, Vekua, 1986). Eisenmann (1999, 2010) agrees with the proximity of the Süssenborn slender species and the equid from Venta Micena but gives a specific rank to *E. granatensis* based on the relatively short protocones compared to *E. altidens*. She considers that *Equus altidens* is too poorly defined and should be used with caution.

Disagreements make it difficult to trace a reliable biochronology for *Equus altidens*. The most extensive suggests the concurrent arrival around 1.8 Ma of the species in Western Asia (*E.* aff. *altidens* from Dmanisi, Georgia, Lordkipanidze et al., 2007) and in Southeastern Europe (Gkeme et al., 2017). Other possibility is that it dispersed to Europe from China around 1.2 Ma (Van der Made, 2013). According to Alberdi and Palombo (2013) *Equus altidens altidens* was first recorded in Italy around 1.5 Ma (Selvella and Pirro Nord LFAs). However, the teeth that have the most affinity (deep postprotoconal valley, elongated protocone), with those of the type locality are around and younger than 1 Ma: Bois de Riquet (Bourguignon et al., 2016; Lozano-Fernández et al., 2019), Soleihlac (Prat, 1980; Lacombat, 2005), Pakefield (Lister et al., 2010), Voigstedt (Musil, 1965), Atapuerca Gran Dolina TD6 (Van der Made, 1999), Huescar-1, Cullar de Baza-1 (Alberdi and Ruiz Bustos, 1989). The site of Venosa-Loreto, slightly younger than Notarchirico with an estimate age around 0.6 Ma (Pereira et al., 2015), could represent its last appearance (Alberdi and Palombo, 2013; **Figure 1**). Some elements (metapodials, teeth) found in the site of Mosbach (0.5 Ma) show affinities with the remains of Süssenborn (Eisenmann, 2008) and merit further investigation.

The equid of the Epivillafranchian site of Untermassfeld (Thuringia, Germany), *Equus wuesti* (Musil, 2001), represents another species, somewhat larger and less gracile (**Table 1**), but less distinct in terms of its proportions than *Equus altidens* (Musil, 2001) (**Figure 4**). Musil (followed by Lister et al., 2010) considered the Untermassfeld horse as the ancestor of *E. altidens*, in spite of the presence of the latter species in localities older than the German site (Palombo and Alberdi, 2017). The site is positioned around the Jaramillo polarity subzone with an age of approximately 1.0 Ma (Kahlke, 2006; **Figure 1**). Unfortunately, no skull material was found and tooth remains are not very numerous whereas the postcranial skeleton is well-represented. Metacarpal has deeper diaphysis and proximal end, the distal tuberosities are very strong (**Table 1**). Descriptions of new and older material of the species and comparisons confirm that *Equus wuesti* represents another species inside the Sussemione group close to but different from the equids of Venta Micena (in particular the teeth) and Akhalkalaki (Eisenmann and Boulbes, in preparation).

Equus suessenbornensis (Wüst, 1900) is a large species with a mozaic of features (Musil, 1969; Gromova and Dubrovo, 1975; Forsten, 1986; Azzaroli, 1990; Alberdi et al., 1998; Eisenmann, 2006a). The main characteristic of the teeth is the high level of enamel folding and converging characters with true horses (caballines) regarded as homoplasy. The upper teeth have an elongated and asymmetric protocone (IP index on M12 = 45, **Table 1**) with a concave lingual border, a wide mesostyle on premolars, a marked groove on styles at least at some distance from the crown, and a wide-based pli caballin. Lower teeth show certain cingulate structures such as protostylid or ectostylid, the vestibular groove is always deep on molars and often in contact with the lingual side (**Figure 3D**). Metapodials are longer and the extremities are robust; diaphysis and more specially the proximal articulation are "flattened" (high PF index, **Table 1**); the distal keel is poorly developed (**Table 1**); the metatarsal is elongated (**Figure 4**). Some authors have considered *Equus suessenbornensis* as the first archaic true horse or an evolutionary intermediate between stenonoids and caballoids (Gromova, 1949). However, the double knot appears to be very different from that characteristic in horses, although more derived than in *E. stenonis* (Forsten, 1986, 1999a; Alberdi et al., 1998; Palombo and Alberdi, 2017). *Equus verae* (Sher, 1971) of north-eastern Siberia (Chukochya, about Jaramillo event), which is characterized by teeth with a similar morphology and metapodials with identical proportions to *Equus suessenbornensis*, could present a synonym (Forsten, 1986) or a very similar species (Eisenmann and Kuznetsova, 2004). The cranium from Kolyma (north-east Siberia), referred to *E. coliemensis* (Lazarev, 1980) and dated to the end of the Early Pleistocene, belongs in the same group (Eisenmann, 2010).

In Europe *Equus suessenbornensis* is also present in Germany in the Middle Pleistocene site of Voigtstedt (Musil, 1965), in the Czech Republic at Stranska Skala (Musil, 1972), in Italy in several localities between the latest Villafranchian (Farneta and Pirro faunal units) to the middle Galerian (Caloi and Palombo, 1987; Alberdi et al., 1988; Alberdi and Palombo, 2013), in Spain at Fuente Nueva-3, Barranco León-5, Cueva Victoria, Huéscar-1, Cúllar de Baza-1, (Alberdi and Ruiz Bustos, 1989; Alberdi, 2010; Alberdi and Piñero, 2015), in France at the sites Bois de Riquet, Nauterie, and Soleilhac (Prat and Thibault, 1976; Prat, 1980; Lacombat, 2005; Bourguignon et al., 2016), in England in the Cromer Forest Bed Formation, Lister et al., 2010). In Eastern Europe *Equus suessenbornensis* was likely present in Ukraine (Tiraspol) (Gromova and Dubrovo, 1975), as well as in Romania (Samson, 1975) and in Western Asia in Georgia (Akhalkalaki) which delivered the best-known collection for the species (Vekua, 1986). The presence of this species in older sites as in Italy (Pirro Nord and Selvella, Alberdi and Palombo, 2013) can be debated. The measurements given by the authors of the specimens that belong to this taxon show a relatively small body size, taking into account the variability of the best known sample of Akhalkalakhi (MT III length between 300 and 330 mm). Other localities, for example Dursunlu in Turkey (1.0 and 0.8 Ma) (Yigit, 1998; Güleç et al., 2009), merit further investigation. Indeed, some teeth seem really characteristic of the species.

Taking into account this wide geographical range from Beringia to Western Europe (Eisenmann and Kuznetsova, 2004), the range of the type species based on material similar to the hypodigm (complex enamel, long protocone, and metapodials with robust extremities) (North-East Siberian, Akhalkalaki, Orce, Cueva Victoria, Süssenborn, Venosa) is comprised between the end of Early Plesitocene around 1.2 and 0.6 Ma (**Figure 1**).

Phylogeny of *Equus altidens/granatensis* and *Equus suessenbornensis*

Scholars are divided about the phylogeny of *Equus altidens/granatensis* and *Equus suessenbornensis*–a local European evolution or a dispersal event from Asia and or Africa. In the scenario proposed by Eisenmann (2010), cf. Introduction, they belong to the new subgenus of *Equus* "*Sussemionus*" and originated probably in North America and are not linked with the stenonid group (*Allohippus* for instance). Sussemionus is defined in reference to the mixture of morphological characters shared in the fossil equids from Süssenborn and extant hemiones (deep postprotoconal groove, multiple plis caballin or with very large base, sometimes very short protocones on upper teeth, and elongated/bilobated metaconids, presence of stylids and deep ectoflexid on lowers).

However, this point of view is not shared by other authors who consider that both species belong to the stenonid group (Forsten, 1986, 1999a; Azzaroli, 1990, 1992; Alberdi et al., 1998; Alberdi and Palombo, 2013; Palombo and Alberdi, 2017). In this scheme a local evolution in Europe from a stenonid stock is proposed for both species. With an overall trend from robust to gracile, *Equus altidens* could represent the latest form of the stenonid group (Alberdi et al., 1998; Piñero and Alberdi, 2015). Intermediate chronological forms in relative proportions (Selvella, Libakos, and Pirro Nord) provide support for this model (Van der Made et al., 2017) at least in Italy, but points of view diverge about the taxonomy of the equids from these localities (De Giuli, 1987; Azzaroli, 1990; Forsten, 1999a; Eisenmann, 2004a, 2006a; Alberdi and Palombo, 2013; Gkeme et al., 2017). Alternative scenarios propose that *E. altidens* evolved from the African species *E. tabeti* (Aïn Hanech, Algeria), and that it dispersed shortly after 1.8 Ma to Europe (Guerrero-Alba and Palmqvist, 1997).

Concerning *Equus suessenbornensis*, some authors highlight the phylogenetic link with *Equus major* (*Equus bressanus*) (Grossouvre and Stehlin, 1912; Alberdi et al., 1998; Forsten, 1999a; Aouadi and Bonifay, 2008; Palombo and Alberdi, 2017). According to Alberdi et al. (1998), the *E. major-E. suessenbornensis* monophyletic group may have stemmed from *E. livenzovensis*. In accordance with this, remains of large equids from the Upper Villafranchian and Lower Galerian are commonly referred to *Equus* ex. gr. *bressanus-suessenbornensis* (Rook et al., 2013). Due to the heterogeneity of the large stenonid group (*E. major-bressanus*) and the hypothesis including *E. suessenbornensis* in the subgenus *Sussemionus*, this link remains uncertain.

Ecology of *Equus altidens* Sensu Lato and *Equus suessenbornensis*

These two species, in addition to the Süssenborn type locality, are frequently found sympatrically in many other deposits. The association is particularly well-documented in Akhalkalaki, Georgia (1.0 to 0.8 Ma) (Vekua, 1986), in several sites in the Guadix-Baza basin in southern Spain between 1.4 and 0.9 Ma (Alberdi and Ruiz Bustos, 1989; Alberdi et al., 1998; Alberdi, 2010), in the region of Murcia Cueva Victoria and Quibas (Alberdi and Piñero, 2015; Piñero and Alberdi, 2015), in Italy between 1.5 and 0.6 Ma (Alberdi and Palombo, 2013) and in France (Bois de Riquet, Bourguignon et al., 2016; **Figure 5**). They could both be represented in the Czech Republic at Stranska Skala (Musil, 1995) and in Romania (Samson, 1975). The co-occurrence of the two species seems to be demonstrated in early Middle Pleistocene England at the West Runton and Pakefield sites (Lister et al., 2010). It seems that at lower latitude (Spain, Italy, France) the slender species is more common than *Equus suessenbornensis* (Alberdi and Piñero, 2015; Bourguignon et al., 2016; Palombo and Alberdi, 2017). It should also be noted that from new discoveries in the site of Untermassfeld *Equus wuesti* is associated with a large form sharing affinities with *E. suessenbornensis* group (Eisenmann and Boulbes, in preparation).

FIGURE 5 | *Equus altidens* **(A)** and *Equus* cf. *suessenbornensis* **(B)** from Bois de Riquet (US2). **(A)** Right proximal metacarpal (BDR-X37b-61b); **(B)** left proximal metacarpal (BDR-Z34d-114).

The large difference in body mass (**Figure 5**) between *Equus altidens* and *Equus suessenbornensis* prevented any interspecific competition between them and led to the use of different ecological niches (Alberdi et al., 1998; Alberdi and Palombo, 2013). According to (Alberdi and Piñero, 2015, p. 325) "the large horses lived on open and dry habitats (steppes), whereas smaller ones lived on more closed and wet habitats (savanna-mosaic, woodlands)." From a locomotor adaptation point of view, the relative length of the *Equus altidens/granatensis* metapodials in comparison with the proximal bones of the limbs, and their gracility, suggests a more pronounced cursorial capacity than in the other Villafranchian species and the frequenting of more open landscapes and certainly more arid biotopes (Eisenmann, 1984, 2010; Caloi, 1995). In addition, the proportions of the muzzle and the morphology of the row of symphyseal incisors show that these two species occupied a particular ecological niche and exploited different food resources (Caloi, 2002). The relatively short and wide muzzle proportions in *Equus altidens* are consistent with a highly specialized grazer diet. *Equus suessenbornensis* has a wide but relatively elongated muzzle that may imply a less strict preference for monocotyledonous short grass. However, during periods of low availability of resources, the diet of these species, in particular *Equus suessenbornensis*, could have been enriched with a certain amount of dicotyledonous plants (Caloi, 2002). Simple enamel folds are observed in species feeding on hard vegetation, while a more complicated enamel pattern is found in species feeding on softer plants (Gromova, 1949; Eisenmann, 2010). The highly folded teeth of *Equus suessenbornensis* could be related to more humid conditions (Eisenmann, 2006a). Besides the size and shape of specific skeletal elements, the fossils of Pleistocene equids have also yielded other information on their diets and habitat use. In particular, studies of tooth wear characteristics and isotopic analyses of teeth have given insight into horse behavior. Mesowear describes the tooth wear patterns that result from an individual animal's diet over a large part of its lifespan (Fortelius and Solounias, 2000; Rivals et al., 2007). Tooth microwear reflects the wear characteristics of the foodstuffs the animal consumed in the days before it died (Walker et al., 1978). The microwear of grazers is characterized by high numbers of scratches and low numbers of pits (Solounias and Semprebon, 2002). Feeding habits reconstructions based on mesowear analysis indicate a high level of abrasion in *Equus altidens*, as demonstrated in the Vallparadis section (level EVT12 and EVT7, respectively, dated to 1.0 Ma and 0.86 Ma) (Strani et al., 2019) and the MIS 17 localities of Pakefield and West Runton in England (Rivals and Lister, 2016). However, microwear scores seem to nuance the strictly "grazer" character of *Equus altidens*, classified as either grazers or seasonal mixed feeders (Valli et al., 2012; Rivals and Lister, 2016; Strani et al., 2019). Such data are, to our knowledge, not available for *E. suessenbornensis*.

The Case of *Equus apolloniensis*

Equus apolloniensis (Koufos et al., 1997), the equid of Apollonia 1 in Greek Macedonia (Platanochori Formation, Mygdonia Basin) dated to about 1.2–0.9 Ma (Koufos and Kostopoulos, 2016), constitutes a different species with many affinities to modern wild asses (Eisenmann and Kuznetsova, 2004; Eisenmann and Boulbes, in preparation). The species is characterized by its medium to large size, a cranium with a short and deep muzzle, short palate, elongated choanae, shallow narial notch, far posteriorly situated orbit, elongated supra-occipital crest; teeth with elongated protocones, deep postprotoconal groove (**Table 1**; **Figure 3F**), rounded double knot and shallow ectoflexid on lower molars; and elongated, and not robust metapodials with deeper diaphysis as *E. altidens*/*E. granatensis* but "flattened" proximal end as *E. stenonis* (**Table 1**); protrusion of the distal is intermediate (**Table 1**). According to Koufos et al. (1997) the species represents a transitional form from the typical *E. stenonis* to the Middle Pleistocene horse *Equus suessenbomensis*. However, the similarities with the current wild donkeys (*Equus africanus*) are very striking in the mandible, morphology of the teeth (central and bilobed protocone, deep postprotoconal groove, shallow vestibular groove on lower molars), general proportions of the limb bones, and the proportions of the metapodials (Eisenmann and Boulbes, in preparation). The geographical distribution of the species appears to be limited to the eastern Mediterranean, as evidenced by its presence in other localities of the Upper Villafranchian in Greece (Koufos et al., 1997) as in Alikes (1.6 Ma, Kahlke et al., 2011), may be in Tsiotra Vryssi and more certainly in the site of Platanochori-1 (both from Mygdonia basin) similar in age than Apollonia P-1 (Konidaris et al., 2015). Its presence is also suspected in Turkey in the upper travertines of the Denizli region in southwestern Anatolia dated between 1.6 and 1.1 Ma (Boulbes et al., 2014; Lebatard et al., 2014). The species is however evoked at the transition of the Lower to the Middle Pleistocene in Spain in the region of Valencia (Cova del Llentiscle de Vilamarxant, Sarrión Montañana, 2008).

CABALLOID OR TRUE HORSES

There is consensus that the lineage of true or caballoid horses emerged in Europe at the beginning of the Middle Pleistocene (Forsten, 1998b), gradually becoming more numerous and replacing the various stenonid species.

Their extensive skeletal plasticity enabled them to survive under a wide range of climatic conditions and environments, from interglacial forests to grass-steppes during glacial episodes (van Asperen, 2010; Saarinen et al., 2016). Their ubiquitous and often abundant presence in iconic Middle Pleistocene palaeontological and archaeological sites have led to an intensive research focus, with researchers such as Von Reichenau (1915), Gromova (1949), Prat (1968), Nobis (1971), (e.g., Eisenmann et al., 1985; Eisenmann, 1988, 1991a,b; Eisenmann and David, 2002) (e.g., Forsten, 1973, 1999b; Forsten and Moigne, 1998) (e.g., Musil, 1975, 1977, 1978, 1984, 1990, 1991) (Guadelli, 1987, 1991), and Kuzmina (1997) publishing extensively on these fossils in the twentieth century, developing methods that are still in use (especially V. Eisenmann's series of measurements; Eisenmann, 1979, 1980, 1981; Eisenmann et al., 1988; Dive and Eisenmann, 1991). Initially, this research focused primarily on describing the fossils. Later work developed a focus on biostratigraphy (e.g., Eisenmann, 1988, 1991a,b; Forsten, 1998b), which has continued into the twenty-first century (e.g., Cramer, 2002; Boulbes, 2010; van Asperen, 2011, 2012, 2013a; Uzunidis, 2017). Such studies identified patterns of variation in the Middle Pleistocene *Equus* lineage which were subsequently interpreted as ecomorphological adaptations (van Asperen, 2010; Saarinen et al., 2016). Since they were an important component of the large vertebrate fauna, Middle Pleistocene equids have also been included in broader studies of diet and habitat use (e.g., Bocherens et al., 1997; Rivals et al., 2008, 2009; García García et al., 2009; Feranec et al., 2010; Pushkina et al., 2014; Rivals and Lister, 2016; Uzunidis et al., 2017), resource partitioning and niche separation (Britton et al., 2012), and taphonomy (Rivals et al., 2015).

One Species or Many Species?

To a novice accessing the literature, one thing stands out immediately: the proliferation of equid species names during the Middle Pleistocene (**Table 2**). Middle Pleistocene caballoid equids exhibit homogeneous overall morphology compared to equids from earlier geological epochs.

The first true horse in Europe, *Equus mosbachensis* (Von Reichenau, 1915) (or *E. ferus mosbachensis*), is perhaps the only one often regarded as a true species (Eisenmann, 1979, 1980; Bonifay, 1980; Crégut, 1980; Eisenmann et al., 1985; Guadelli and Prat, 1995; Langlois, 2005; Boulbes, 2010; Palombo, 2014; Palombo and Alberdi, 2017; Uzunidis et al., 2017). *Equus mosbachensis* presents some "archaic" morphological characters: presence of the tendon insertion of the anterior brachialis muscle on the inner edge of the diaphysis of the radius, strong supra-articular tuberosities on metapodials, a large size and slender general build. Other characters are specific, such as variation the of protoconal index (low and sub-equal between P4 and M1). *Equus mosbachensis* is clearly identified in Mauer (Nobis, 1971), dated by combined ESR/U-series and IR analysis at 609 ± 40 ka and correlated to MIS 17/15 (Wagner et al., 2011), then in the eponymous site of Mosbach 2 which yielded a very rich assemblage. Also in Germany, some typically caballine and teeth discovered at Süssenborn (MIS 16, 0.64–0.62 Ma, Kahlke, 2014) could represent some of the oldest evidence (Forsten, 1986; Eisenmann, 2008). West Runton is the oldest site in England

TABLE 2 | Selected species names used in the literature for Middle and Late Pleistocene European caballoid equids (NB many variants on these names also occur but are not included here).

Species	MIS	Selected references
Equus mosbachensis Von Reichenau, 1915 *E. m. tautavelensis* *E. m. campdepeyri* *E. m. micoquii* *E. m. palustris*	16–6	Von Reichenau, 1915; Nobis, 1971; Bonifay, 1980; Crégut, 1980; Eisenmann et al., 1985; Eisenmann, 1988, 1991a,b; Musil, 1991; Guadelli and Prat, 1995; Kuzmina, 1997; Forsten and Moigne, 1998; Langlois, 2005; Uzunidis, 2017
Equus steinheimensis Von Reichenau, 1915	11–8	Nobis, 1971; Mourer-Chauviré, 1972; Bouchud, 1978; Eisenmann, 1988, 1991a; Forsten and Moigne, 1998; Forsten, 1999b
Equus torralbae Prat, 1977	9	Prat, 1977; Martín Penela, 1987; Eisenmann et al., 1990; Sesé and Soto, 2005; Cerdeno and Alberdi, 2006
Equus achenheimensis Nobis, 1971	8–6	Nobis, 1971; Eisenmann, 1991a; Forsten, 1998b; Mourer-Chauviré et al., 2003; Boulbes, 2010
Equus f. taubachensis Freudenberg, 1911	7–5e	Von Reichenau, 1915; Musil, 1975, 1977, 1978, 1984, 1990; Eisenmann, 1991a,b; Foronova, 2006
Equus f. piveteaui David and Prat, 1962	6	Prat, 1968; Nobis, 1971; Bouchud, 1978; Eisenmann, 1988, 1991a; Griggo, 1995; Forsten, 1999b; Guadelli, 2007; Uzunidis, 2017
Equus f. germanicus Nehring, 1884	5–3	Von Reichenau, 1915; Nobis, 1971; Eisenmann et al., 1985; Guadelli, 1987; Eisenmann, 1988, 1991a,b; Forsten and Ziegler, 1995; Forsten, 1999b; Eisenmann and David, 2002
Equus f. antunesi Cardoso and Eisenmann, 1989	Late Pleist.	Cardoso and Eisenmann, 1989; Cerdeno and Alberdi, 2006
Equus f. gallicus Prat, 1968	End 3–2	Prat, 1968; Mourer-Chauviré, 1980; Eisenmann et al., 1985; Guadelli, 1987, 1991; Eisenmann, 1988, 1991a; Cardoso and Eisenmann, 1989; Eisenmann and David, 2002; Crégut-Bonnoure et al., 2018
Equus f. latipes Gromova, 1949	3–2	Nobis, 1971; Belan, 1985; Eisenmann, 1991a,b; Kuzmina, 1997; Spassov and Iliev, 1997; van Asperen et al., 2012
Equus f. arcelini Guadelli, 1991	2	Guadelli, 1987, 1991; Eisenmann, 1988, 1991a; Eisenmann and David, 2002; Bignon, 2003; Bignon et al., 2005; Valensi and Boulbes, 2018
Equus ferus Boddaert, 1785		Nobis, 1971; Eisenmann, 1991a,b; Cramer, 2002; Boulbes, 2010; van Asperen, 2010, 2012, 2013b
Equus caballus Linnaeus 1758		Nobis, 1971; Eisenmann, 1988, 1991a,b; Kuzmina, 1997; Cramer, 2002; Boulbes, 2010

that contained material of the species (Lister et al., 2010), of pre-Elsterian age, and is correlated with an MIS 17 fauna (Preece and Parfitt, 2008). Other regions of southern and western Europe also show the presence of this horse at the beginning of the Middle Pleistocene: in Spain in the Middle Pleistocene levels of the Vallparadís section (EVT3) of a slightly more recent age than 0.6 Ma based on the small mammal fauna (Aurell-Garrido et al., 2010; Madurell-Malapeira et al., 2010; Martínez et al., 2014) or in Sierra de Atapuerca (Galeria TG8, Gran Dolina TD10, Van der Made, 2013). In Italy the first true horses are recognized in the Isernia faunal unit (Palombo, 2014) at Notarchirico (about 0.6 Ma; Pereira et al., 2015), and perhaps earlier with the "caballine equid" from Cesi (Brunhes lower to 0.7 Ma, Ficcarelli et al., 1997; Palombo, 2014). There is no chronological consensus on the disappearance of the *E. mosbachensis* group or even on the taxonomy of the different forms or subspecies ascribed to it (*E. m. tautavelensis* Crégut, 1980, Caune de l'Arago; *E. m. campdepeyrii* Guadelli and Prat, 1995, Camp-de-Peyre; *E. m. palustris* Bonifay, 1980, Lunel-Viel; *E. m. micoquii* Langlois, 2005, Micoque) because of the numerous regional and chrono/ecotype variations. *Equus mosbachensis* could extend to the end of Middle Pleistocene during MIS 6 (Guadelli, 2007; Uzunidis, 2017), but populations similar to the type-series are generally Cromerian in age, or up to MIS 9 as in Schöningen (Channel II) for example (Van Kolfschoten et al., 2015; **Figure 1**).

This is not unexpected, since interspecific variation between extant species of equids is relatively low in comparison with other large mammal lineages, making it difficult to distinguish between modern equid species based on skeletal morphology (Eisenmann, 1979, 1986; Eisenmann and Beckouche, 1986; Dive and Eisenmann, 1991; Eisenmann and David, 2002). However, clear patterns of variability in terms of dental and skeletal proportions can be identified in Middle Pleistocene caballoid equid fossils. This variability has been interpreted as reflecting an evolutionary lineage developing through various (chrono)species (Eisenmann and Kuznetsova, 2004). Whether these can be regarded as species or subspecies, chronospecies or ecomorphs depends largely on an assessment of the extent of this variation between fossil assemblages as compared to intra- and interspecific variation in modern equids (van Asperen, 2013b).

Sexual dimorphism, both in size and in shape, and age-related size and shape variation in adult skeletal elements is insignificant in modern equids (Winans, 1989; van Asperen, 2013b). Whilst male individuals are on average slightly larger than females, body size considerably overlaps between the sexes (Kuzmina, 1997; van Asperen, 2013b). This implies that any size and shape differences that can be observed between fossil assemblages reflect real population differences. However, whilst such size and shape differences can certainly be observed, taken as a whole, the Middle Pleistocene European horse lineage, covering a time span of about 300,000 years, is not more variable than modern ponies or such highly homogeneous groups as Arabian horses or *Equus przewalskii* (van Asperen, 2013b). Furthermore, there is no unidirectional, evolutionary trend in size and shape. Instead, morphology fluctuates over time (Forsten, 1993; Eisenmann and David, 2002; Eisenmann, 2004b; van Asperen, 2010). In addition to observations on skeletal morphology, studies of equid genetic variation also indicate that Middle Pleistocene equid taxonomy shows a degree of oversplitting (Weinstock et al., 2005; Orlando et al., 2009).

Taking these considerations into account, here we follow the guidelines of the International Commission on Zoological Nomenclature (ICZN, 2003; see also Cramer, 2002; van Asperen, 2013b) and refer to all European late Middle Pleistocene and Upper Pleistocene caballoid equids as *Equus ferus* Boddaert, 1785, although this taxon, commonly chosen for Pleistocene wild horses, remains questionable (Guadelli and Delpech, 2000; Eisenmann, 2006b). The variation observed between assemblages follows certain patterns that can be interpreted as ecomorphological variation, and the resulting groups are best referred to as ecomorphs, or, at most, subspecies of *E. ferus*.

Ecomorphological Patterns

The European Middle Pleistocene was characterized by high-amplitude glacial–interglacial cycles, producing an alternation of a wide range of environments ranging from glacial deserts to continental steppe-like environments and temperate forests. Remains of caballoid horses have been found in sediments deposited in virtually all these environments, often in abundance and with good preservation. Although, as we have argued above, all these remains can be assigned to a single species, the variation in temperature, humidity, vegetation openness, and the character of the substrate exerted fluctuating selective pressures on certain skeletal characteristics. Adaptive variation produced several ecomorphs whose morphology reflects the environmental conditions (van Asperen, 2010). The cyclical nature of the climatic changes thus led to cyclical fluctuations in caballoid morphology (Forsten, 1993; Eisenmann and David, 2002; Eisenmann, 2004b; van Asperen, 2010). The influence of these environmental conditions on horse morphology was mediated through diet, thermoregulation and locomotion.

Muzzle

The main differences in cranial proportions of caballine Pleistocene Equids concern the variation in the proportions of the muzzle (Eisenmann, 2014). Despite attempts to detect an evolutionary pattern, the proportions of the muzzle always find an explanation in local climatic conditions. However, whether these differences in proportions result from a micro-adaptive phenomenon or phenotypic plasticity as acclimatization remains unclear. A short and broad muzzle could represent an adaption to a cold climate (following Allen's rule) and grazer specialization. Examples of cold adapted caballoid equids with a short and broad muzzle are found in Middle Pleistocene glacial deposits (Bellai, 1998; Boulbes, 2014; Caune de l'Arago, MIS 14–12, Eisenmann et al., 1985; Lumley et al., 2015) or from the Last Glacial Maximum at the end of the Upper Pleistocene (MIS 2) (Coulet des Roches, *E. ferus gallicus*, Crégut-Bonnoure et al., 2018). On the other hand, more elongated muzzles often associated with narrower proportions come from temperate climatic conditions as in the case of the interglacial equid from Lunel-Viel (Bonifay, 1980; Eisenmann et al., 1985) or the Late Pleistocene horse from Portugal *E. ferus antunesi* (Cardoso and Eisenmann, 1989). Intermediate morphs could also reflect interstadial conditions. Reconstruction based on the proportions of the symphysis leads to the same results (Caloi, 2002; Bignon, 2003).

Teeth

Size and Shape

Tooth size and shape is influenced primarily by diet. Equids are generalized grazers (Salter and Hudson, 1979; Guthrie, 1984; Feranec, 2007a; see below). Several features of the dentition of Middle Pleistocene caballoids have been connected with specific dietary pressures. A larger occlusal surface enables the animal to process more food (MacFadden, 1988). Although horses can survive on a low-quality diet, they need a high and relatively diverse food intake (Salter and Hudson, 1979; Duncan et al., 1990). Hindgut fermenters such as horses show an increase in length of the premolar row and a widening of the teeth with an increase in the amount of browse in the diet (Janis, 1990).

In general, tooth size shows relatively little variation over the Middle Pleistocene. And whilst qualitative characteristics of the tooth occlusal surfaces can vary greatly within assemblages, variation between assemblages is insignificant. This may be due to the fact that the dentition is generally less phenotypically plastic and thus reacts more slowly to environmental factors than e.g., limb bones (Hillson, 2005). However, differences in size are sometimes recorded: glacial horses, such as for example those of Arago cave (MIS 14 to MIS 12), exhibit very large teeth ("macrodont"), relative to the size of the postcranial elements (Boulbes, 2014) (**Figure 6**). An explanation could be that this horse lived under glacial climatic conditions in a steppic environment with low-quality foodstuffs, necessitating a high food intake. A wider occlusal surface is also an advantage when consuming more abrasive grasses (Gromova, 1949; Guadelli, 1987; Eisenmann, 1991b; Delpech et al., 2000). In the case of the Arago horse, a high level of abrasive food is indeed inferred from mesowear and microwear analysis (Kaiser and Franz-Odendaal, 2004; Rivals et al., 2008). Teeth from British sites tend to be somewhat larger than those from continental sites, being relatively wide with relatively long premolar rows (van Asperen, 2010). This suggests a higher food intake and/or a higher proportion of browse in the diet, which may be due to the more oceanic climate, and thus denser and to horses less hospitable interglacial forests, of the British Isles compared to most of continental Europe.

Protocone length

Eisenmann (1991b) grouped caballoid horses into three types based on the length of protocone of their upper teeth. Longer protocones are more resistant to wear and thus better adapted to abrasive food sources (MacFadden, 1988). Although the size differences are not statistically significant, in general the pattern holds for Middle Pleistocene caballoids, but there are many exceptions (van Asperen, 2009a,b). Horses of Type I have shorter protocones on the upper third and fourth premolars (P3/4) than on the upper first and second molars (M1/2), and are generally found in temperate climates. Kuzmina (1997)

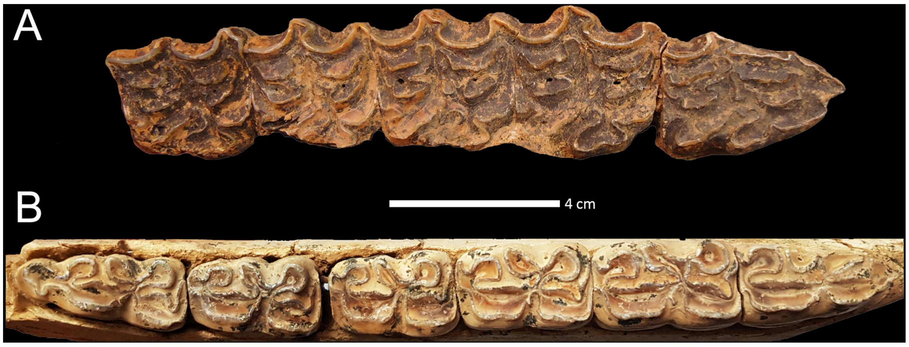


FIGURE 6 | *Equus mosbachensis tautavelensis* from lower level Q (CMI) of Arago cave. **(A)** Right maxillary with P4-M3 (G13-GEQ1-1290); **(B)** Right mandibular with P2-M3 (I8-IZPQ3-2160). Occlusal length of upper P3 **(A)** is about 36,8 mm.

correlates long protocones on the upper molars with forest-steppe or forest conditions. Type I is typical for such temperate assemblages as British MIS 9 and 7 material and horse remains from Achenheim, Biache-Saint-Vaast, Weimar-Ehringsdorf and Taubach (Nobis, 1971; Auguste, 1995; van Asperen, 2009a,b), but also characterizes the horse from Abri Suard (layers 5-6, MIS 6) (Prat, 1968; Eisenmann, 1991b). The majority of Upper Pleistocene horses is included in this group (Guadelli, 1987; Eisenmann, 1991b; Fourvel et al., 2014).

Horses of Type II show the opposite pattern, with relatively long protocones on the P3/4 and shorter protocones on the M1/2, and are often correlated with cold climatic conditions. The cold MIS 6 assemblage from Wannen belongs to Type II, but the type seems to be rare. LGM horses from MIS 2 (Magdalenian) are also included in this group (Eisenmann, 1991b).

Finally, horses of Type III, associated with cool to cold environments, have short protocones on both P3/4 and M1/2. The group of Type III horses includes assemblages from temperate sites such as Steinheim, Orgnac 3, Biache-Saint-Vaast, and British MIS 11 sites, as well as sites dating from colder periods, such as the MIS 6 sites of Schweinskopf and Romain-la-Roche (van Asperen, 2009a; Boulbes, 2010).

Some samples do not fit any Type, with long protocones on both the premolars and the molars (e.g., British MIS 6 and Schöningen 13II-4 samples; van Asperen, 2009a). Uzunidis et al. (2017) carried out a direct test of the relationship between protocone length and the abrasiveness of the diet (as reflected in tooth microwear, Solounias and Semprebon, 2002), and found no correlation. Admittedly, their study did not differentiate between premolars and molars, but together these results indicate the length of protocone should be used with caution to infer environmental conditions.

Body Size, Limb Element Proportions, and Robustness of the Limbs

Body size is a complex and highly plastic trait, which is influenced by a large number of factors. Thermoregulatory pressures lead to larger body size in colder (Bergmann's rule) or drier climates, whereas closely related animals in warmer or more humid climates tend to be smaller (Mayr, 1956; James, 1970; Lindstedt and Boyce, 1985; Blackburn et al., 1999). In colder climates, limbs tend to be shorter than in warmer climates (Allen's rule). Together, these body shape changes produce a reduced ratio of surface area to body mass and thus reduced heat loss in colder and drier climates. Furthermore, if a similar bodyweight is supported by shorter legs and muscles, the leg bones will be more robust, which provides further thermoregulatory advantage (Gregory, 1912; Thomason, 1986; Tilkens et al., 2007).

Animals of larger body size have enhanced starvation resistance (Lindstedt and Boyce, 1985; Blackburn et al., 1999). Such animals are more likely to survive seasons of scarcity and profit from increased resource availability after periods of high mortality, although short growing seasons may limit growth potential. In contrast, small body size may facilitate predator avoidance in densely vegetated environments (Bro-Jørgensen, 2008).

Middle Pleistocene

These factors combine to produce a complex pattern of body size and shape variation during the glacial-interglacial cycles of the Middle Pleistocene (**Figure 7**). Glacial horses are generally smaller and more robust than interglacial horses (Collinge, 2001; Cramer, 2002; Guthrie, 2003; van Asperen, 2010). This is particularly pronounced in British samples from low-productivity periglacial desert environments dating to MIS 6 (Green et al., 1984; Parfitt et al., 1998; Murton et al., 2001). On the other hand, horses from continental sites from MIS 6 (*E. achenheimensis*, Romain-la-Roche; *E. f. piveteaui*, Abri Suard 5-6) have a larger body size. The MIS 6 glaciation was one of the most extreme of the Middle Pleistocene (Shackleton, 1987; Reille et al., 2000; Ehlers et al., 2004; Laban and Van der Meer, 2004). In contrast, during the less extreme glacials of MIS 8 and 10, a relatively diverse steppe vegetation (De Beaulieu and Reille, 1995) allowed the horses to grow to larger body size (van Asperen, 2010) (**Figure 7**).

Within the interglacial assemblages, essentially two morphologies can be distinguished. The mosaic steppe vegetation of phases with a long growing season and a more continental climate presented the horses with an environment that they are extremely well-adapted to. As a consequence, they were able to

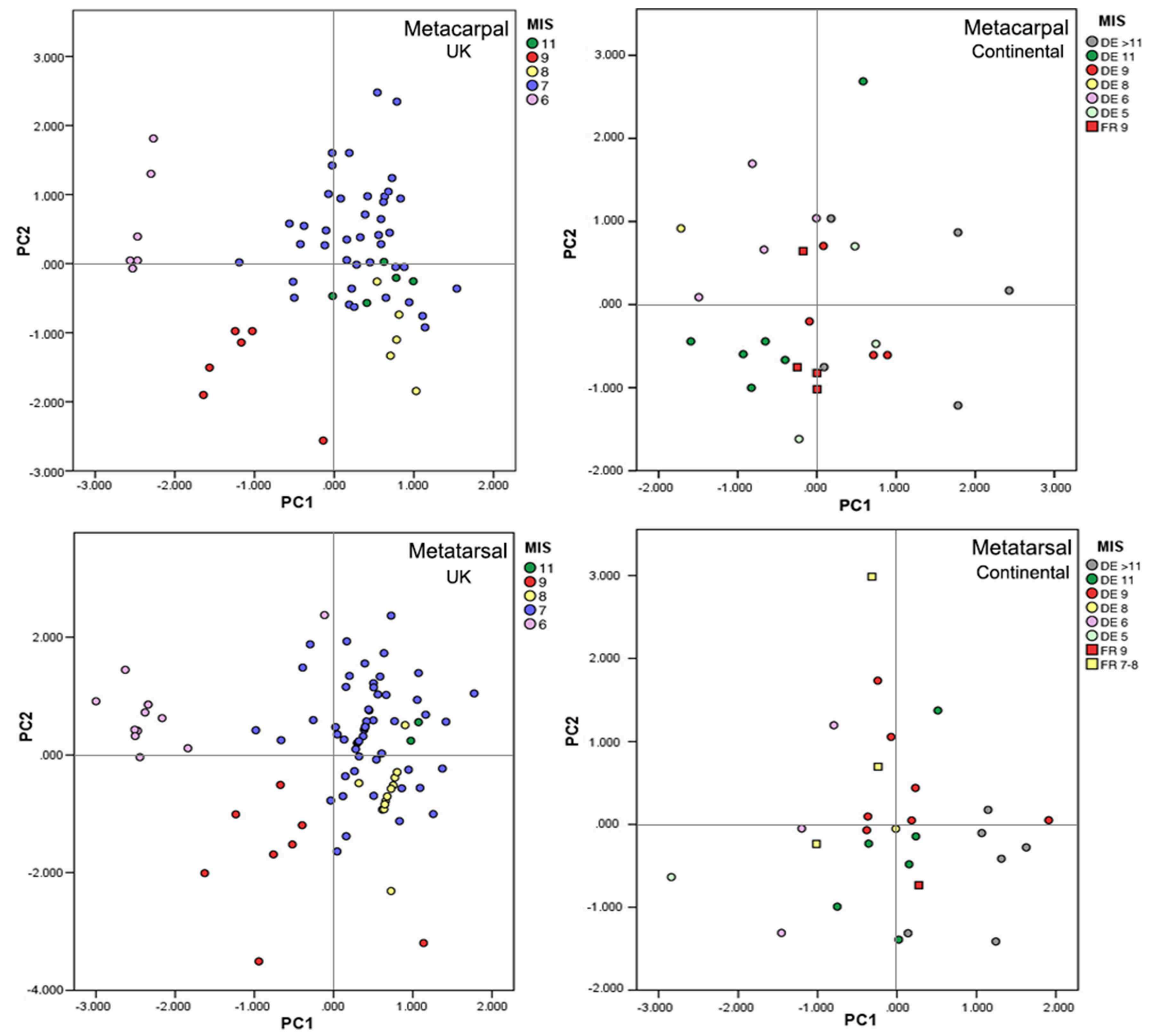


FIGURE 7 | Principal component analysis of complete caballoid equid metacarpals and metatarsals from late Middle Pleistocene British sites and continental Europe; PC2 plotted against PC1 (modified from van Asperen, 2010, Copyright © 2010 Elsevier BV, with permission from Elsevier); PC1 generally relates to overall size, while PC2 tends to reflect robusticity. Supplementary data available in van Asperen (2010).

grow to a large size, with relatively robust limbs, though less robust than their glacial counterparts (van Asperen, 2010). Such large-sized, robust horse remains are found in British sites dating from the later, relatively continental phases of MIS 7 (Schreve, 2001) and on continental MIS 9 and MIS 7 sites. The higher seasonality experienced by populations from continental regions led to somewhat larger body size than in the more oceanic climates of Britain (van Asperen, 2010) (**Figure 7**).

In contrast, the second group of interglacial horses has relatively small body size and slender limb bones. Assemblages with such characteristics are found in contexts with indications of densely vegetated habitats and oceanic conditions, representing a far less favorable environment for grazing-adapted species. These morphologies are found in British MIS 9 sites and some continental sites of uncertain date, such as "*E. steinheimensis*" from Steinheim (MIS 11? van Asperen, 2010, 2013a), and the horses from Orgnac (MIS 9–8, Forsten and Moigne, 1998; Moncel et al., 2005) and Lunel-Viel (MIS 11–10, Brugal and Boudadi-Maligne, 2011). The two laters are also characterized by robust diaphysis in relation to substrat and humidity gradient (see below). Small sized horses also present in Acheulean sites in the Iberian Peninsula (*E. torralbae*, Torralba, Prat, 1977; the horse from the site of cueva del Ángel, MIS 9–7, Falguères et al., 2019) could correspond to the same pattern and/or a latitudinal gradient.

British horse remains dating from MIS 11 and continental horse remains dating from MIS 5 have an intermediate morphology, being larger than the horses in the second group but somewhat more slender than the horses of the first group (van Asperen, 2010). It may be significant that horse remains are scarce in faunal assemblages dating from these phases, indicating that population sizes were small, so that these animals were able to grow to a relatively large size regardless of the probably densely forested habitats they inhabited.

Late Pleistocene

From the end of the Middle Pleistocene and during the Late Pleistocene, the caballoid horses underwent a general decrease in

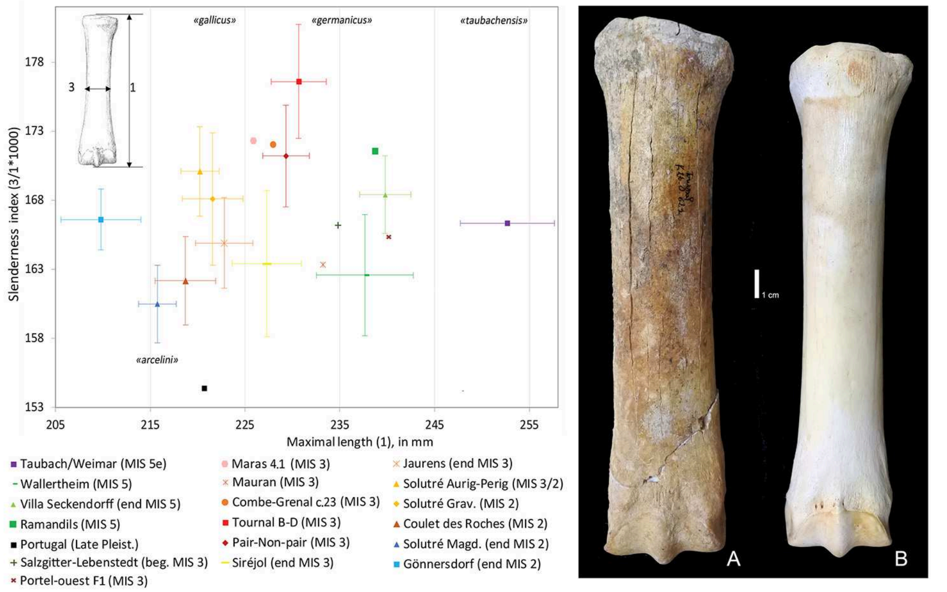


FIGURE 8 | Bivariate diagram of slenderness index (SI 1) in relation to the maximal length of the metacarpal. Slenderness index (SI 1): breadth at the middle of the diaphysis (3)/maximal length (1)*1,000. Confidence interval scale bars (95%) for series with more than 5 specimens. Data: Taubach/Weimar (Eisenmann, pers. comm.); Wallertheim (Nobis, 1971); Villa Seckendorff, Salzgitter-Lebenstedt, Solutré Gravettian, Gönnersdorf (Cramer, 2002); Combe-Grenal, Solutré Aurignacian-Perigordian (Guadelli, 1991); Mauran (Eisenmann and David, 1994); Pair-non-Pair (Prat, 1968); Siréjol, Jaurens (Eisenmann, 2019); Ramandils, Portel-Ouest, Abri du Maras, Tournal B/D, Coulet des Roches (Boulbes, pers. data); Portugal (Cardoso and Eisenmann, 1989). Metacarpals of Late Pleistocene horses. **(A)** *Equus ferus germanicus* from Tournal (K26-0-621, level B, MIS 3); **(B)** *Equus ferus gallicus* from Coulet des Roches (M4-814, MIS 2).

size, which also resulted in the creation of several chronological subspecies (*E. f. taubachensis*, *E. f. germanicus*, *E. f. gallicus*, *E. f. arcelini*, Prat, 1968; Eisenmann, 1991b; Guadelli, 1991). This trend is for example well-illustrated in the length of the metacarpal (**Figure 8**) and based on a method using the Variability Size Index V.S.I. (Cramer, 2002; Magniez et al., 2017). The decrease in body size during the Late Pleistocene constitutes a gradual process of adaptation to climatic change, but without speciation (Forsten, 1996). This could be attributed to adaptive pedomorphism or dwarfism (Gould, 1976; Guthrie, 1984; Forsten, 1988, 1996) to maintain population densities in an increasingly fragmented or constraining environment by increasing the rate of population growth (e.g., through the shortening of the gestation period) for the survival of the species Forsten, 1993). This could be an adaptive response to rapid changes in climate during this period (Magniez and Boulbes, 2014). Size reduction among late Pleistocene horses also provides a useful biochronological marker (Magniez and Boulbes, 2014). Even if there are exceptions: the horse of Portel-Ouest cave (levels F) is larger than those of the contemporary sites of MIS 3, perhaps resulting from a regional particularism.

In addition to this decrease in body size, it is also possible to detect variations in certain skeletal proportions. As during the Middle Pleistocene, the robustness of the diaphysis of the metapodials shows the most important pattern (**Figure 8**). Following the distribution of the currently recognized species, the robustness of the diaphysis of the metapodials correlates well with moisture levels (Eisenmann, 1984). For example, the metacarpal from the Mousterian layers of Tournal B-D and Abri du Maras (level 4.1) (*E. f. germanicus*, South of France, MIS 3) have a relatively robust diaphysis, which reflects the high humidity recorded in these levels (Echchat, 2008; Magniez and Boulbes, 2014; Daujeard et al., 2019) (**Figure 8A**). On the other hand, the metacarpal of the horse from Coulet des Roches (South France, MIS 2) is slender in relation to the hard substrate frequented as demonstrated by other proxies (Crégut-Bonnoure et al., 2018) (**Figure 8B**). The Late Pleistocene horse from Portugal, *E. ferus antunesi*, even more gracile, was probably adapted to rather dry climate and to a hard ground (Cardoso and Eisenmann, 1989) (**Figure 8**). These rapid and reversible variations in the proportions of the diaphysis seem, in this case, to be related to phenotypic plasticity.

Another pattern concerns the variation in the general proportions of the limb and in particular the relationship between the lengths of metacarpal and metarsal (**Figure 9**). In the lineage of the Upper Pleistocene horses, the length of the metacarpal decreased faster than that of the metatarsal. These differences could reflect an evolution pattern and/or an adaptation to the openess of the environment and the density of the vegetation. Indeed, Eemian (MIS 5e) horses have caricatural proportions with a very long metacarpal compared to the metatarsal; horses from MIS 3 to a lesser degree have a long metacarpal and are often associated with mozaic landscapes; forms from MIS 2, correlated with open landscapes, have a longer metatarsal (**Figure 10**). Such differences have also been noticed in extant species, the metatarsals are especially short in two species of zebras, *Equus burchelli* and *Equus zebra* (Eisenmann, 1979; Groves and Willoughby, 1981), which occasionally frequent wooded environments (Eisenmann, 1984).

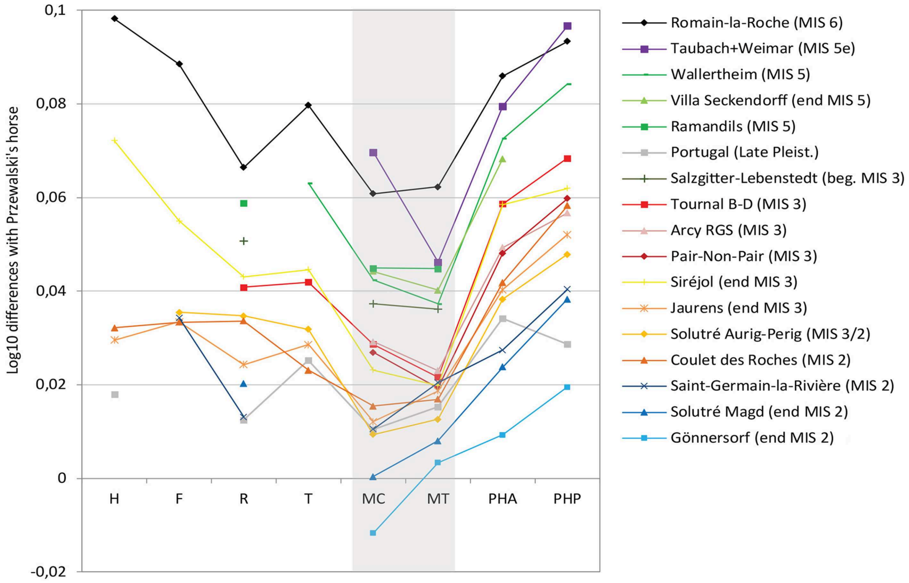
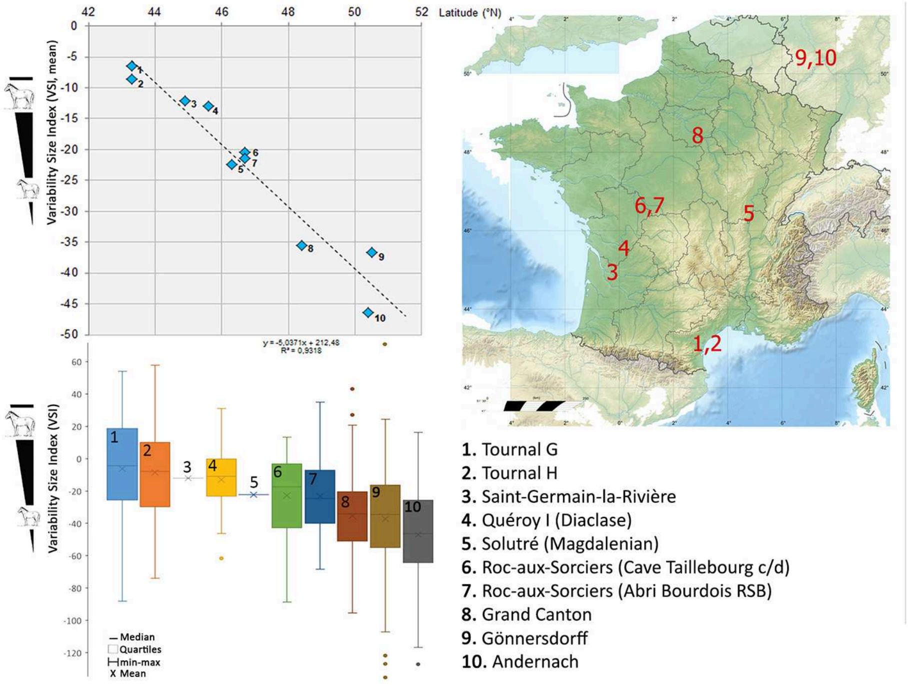


FIGURE 9 | Simpson's ratio diagram of bone lengths of European Late Pleistocene true horses. Reference: Przewalski's horse (Eisenmann, 1991a). H, Humerus; F, Femur; R, Radius; T, Tibia; MC, Metacarpal; MT, Metatarsal; PH1A, First Anterior Phalanx; PH1P, First Posterior Phalanx. Data: Romain-la-Roche (Boulbes, 2010); Taubach-Weimar (Eisenmann, pers. com.); Wallertheim, Villa Seckendorff, Gönnersdorf (Cramer, 2002); Ramandils, Tournal B-D (Boulbes, pers. data); Siréjol (Eisenmann, 2019); Jaurens (Eisenmann, 1991a); Solutré (Guadelli, 1991); Coulet-des-Roches (Crégut-Bonnoure et al., 2018); Saint-Germain-la-Rivière (Prat, 1968).



1. Tournal G
2. Tournal H
3. Saint-Germain-la-Rivière
4. Quéroy I (Diaclase)
5. Solutré (Magdalenian)
6. Roc-aux-Sorciers (Cave Taillebourg c/d)
7. Roc-aux-Sorciers (Abri Bourdois RSB)
8. Grand Canton
9. Gönnersdorff
10. Andernach

FIGURE 10 | Variability Size Index (VSI, cf. Meadow, 1999) of horse populations from the end of MIS 2 (Magdalenian). Standard: Jaurens (Mourer-Chauviré, 1980; Eisenmann, 2019). Gönnersdorf, Andernach (Cramer, 2002); Tournal (Boulbes, pers. data); Roc-aux-Sorciers (Boulbes and Valensi, unpublished data) Saint-Germain-la-Rivière (Prat, 1968); Quéroy I, Grand Canton (Véra Eisenmann, pers. com.); Solutré Magdalenian (Guadelli, 1991).

Magdalenian cline

The end of the Pleistocene offers a fine chronological resolution to detect size variation with numerous well-dated sites. The size index (V.S.I., see Meadow, 1999) in relation to latitude (**Figure 10**, **Table S1**) shows a progressive and statistically significant decrease in the body size of Magdalenian horses from southern France to northern Europe. The pattern of this geographical cline is clearly visible: series coming from the same latitude have an equivalent size. Mediterranean horses are a little larger than those from southwestern France, which are themselves more robust than those from central France; horses from the Paris Basin and the Rhineland in Germany are smaller.

These regional differences can be compared with the ^{15}N nitrogen gradient and could be explained by an earlier onset of climatic improvement in the south compared to the northern and/or continental regions after the Last Glacial Maximum (Drucker et al., 2003, 2012; Stevens and Hedges, 2004; Stevens et al., 2009). Access to more resources in more southerly regions would have favored maintaining an equal size in the south of France. These results reflect the regional mosaic of the Late Glacial horse populations (Kaagan, 2000; Cramer, 2002; Bignon et al., 2005; Bignon and Eisenmann, 2006; Magniez et al., 2017).

Breadth of the Third Phalanx

The third phalanx is the skeletal element that interacts most closely with the substrate in locomotion. In comparison with other equids, caballoid horses have relatively broad third phalanges. Broad third phalanges are thought to be an adaptation to soft substrates, providing a larger contact area and broader distribution of weight (Eisenmann, 1984; Forsten, 1988; Kuzmina, 1997; Foronova, 2006). Although this characteristic has been analyzed for Middle Pleistocene equids (van Asperen, 2010), this interspecific pattern does not seem to be reflected in variation at an intraspecific level.

Study of Late Glacial (LG) horses (Bignon and Eisenmann, 2006) demonstrates the homogeneity in proportions of the third phalanges at a local scale between different areas, according to the authors p. 169 “related to the global climatic context and the local ecology, namely the food exploitation by horses of river banks and marshes vegetation.” New data coming from LGM and LG levels of the site of Coulet des Roches identify slightly narrower proportions than contemporaneous populations, showing that horses at this site frequented less heavy or harder ground habitats (Crégut-Bonnoure et al., 2018) as in the case of the horse from Portugal, *E. f. antunesi* (Cardoso and Eisenmann, 1989). In contrast, the Late Pleistocene horse *E. f. latipes* (Gromova, 1949) from the Paleolithic sites of Kostenki, Russian Valley, Don River (Kuzmina, 1997) and Mezin, Desna basin, Ukraine (Belan, 1985) show extremely wide third phalanges.

Diet and Habitat

Regardless of climatic conditions, Middle Pleistocene horse mesowear has the characteristics of a grazer (e.g., Rivals et al., 2008; Rivals and Lister, 2016; Uzunidis et al., 2017). In grazers, the abrasive nature of the foodstuffs consumed, as well as the relatively high amount of grit found on plants growing at ground level, produce an abrasion-dominated wear pattern with round or blunt cusps with low relief (Williams and Kay, 2001). Middle Pleistocene horses often have some of the highest mesowear scores, and therefore the most abrasive diets, among the species represented in the faunal assemblages (e.g., Rivals et al., 2008). However, occasionally horse populations show variation in mesowear, ranging from grazer to mixed feeder with a significant amount of browse in the diet (e.g., Rivals et al., 2009, 2015). Interglacial horse assemblages are often characterized by a higher amount of variation in diet than glacial assemblages (Rivals et al., 2009).

In contrast to their generally grazer-like mesowear signature, Middle Pleistocene horse microwear is more variable, ranging over the entire spectrum from grazer to browser (e.g., Rivals et al., 2009, 2015; Rivals and Lister, 2016). The same assemblage can have a grazer-like mesowear pattern but a browser-like microwear pattern, possibly due to seasonal variation in diet (Uzunidis et al., 2017). One problem with a browsing microwear signature is that it is not possible to distinguish between browsers eating low herbaceous browse (forbs) or trees and shrubs (Rivals and Lister, 2016). Przewalski horses, for example, consume large amounts of dicotyledons (Schulz and Kaiser, 2013).

Animals that feed on different kinds of foodstuffs tend to have different ratios of carbon and nitrogen isotopic values in their tooth and bone collagen. Carbon isotope values relate to the different photosynthetic pathways used by plants, known as the C3, C4, and CAM pathways. The European Middle Pleistocene is strongly dominated by C3 plants. However, within C3 plants, there is further fractionation between woody and herbaceous plants depending on the openness of the landscape, known as the canopy effect (Heaton, 1999; Drucker et al., 2008). As a result, differences in feeding behavior can lead to different δ^{13}C values in herbivores (Feranec, 2007b). Nitrogen isotopic values vary primarily with the trophic level at which the species feeds (Bocherens and Drucker, 2003).

Mean δ^{13}C values for Middle Pleistocene horses tend to reflect grazing in open forest or grassland (e.g., García García et al., 2009; Feranec et al., 2010; Pushkina et al., 2014). However, δ^{13}C values reflecting foraging in more closed habitats also occur, mainly in temperate assemblages such as those from Steinheim (MIS 11?) and Neumark-Nord (MIS 5e; e.g., Britton et al., 2012; Pushkina et al., 2014). Pleistocene equids tend to have slightly lower δ^{13}C values than bovids, which may be due to differences in digestive physiology (Britton et al., 2012). There is also variation in horse δ^{15}N values, to the degree that at some sites, horses appear at a higher trophic level than bovids, their closest competitors for food resources (ibid.). This could be due to the horses consistently selecting lower-quality forage and the way in which their non-ruminant digestive system processes this forage. However, it is more likely that equids and bovids flexibly adapted their feeding strategies to resource availability and the density of herbivores feeding on the same plants (Menard et al., 2002; Britton et al., 2012).

EUROPEAN WILD ASS *Equus hydruntinus*

Equus hydruntinus, also known as the European wild ass, was first described by Regalia (1907) at the start of the twentieth century from the Upper Paleolithic cave site of Romanelli (Italy), to be precise, in the Upper Complex (≪ Terre brune ≫) attributed to the Epigravettian (Sardella et al., 2018). An exhaustive study of its anatomy and its geographical distribution was made by

Stehlin and Graziosi (1935). Many authors have designated *Equus altidens* (or *Equus granatensis* Eisenmann, 1999) as the probable ancestor of *Equus hydruntinus* (Musil, 1969; Forsten, 1986, 1990, 1999a; Azzaroli, 1992; Eisenmann, 1992; Alberdi et al., 1998; Alberdi and Palombo, 2013). This scenario is based in particular on assemblages of intermediate size and chronology (Petralona, Cullar de Baza-1, Venosa) (Van der Made et al., 2017). Affinities with *E. tabeti* (Aïn Hanech) and *E.* cf. *tabeti* (Oubeidiyeh) (Guerrero-Alba and Palmqvist, 1997; Eisenmann, 1999) have also been identified. In contrast, current thinking favors a new arrival from Asia over a local evolution in Europe (Eisenmann, 1992; Palombo and Alberdi, 2017). According to this model, *Equus hydruntinus* would have entered to occupy the ecological niche left vacant by *Equus altidens* (Palombo and Alberdi, 2017). At the maximum extent of its geographical expansion in the Late Pleistocene, the distribution of *Equus hydruntinus* extended from Europe to the south-west of Asia (Middle East, Caucasus) and probably into North Africa (Uerpmann, 1987; Wilms, 1989; Orlando et al., 2006). During the Holocene, the contraction of the steppe, the significant fragmentation of its geographical distribution and distinct subpopulations, and human exploitation progressively caused its disappearance between the Neolithic and the Iron Age (Spassov and Iliev, 2002; Crees and Turvey, 2014), more precisely, according to palaeogenetic information, during the Bronze Age (Bennett et al., 2017). As this hypothesis is subject to certain limitations (cf. Nores et al., 2015), it cannot be excluded that the enigmatic ≪ zebro ≫ mentioned in numerous Medieval manuscripts from the Iberian Peninsula corresponds to *Equus hydruntinus* (Antunes, 2006).

Systematics and Phylogeny

It was not until the start of the twenty-first century that the enigma of the phylogeny of *Equus hydruntinus* was significantly resolved through the contribution of studies of ancient DNA. Hitherto, the systematic position of this equid had long been disputed. The species was variously included in the subgenus ≪ *Asinus* ≫ (Stehlin and Graziosi, 1935; Gromova, 1949), or ≪ *Hemionus* ≫ (Azzaroli, 1992), placed close to the zebras (Davis, 1980; Bonifay, 1991), seen as the last representative of the Plio-Pleistocene group of the ≪ stenonids ≫ (Forsten, 1986, 1990, 1999a; Forsten and Ziegler, 1995; Alberdi and Palombo, 2013), or even considered as belonging to a separate ≪ *Hydruntinus* ≫ genus (Radulesco and Samson, 1965). These multiple hypotheses regarding its affiliation are related to the mosaic of characteristics found in the skeleton and dentition of this species: gracility and cursorial proportions of the limbs as in the hemiones, very short protocones as in the ≪ stenonids≫, a deep ectoflexid as in the zebras (Eisenmann and Mashkour, 1999). It was not until the start of the twenty-first century, with the significant study of the morphology of two crania from the site of Kabazi II (Crimea), that the proximity of *Equus hydruntinus* to the hemiones became clearer (Burke et al., 2003). The rise of palaeogenetics allowed this affiliation to be confirmed by many mitochondrial sequences (Orlando et al., 2006, 2009). The last palaeogenetic studies to date do not definitively support the classification of *E. hydruntinus* as a distinct species and places it among the Asiatic wild asses (Bennett et al., 2017).

From a morphological and metrical point of view, many characteristics indeed distinguish between *Equus hydruntinus* and *Equus hemionus*. The principal differences can be found in the cranium and teeth. The crania from the site of Kabazi II, and above all the complete cranium from the Emine-Bair-Khosar cave, reveal the main differences with *E. hemionus*: the length of the palate is greater, the muzzle is proportionally very short and relatively wide, the naso-incisival incision is clearly much shorter (Burke et al., 2003; Orlando et al., 2006; Eisenmann et al., 2008; van Asperen et al., 2012) (**Figure 11**). The species is often referred to as microdont, meaning that the teeth are relatively small in proportion to the postcranial skeleton, but it is also characterized by a high degree of hypsodonty (Stehlin and Graziosi, 1935; Eisenmann and Baryshnikov, 1995; Eisenmann et al., 2008). The mesio-distal length of the M^3 is always shorter than that of the M^2 (Bonifay, 1991; Boulbes, 2009). The variation in the protoconal index within the tooth row is also different from that of hemiones, with notably an IP which increases from the P^4 to the M^1 (Eisenmann and Patou, 1980; Cardoso, 1995; Boulbes, 2009). The relative proportions of the limb bones are close to those of hemiones, however, the MC III is proportionally shorter than the MT III (Eisenmann et al., 2008). The frequency of the presence of the small facet for the trapezoid varies between different species of hemiones, but it is more often present than in *Equus hydruntinus*. The metacarpals and metatarsals of *E. hydruntinus* have somewhat more robust diaphyses (which are also thicker) (Eisenmann et al., 2008; van Asperen et al., 2012). On the other hand, relatively to the length of the bone (variable 1), the epiphyses (5 to 14) are less developed (**Figure 12**). Finally, the distal keel (12) shows proportionally less protrusion. Other morphological criteria for the different skeletal elements show the ≪ primitive ≫ character state (Bonifay, 1966, 1991; Prat, 1968; Boulbes and Rillardon, 2010).

Biochronology

The appearance of *Equus hydruntinus* in the European fossil record is not synchronous across all geographical provinces, which can be partly explained by its rareness.

It seems that the oldest remains of this species in Europe can be found in Spain, in the Middle Pleistocene levels of the section of Vallparadís (*E.* cf. *hydruntinus*, level 11, EVT3), which is dated to a little later than 0.6 Ma on the basis of the small mammal fauna (Aurell-Garrido et al., 2010; Madurell-Malapeira et al., 2010; Martínez et al., 2014). In the complex of the Sierra de Atapuerca, *Equus* cf. *hydruntinus* was identified at Gran Dolina from level TD 10, correlated with MIS 11-9 (Saladié et al., 2018), in particular from the top of this level (TD 10.2 et TD 10.1), and at Galeria in levels GIIb and GIIIa (Rodríguez et al., 2011; Van der Made, 2013).

In Italy, the first appearance of *Equus hydruntinus* forms one of the chronological markers of the Middle Aurelian faunal assemblages (Vitinia FU, MIS 8.5 and 7) (Marra et al., 2014, 2018). In France, de caves of Lunel-Viel have long been considered to harbor the oldest remains of the species (Bonifay, 1991). Other fossils from this country could be even older, in particular those

FIGURE 11 | Skull of *Equus hydruntinus* from the site Emine-Bair-Khosar, Crimea; catalog no. Ba2 384 (photo E. van Asperen; scale in cm; reprinted from van Asperen et al., 2012 © Palaeontological Association February 2012). **(A)** Lateral view; **(B)** Occlusal view.

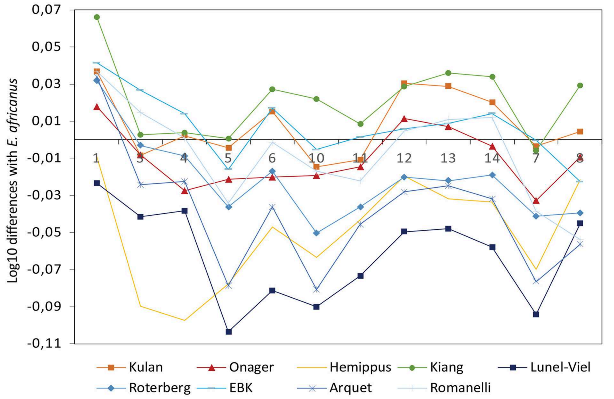


FIGURE 12 | Simpson's ratio diagram of metacarpals from subspecies of extant Hemiones and *Equus hydruntinus*. Reference: *Equus africanus* (Eisenmann, 2019). Measurement system (Eisenmann, 2019): 1-Maximum length, 3-Breadth at the middle of the diaphysis, 4-Depth of the diaphysis at the same level, 5-Proximal articular breadth, 6-Proximal articular depth, 7-Diameter of the facet for capitatum, 8-Diameter of the facet for hamatum, 10-Distal supra-articular breadth, 11-Distal articular breadth, 12-Depth of the sagittal crest, 13-Minimum depth of the medial condyle, 14-Maximum depth of the medial condyle. Data: Hemiones, *E. hydruntinus* from Roterberg and Romanelli (Eisenmann, 2019); *E. hydruntinus* minor from Lunel-Viel, *E. hydruntinus davidi* from Arquet (Boulbes, pers. data); *Equus hydruntinus* from Emine-Bair-Khosar (van Asperen et al., 2012).

from the *loess anciens inférieurs* at Achenheim (Forsten, 1996, ex *E. wernerti* ≫) and an isolated tooth from the site of Orgnac 3 (Aouraghe, 1992). *Equus hydruntinus* is absent from certain very rich fossiliferous sequences, such as those from the Middle Complex of La Caune de l'Arago (MIS 14 to 12) (Moigne et al., 2006). The species is mentioned with caution for the Somme basin in the upper unit (Marne Blanche) of the quarry Carpentier d'Abbeville, recently dated and correlated with MIS 15 (Antoine et al., 2016).

In Germany, *Equus hydruntinus* is present at Schöningen 13II-4, correlated with the Reinsdorf Interglacial (MIS 9) (Van Kolfschoten et al., 2015) and Steinheim (Forsten, 1999b), the chronological position of which is subject to debate (MIS 11?). In the British Isles, the first appearance of the species is reported during the course of MIS 11 (Pettitt and White, 2012), especially from a number of isolated teeth from the site of Swanscombe (Hoxnian=Holsteinian) (Schreve, 1997; Bridgland and Schreve, 2004).

In the light of these finds and the review of the literature, it seems that the chronological range of *E. hydruntinus* extends in Europe from the start of the late Middle Pleistocene until the Holocene (**Figure 1**). Its presence in levels dated toward 0.6 Ma in the North of Spain (and perhaps in the North of France), and in contemporary sites in Transcaucasia (Baryshnikov, 2002) and Acheulean sites from central Syria and the site of C-Spring Azrak in Jordan (Clutton-Brock, 1989; Reynaud Savioz and Morel, 2005) could suggest a first incursion of the species during the MIS 15 interglacial followed later by a second wave of migration from MIS 11-9.

Sub-species or Ecomorphotypes of *Equus hydruntinus*

Several forms of *Equus hydruntinus* have been described in the palaeontological literature in addition to the type first described by Stehlin and Graziosi (1935) from Romanelli. The name of the subspecies *Equus hydruntinus minor* indicates the small body size of the population from Lunel-Viel (Bonifay, 1991). It is possible that this form recurred over the course of the chronological range of *E. hydruntinus* (Boulbes and Rillardon, 2010). The description of this form was based on abundant material, including a cranium, but its affiliation with *Equus hydruntinus* has been questioned by certain authors (Azzaroli, 1990; Van der Made et al., 2017). *Equus hydruntinus danubiensis*, in contrast, represents a large-bodied form described by Samson (1975) from Romania. Eisenmann et al. (2008) also include the fossils of a gracile equid from Petralona (*E. petraloniensis*, Tsoukala, 1991; Tsoukala and Guérin, 2016), dated to 0.4 Ma, within the variation of the species: "*E. hydruntinus petraloniensis.*" According to certain authors, the slender equid from Venosa, considered to be one of the last representatives of *Equus altidens* (Alberdi and Palombo, 2013), could already represent *Equus hydruntinus* (Forsten, 1999a).

Another form, *Equus hydruntinus davidi*, defined by Alimen (1946) based on a single tooth from the Mousterian site of Saint-Agneau (Charente), has a longer protocone. This taxon was subsequently used by Prat (1968) to characterize the elongation of this dental character observed in many sites in the south-west of France post-dating the ≪ first Würmian stage ≫. Following Prat's work, *Equus hydruntinus davidi* has also been identified from other sites in the south of France (Eisenmann and Patou, 1980; Crégut-Bonnoure and Granier, 1982; Guadelli, 1995; Boulbes, 2009). Differences between teeth from Ramandils cave (MIS 5, Rusch et al., 2019) and Crouzade cave (MIS 3, Saos

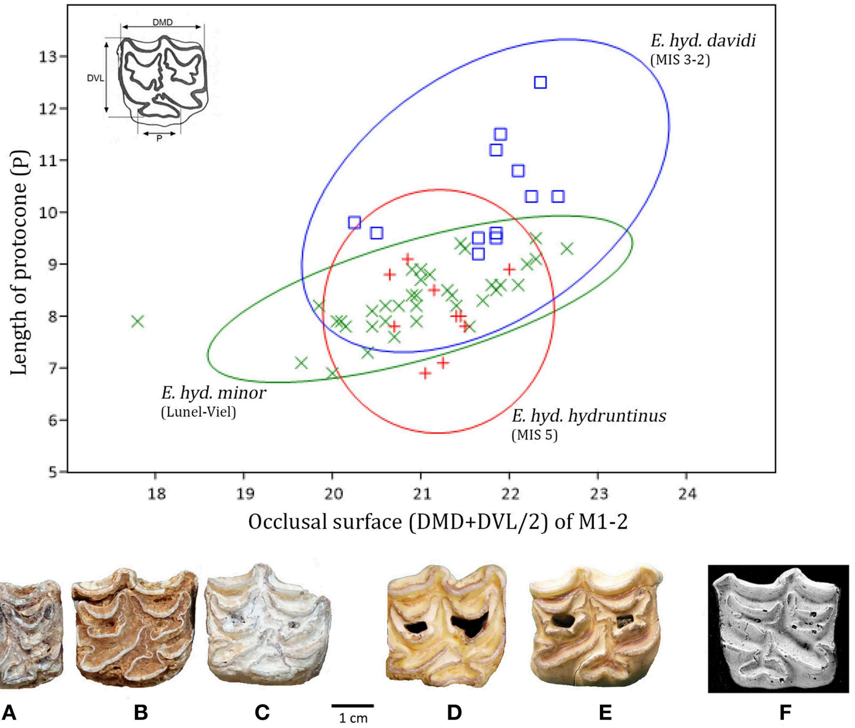


FIGURE 13 | Bivariate plot of protocone length vs. occlusal surface of M1-2. Occlusal surface: average occlusal dimension [(DMD + DVL)/2]. Confidence ellipsoid (95 %). Data: *E. hydruntinus minor* (Lunel-Viel); *E. hydruntinus hydruntinus* (Ramandils, MIS 5); *E. hydruntinus davidi* (Crouzade, Arquet, MIS 3 and Valorgues, MIS 2) (Boulbes, pers. data). Upper teeth of *Equus hydruntinus*. **(A–C)** right P3, P4, M1 from Ramandils cave (*E. h. hydruntinus*); **(C, D)** right M1 and P4 from Crouzade cave (***E****. h. davidi*); **F**: right P4 of *Equus graziosii* (from Eisenmann, 2006a).

et al., 2019) is for example demonstrative (**Figure 13**). Another pattern (connected to the variation of protocone) is the reduction of the depth of vestibular groove on lower molars (Boulbes, 2009). These trends (fixed after MIS 3) could reflect a response to environmental pressures (genetic assimilation), the increase in the length of the protocone favored by the consumption of more abrasive food in cold and steppe climatic context (Boulbes, 2009). Guadelli and Delpech (2000) propose that the geographical barrier posed by the Alps could have fostered the independent evolution of western populations compared to those in the Italy-Balkans province, where populations with dental proportions similar to the type from the Romanelli caves persisted. However, isolated observations show that the morphotype with a long protocone could also have been present in Italy (Conti et al., 2010). The upper teeth of the enigmatic *Equus graziosii* (Azzaroli, 1979) (Maspino, Italy, Late Pleistocene) resemble those of the morph *E. hydruntinus davidi* (**Figure 13F**). This species is related to asses (Azzaroli, 1979; Eisenmann, 2006a); proximity with *E. hydruntinus* has been already pointed by Caloi (1995). This morphotype was also developed on the other side of the Pyrenees in the north-east of Spain, on the site of Teixoneres, dated to MIS 3 (Álvarez-Lao et al., 2017). *Equus hydruntinus davidi* was also identified from one late Würmian site in Portugal (Cardoso, 1995). We note here the fact that these late populations from the south of France and the north of Spain are more closely similar to hemiones in their morphological characteristics (convergences). The palaeogenetical study (Bennett et al., 2017) supports the hypothesis that hydruntine population could have gone through a bottleneck during the last two glacial periods and that Europe could have been recolonized from a refugial population, as proposed earlier on morphological grounds (Boulbes, 2009).

Ecology of *Equus hydruntinus*

Like the hemiones, *Equus hydruntinus* was adapted to semi-arid, steppic conditions and shows a preference for temperate climates, although it could tolerate limited cold (Prat, 1968; Delpech, 1984; Eisenmann, 1984; Azzaroli, 1990; Bonifay, 1991; Burke et al., 2003; Palombo and Alberdi, 2017). According to Abbazzi et al. (1996), *Equus hydruntinus* is primarily adapted to dry Mediterranean conditions and does not necessarily depend on the presence of open landscapes. However, a preference for open biotopes is corroborated by the Holocene distribution of the species, reduced especially to open landscapes in southern and eastern Europe (Crees and Turvey, 2014). Its relationship with temperature is more difficult to ascertain. The species shows a preference for more temperate climates (Caloi, 1995; Forsten and Dimitrijevic, 2004), but it is also present in cool or cold climatic contexts (Prat, 1968; Boulbes, 2009). van Asperen et al. (2012) remark that the crania of *E. hydruntinus* can be distinguished from related equids by their relatively short muzzles, which indicates an adaptation to cold climatic conditions.

At Steinheim, *E. hydruntinus* is characterized by δ^{13}C values that are clearly higher than those for *E. ferus* (Pushkina et al., 2014). Variation in the δ^{18}O and δ^{13}C values show that *E. hydruntinus* "occupied an ecological niche between the true horses, which inhabited shrubland, and the bovids of the grasslands, similar to that of the wooly rhinoceros, although with a slightly higher temperature and more closed vegetation" (p. 175, Pushkina et al., 2014). However, *E. hydruntinus* seems to have been less tolerant of climatic variations than the true horses, forcing it to adapt or, where appropriate, to migrate. The high chronological resolution of numerous well-dated sites indeed allows us to posit several phases of displacement of its geographical range over the course of the second half of the Late Pleistocene (Delpech, 2003). During the coldest phases of the Last Glacial Maximum (LGM) the species retreated to the peninsulas of southern Europe (Wilms, 1989; Crees and Turvey, 2014), a scenario that would also have characterized preceding glacial episodes (Boulbes, 2009). For example, its presence is confirmed at the start of MIS 4 in a relatively arid climate in Calabria (southern Italy), where a Mediterranean influence persisted (Marra and Bellomo, 2008). During cold episodes, *Equus hydruntinus* is accompanied by species that are very well-adapted to such a climate, such as for example *M. primigenius* and *C. antiquitatis* in the northeast of Spain (Álvarez-Lao et al., 2017), and *Saiga tatarica* and *Rangifer tarandus* in the south of France (Crégut-Bonnoure and Paccard, 1997).

REMARKS AND CONCLUSION

The main dispersal event concerning *Equus* in Europe (newcomers, *in situ* and anagenetic evolutionary processes)—first *Equus*, turnover during the post-Olduvai late Villafranchian, caballoid horse's emergence—are connected to major climatic change and document turnover of large mammal communities as well-demonstrated by Palombo and Alberdi (2017). The difficulty with regard to equid morphology is to discriminate between evolutionary and ecomorphological traits. The problem is even more complex because recent equids are known for their high level of plasticity and intra-specific variation, while differences between species are relatively low. Progressive characters such as elongation of the protocone, reduction of the ectoflexid, cursorial adaptations, and protrusion of the distal keel of the metapodials are variable at specific level and could have ecological significance. Despite this difficulty to draw up a phylogenetical and biochronological framework, it is possible to calibrate certain general patterns of evolution. Thus, emergence of elongated protocones in Europe for example can be dated between 1.2 and 0.7 Ma in supposed independant lineages (*E. suessenbornsis*, *E. apolloniensis*, *E. altidens*, *E. mosbachensis*) at the time of fundamental changes in the behavior of glacial cycles during the Quaternary glaciations and the expansion of open and dry environments.

The inventory of the different stenonid forms shows that at the time of the emergence of this group more than 2 million years ago, a wide range of morphologies occur—large, small, robust, slender—as well as combinations of these types. In contrast, the morphology of the teeth (more genetically dependent) seems to be less subject to variation. As a consequence, evolutionary models based on trend of size and/or gracilization are hard to demonstrate. Large and very large stenonids form a heterogeneous group and revision is needed to clarify their taxonomy and temporal distribution.

From the late Early Pleistocene to early Middle Pleistocene many fossils are assigned to *Equus altidens*. However, the morphology of the teeth of the Süssenborn equid seems too derived to be included in the variation of all the slender equids from this period. *E. granatensis* is well-defined and the primitive pattern of the teeth (very short protocones and especially very deep ectoflexids on molars and sometimes deep on premolars) casts doubt on an evolution from a stenonid stock. The presence of the more robust *E. wuesti* at around 1.0 Ma with proportions of limbs and teeth close to *E. granatensis* complicates the problem. Revision of this group is needed to solve the question of whether *E. granatensis* was an endemic species from the south of Spain, a primitive representative of *E. altidens* or an ecomorphotype (Palombo and Alberdi, 2017). The detailed study of the Epivillafranchian key sites of Vallparadis (Aurell-Garrido et al., 2010) and Bois de Riquet (Bourguignon et al., 2016) would certainly provide new information.

The large *E. suessenbornensis* has a wide geographical range from Beringia to Western Europe which is accompanied with little variation in terms of morphology and proportions. In contrast, slender species split in several geographical provinces. Interesting is the succession and regionalization of co-occurrences of equids in the course of Early and Middle Pleistocene: *E. suessenbornensis*-*E. granatensis*/*E. altidens* or *E. wuesti* in western and central Europe and *E. mygdoniensis*-*E. apolloniensis* around the eastern Mediterranean. The latter seems not to be linked to stenonid s. s. or *E. suessenbornensis* but could represent a step within the lineage of asses soon after their differentiation (Eisenmann and Boulbes, in preparation) in accordance with DNA and palaeogenetic projections (Jonsson et al., 2014; Bennett et al., 2017). These lineages finally were replaced by the more generalist caballoid horse group at the beginning of Middle Pleistocene.

Despite the overall homogeneous morphology of true horses during the Middle Pleistocene, paradoxically the ecomorphological adaptations described above coupled with some evolving traits provide real biochronological details in a given geographical province. Since the exact combination of the environmental factors that influence horse morphology subtly varies between the different glacials and interglacials, each oxygen isotope stage was characterized by a specific morphology, as outlined above. However, some caution needs to be taken in using horse morphology as a biostratigraphic indicator. First, the patterns sketched above were identified in northwest and central European horses or south of France, and cannot be transposed directly on other regions, such as southern or eastern Europe, where climatic conditions may have been significantly different. Second, due to the relatively homogeneous morphology of Middle Pleistocene horses, assemblages analyzed must be sufficiently large to produce statistically significant results. Although there is clear variation between ecotypes, there is also a significant amount of overlap, so any attempt to determine the affinities of small numbers of specimens must be regarded as preliminary. Finally, due to these overlaps and the small differences between ecotypes, it is advisable to apply a range of analytical methods to new assemblages to identify their morphology. Statistical methods such as principal component analysis and discriminant function analysis can disentangle more subtle variations (van Asperen, 2010, 2012). In this regard, recent developments using geometric morphometric approaches (on enamel patterns in particular) provide good phylogenetic and taxonomic markers (Barrón-Ortiz et al., 2017; Cucchi et al., 2017; Hanot, 2018) that may be complementary to traditional morphometry. Comparisons between the results of different methods can aid in solving the question of the phylogeography and regionalization of horses in Europe. Combining metric/morphological data with studies of tooth wear characteristics (mesowear, microwear) and isotopic analyses of teeth (Saarinen et al., 2016; Uzunidis et al., 2017) is the best way to ensure the robustness of palaeoecological inferences from ecomorphological patterns and their use as a proxy.

Several questions remain to be solved concerning *Equus hydruntinus*. In the first place, its origin, namely whether it corresponds to a local evolution in Europe or whether it entered Europe in one or more waves of migration from Asia. The detailed study of the oldest fossils (Vallparadis) and comparisons with intermediate forms to *E. altidens* (Venosa, Petralona) will provide essential information. Secondly, its status as a distinct species or subspecies of *Equus hemionus*. Paleontology has demonstrated the existence of many distinct morphological characters between *Equus hydruntinus* and *Equus hemionus* although most are plesiomorphic. The presence in *E. hydruntinus* of the mitotype of *Equus hemionus* (samples from 100 Ka) in association with distinctive morphological characteristics implies that *Equus hydruntinus* can be seen as an ecomorph or a subspecies of *Equus hemionus* (Bennett et al., 2017). However, according to the first appearance date of the species (0.6 Ma), it is also not impossible to consider that in the recent history of the taxon (0.1 Ma) gene transfer took place by introgressive hybridization. The sympatric cases noted between the two species in the Eemian, notably in the Binagady site (Azerbaidjan) (Eisenmann and Mashkour, 1999), followed by numerous observations during the Upper Pleistocene of characters convergent with the hemiones could support this hypothesis. The particular form of *Equus hydruntinus davidi* from southern France and the enigmatic *Equus graziosii* from Italy require further reflection. Palaeogenetic investigations, not only on the mitochondrial DNA but also the nuclear DNA, will in parallel have to multiply on fossils of various geographical origins. Given the difficulties with their identification, it is also not impossible to rule out the existence of several small, slender equidae in Western Europe including *Equus hydruntinus*, *Equus hemionus* and possibly other forms not recognized until now.

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript and/or the **Supplementary Files**.

AUTHOR CONTRIBUTIONS

NB and EA wrote sections of the manuscript. Both authors contributed to manuscript revision, read, and approved the submitted version.

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What Is *Equus*? Reconciling Taxonomy and Phylogenetic Analyses

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Interest in the origin and evolution of *Equus* dates back to over a century, but there is still no consensus on the definition of the genus or its phylogenetic position. We review the placement of *Equus* within several phylogenetic frameworks and present a phylogenetic analysis of derived Equini, including taxa referred to *Equus*, *Haringtonhippus*, *Dinohippus*, *Astrohippus*, *Hippidion*, and *Boreohippidion*. A new, morphology-based phylogenetic tree was used as an initial hypothesis for discussing what taxa *Equus* encompasses, using four criteria previously used to define the genus category in mammals: phylogenetic gaps, uniqueness of adaptive zone, crown group definition, and divergence time. According to the phylogenetic gaps criterion, *Equus* encompasses clade 6 (*Ha. francisci* = *E. francisci*, *E. conversidens*, *E. quagga*, *E. hemionus*, *E. mexicanus*, *E. ferus*, *E. occidentalis*, and *E. neogeus*) based on morphological synapomorphies. *Equus* is assigned to clade 6, or possibly clade 7, according to the uniqueness of adaptive zone criterion. The crown group criterion places *Equus* at clade 6. Based on the time-calibrated phylogeny of Equini, the divergence time criterion suggests that *Equus* encompasses clade 9. This clade comprises all taxa traditionally assigned to *Equus* analyzed in our study, including the eight taxa listed above as well as *E. stenonis*, *E. idahoensis*, and *E. simplicidens*; the latter two are sometimes referred to the subgenus *Plesippus* and the former to the subgenus *Allohippus*. With the exception of the divergence time criterion, the results of our evaluation are congruent in identifying clade 6 as the most suitable position for *Equus*. The taxonomic implications of delimiting *Equus* to clade 6 in our phylogenetic tree include elevation of *Allohippus* and *Plesippus* to generic rank, assignment of a new genus to "*Dinohippus*" *mexicanus*, and synonymy of *Haringtonhippus* with *Equus*.

Keywords: phylogeny, taxonomy, Equidae, *Equus*, *Dinohippus*, *Haringtonhippus*, *Allohippus*, *Plesippus*

INTRODUCTION

The origin and evolution of the genus *Equus* has been of particular interest to paleontologists for over a century (e.g., Marsh, 1879; Gidley, 1907; Matthew, 1924, 1926; Stirton, 1940, 1942; Lance, 1950; Dalquest, 1978, 1988; Bennett, 1980; MacFadden, 1984; Azzaroli, 1988, 1992; Hulbert, 1989; Prado and Alberdi, 1996; Kelly, 1998; MacFadden and Carranza-Castañeda, 2002). There are several evolutionary hypotheses for the genus and the definition of the generic name across those hypotheses has varied. Since the 1980s, discussions concerning the phylogenetic position of the genus have centered primarily on the position of some named species of *Dinohippus* with respect to *Equus* (e.g., Bennett, 1980; MacFadden, 1984; Azzaroli, 1988, 1992; Hulbert, 1989; Prado and Alberdi, 1996; Kelly, 1998). In that sense, our understanding of what constitutes the genus has been relatively stable, with discussions of taxonomy restricted to the base of the tree. In contrast, a recent molecular study suggested a taxonomic scheme that departs from previous taxonomies in that *E. francisci*, a species previously nested within *Equus*, is placed in a new genus, *Haringtonhippus* (Heintzman et al., 2017). That interpretation implicitly constrains the definition of the genus to the crown group and has potential implications for the taxonomy of horses traditionally assigned to *Equus*. In this study, we review the use of the generic name *Equus* within several phylogenetic frameworks and outline four criteria previously used to define a genus. We then examine the concept and contents of *Equus* based on a new phylogenetic analysis of derived Equini given those criteria. As is the case with any phylogenetic hypothesis, we acknowledge that the tree we present will be revised as new data and new specimens are studied. Nonetheless, our phylogenetic results offer a working hypothesis for discussing distinct paradigms for understanding higher level taxonomy, particularly in regards to the definition of the genus *Equus*.

Contextual Framework

Under a Linnaean taxonomic scheme, *Equus* is included within the subfamily Equinae and the tribe Equini (MacFadden, 1992). *Equus* is hypothesized to have originated in North America (e.g., Bennett, 1980; MacFadden, 1984; Azzaroli, 1988, 1992; Hulbert, 1989; Prado and Alberdi, 1996; Kelly, 1998; MacFadden and Carranza-Castañeda, 2002). Some early phylogenetic hypotheses proposed that *Equus* originated from derived species of *Pliohippus*, within the subgenus *Astrohippus* (Osborn, 1918; Stirton, 1940). Later studies separated derived species of *Pliohippus* into two distinct genera, *Astrohippus* and *Dinohippus* (Quinn, 1955), and proposed several hypotheses for the origin of *Equus*. Some studies suggested that *Equus* evolved from a species of *Dinohippus*, such as *D. mexicanus* or *D. leidyanus* (e.g., Lance, 1950; Webb, 1969; Bennett, 1980; MacFadden, 1984; Azzaroli, 1988, 1992). Others posited a polyphyletic origin from both *Astrohippus* and *Dinohippus* (Dalquest, 1978) or from a separate genus, such as *Eoequus* (Quinn, 1955), a taxon later considered a junior synonym of *Protohippus* (Hulbert, 1988).

Morphological phylogenetic analyses conducted since the 1980s support the close phylogenetic affinity of derived members of *Dinohippus*, such as *D. mexicanus*, to early representatives of *Equus*, including *E. simplicidens* (Bennett, 1980; Hulbert, 1989; Prado and Alberdi, 1996; Kelly, 1998). Some of these studies identified "*D.*" *mexicanus* as the sister group of *Equus* (Kelly, 1998). Other studies suggested including "*D.*" *mexicanus* within *Equus* (Prado and Alberdi, 1996) or even including "*Dinohippus*" s.l. within *Equus* (Hulbert, 1989). Regardless of placement, the debate over the delimitation of "*Equus*" has been largely along the stem of the equid tree. Branches of Plio-Pleistocene Equini taxa, other than *Hippidion*, have traditionally been considered species of *Equus*.

In contrast to previous studies, the recent naming of a new genus (*Haringtonhippus*; Heintzman et al., 2017) on the basis of molecular data and estimated divergence times for extant and some fossil equids has potentially significant taxonomic implications for branches of the equid tree. Specifically, the study constrained the definition of *Equus* to the crown group (Heintzman et al., 2017), implicitly excluding many stem-group species from *Equus* without explicitly assigning them to any other genus. In that context, we saw an opportunity to explore a deeper philosophical question about the criteria for defining genera, and how those criteria bear on the placement of *Equus* and the validity of taxa traditionally referred to *Equus*.

DEFINITION AND DELIMITATION OF MAMMALIAN GENERA

The literature on species concepts and naming of species is extensive (e.g., Mayr, 1940, 1942, 1963; Simpson, 1961; Ghiselin, 1966, 1974; Van Valen, 1976; Paterson, 1978, 1985; Wiley, 1978; Cracraft, 1983, 1997; de Queiroz and Donoghue, 1988; Templeton, 1989; Mayden, 1997, 2002; de Queiroz, 1998, 2007; Groves, 2004). In contrast, discussions on higher Linnaean taxonomic categories (e.g., the genus) are less numerous. Nonetheless, different authors discussed the meaning and relevance of the genus and proposed various criteria for recognizing and delimiting this higher taxonomic category in a consistent way (e.g., Mayr, 1950, 1969; Cain, 1956; Michener, 1957; Inger, 1958; Simpson, 1961; Hennig, 1966; Dubois, 1987, 1988; Groves, 2001, 2004; Vences et al., 2013). We note that some authors have discussed limitations of the Linnaean classification system and proposed to abandon it (e.g., de Queiroz and Gauthier, 1992; Ereshefsky, 2001; Zachos, 2011) or to combine it with different approaches (Kuntner and Agnarsson, 2006). Therefore, new approaches to nomenclature have been advanced in recent decades (e.g., Papavero et al., 2001; Béthoux, 2007; Cantino and de Queiroz, 2010), but they have not been fully integrated across the Tree of Life. As a result, the Linnaean system continues to form the primary framework used to study and communicate about past and present biodiversity (Vences et al., 2013), particularly in regard to the binomial name (genus and species).

The only widely accepted criterion for delimiting a genus or other higher taxonomic categories is monophyly (Hennig, 1966; Mayr, 1969; Groves, 2001, 2004; Vences et al., 2013). Only monophyletic groups that are well-supported should be named as Linnaean taxa (Vences et al., 2013). Other criteria previously applied to delimitation of extant and extinct genera of mammals are: (1) phylogenetic gaps, (2) uniqueness of adaptive zone, (3) crown group definition, and (4) divergence time (Hennig, 1966; Mayr, 1969; Groves, 2001, 2004; Vences et al., 2013). Some authors advocate for the use of two or more of these criteria, in addition to monophyly, to delimit genera and other higher taxa (e.g., Hennig, 1966; Mayr, 1969), and summary of these criteria is as follows.

Phylogenetic Gaps

The identification of phylogenetic gaps is a criterion that has been used for delimiting genera as well as other higher taxonomic categories (Mayr, 1969). The gaps between taxa and the relative size of those gaps are the result of evolutionary processes (e.g., speciation, extinction, evolutionary and adaptive radiations, and unequal rates of evolution; Mayr, 1969). Specifically, Mayr (1969) defined the genus as "a taxonomic category containing a single species, or a monophyletic group of species, which is separated from other taxa of the same rank [other genera] by a decided gap" (Mayr, 1969, p. 92). In the context of phylogenetic analyses, the gaps between taxa can be measured by the number of synapomorphic traits. In order to facilitate information retrieval and limit redundancy in taxonomic classifications, Mayr (1969) suggested the size of the gap could vary depending on the size of the taxon.

Uniqueness of Adaptive Zone

Simpson (1944) proposed the concept of adaptive zone as a key component of evolutionary change. An adaptive zone corresponds to a particular mode of life or a unique ecological situation (e.g., Simpson, 1944, 1953; Mayr, 1950, 1969; Wood and Collard, 1999; Vences et al., 2013). Under this concept, the occupation of a new adaptive zone by a taxon results in significant evolutionary change (Simpson, 1944). Some authors suggest that this evolutionary change should be reflected at one or more higher categories in the taxonomic classification (Mayr, 1969). Under this perspective, the difference in the occupation of an adaptive zone contributes to the width and the sharpness of phylogenetic gaps between taxa (Mayr, 1969). Therefore, a genus is considered to consist of a species or group of species of common ancestry that occupy a different adaptive zone from the one occupied by species of another genus (Mayr, 1950, 1969).

Crown Group Definition

With the advent of phylogenetic systematics the definition of taxa shifted to a nominalist perspective (de Queiroz, 1994). The essentialist perspective starts from the assumption that the taxon exists, then tries to discover its essential traits, and then refers all organisms with these traits to the taxon in question (de Queiroz, 1994). The nominalist perspective instead assumes that the limits of named taxa are arbitrary conventions, and then proceeds to spell these conventions out. Thus, phylogenetic nomenclature defines taxon names explicitly by anchoring them to defined points on the phylogenetic Tree of Life (de Queiroz, 1994). For example, Mammalia has been defined as the last common ancestor of monotremes and therians plus all descendants of that ancestor (Rowe, 1988; Rowe and Gauthier, 1992). This is a crown group definition of Mammalia (de Queiroz, 1994). In the case of *Equus*, the last common ancestor of all extant species assigned to *Equus* and all descendants of that ancestor, is the crown group definition of the genus.

Divergence Time

Some researchers suggest that a taxonomic arrangement above the species level should ideally not only provide information about evolutionary relationships, but should also reflect the approximate divergence times of the different taxonomic ranks (e.g., Hennig, 1966; Avise and Johns, 1999; Groves and Grubb, 2011). In the particular case of the genus, Groves (2001, 2004) and Groves and Grubb (2011) indicated that the cutoff point for assigning generic status to monophyletic groups of species could be placed at about the Miocene-Pliocene boundary (4–7 Ma). This cutoff point is based on a principle of least violence (which aims at preserving as many traditional genera as possible) and a survey of mammals whose fossil record or molecular divergence estimates are well-known (Groves, 2001, 2004). Under the divergence time criterion, species are regarded as distinct genera if they diverged well-before the Miocene-Pliocene boundary. This approach was intended to make the delimitation of genera a more objective endeavor (Groves, 2001, 2004; Groves and Grubb, 2011).

WHAT IS *EQUUS*? DELIMITATION OF THE GENUS BASED ON FOUR CRITERIA

The question "What is *Equus*?" is a philosophical one that ultimately relates to the evolutionary paradigm under which individual researchers are operating and the research questions that are being asked. In this sense, the question we pose in the title of the paper may have different answers depending on the paradigm under consideration. What *Equus* is, under these varying paradigms, has implications for how we communicate knowledge about the evolutionary and taxonomic history of horses. Perhaps the more valuable question is not "What is *Equus*?," but rather "How variable is the taxonomic content of *Equus* in a given phylogenetic tree, under very distinct paradigms for understanding higher-level taxonomy?" Therefore, we conducted a phylogenetic analysis of derived Equini and examined the placement of the name "*Equus*" within the resultant phylogenetic tree given the four criteria discussed above for delimiting extant and extinct genera of mammals.

Phylogenetic Analysis

We performed a phylogenetic analysis of derived Equini using a matrix of 32 morphological characters and 21 Equini taxa, including *Astrohippus stocki*, *Boreohippidion galushai*, *Dinohippus leardi*, *D. leidyanus*, *D. interpolatus*, *D. mexicanus*, *Equus conversidens*, *E. ferus*, *E. hemionus*, *E. idahoensis*, *E. mexicanus*, *E. neogeus*, *E. occidentalis*, *E. quagga*, *E. simplicidens*, *E. stenonis*, *Haringtonhippus francisci*, *Hippidion saldiasi*, *Hi. principale* and two outgroup taxa, *Acritohippus stylodontus,* and *Pliohippus pernix* (**Table 1**). Our study sample included holotype and referred specimens (**Table A1**). We gathered data

TABLE 1 | Taxa and character matrix used in the phylogenetic analysis conducted here.

	CH1	CH2	CH3	CH4	CH5	CH6	CH7	CH8	CH9	CH10	CH11	CH12	CH13	CH14	CH15	CH16	CH17	CH18	CH19	CH20	CH21	CH22	CH23	CH24	CH25	CH26	CH27	CH28	CH29	CH30	CH31	CH32
Acritohippus stylodontus	0	0	0	0	?	?	0	0	0	0	1	0	0	1	0	?	0	?	?	0	0	0	0	0	0	?	?	0	?	0	0	0
Pliohippus pernix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astrohippus stocki	1	?	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	1	1	?	0	1	1	2	2	0	1	0	0	0	0
Boreohippidion galushai	2	0	0	0	0	1	0	1	?	0	0	0	1	1	0	2	1	0	0	0	1	0	3	2	1	1	1	0	2	0	1	0
Dinohippus interpolatus	1	0	[01]	1	0	1	0	0	1	0	0	0	1	0	0	1	1	0	1	0	1	0	2	2	1	2	0	0	1	0	0	0
Dinohippus leardi	?	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	1	0	1	0	1	0	2	2	1	2	0	0	0	0	0	0
Dinohippus leidyanus	1	0	0	1	1	1	0	1	?	0	0	0	1	0	0	1	1	0	1	0	1	0	2	2	1	2	0	0	1	0	0	0
Dinohippus mexicanus	1	0	0	1	1	1	1	0	1	0	1	1	0	1	0	1	1	0	1	0	1	0	1	1	2	2	0	0	1	1	1	0
Equus conversidens	1	0	1	?	?	?	1	1	?	1	1	0	2	1	1	1	1	1	1	1	?	1	5	3	2	2	2	1	1	2	1	0
Equus ferus	1	0	1	?	?	?	0	1	?	1	[01]	0	1	1	1	2	1	1	1	1	?	1	5	3	2	2	2	1	2	2	1	1
Equus hemionus	1	0	1	?	?	?	1	1	?	1	1	1	0	1	1	1	1	1	1	1	?	1	5	3	2	2	2	1	1	2	1	0
Equus idahoensis	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	1	1	0	1	[01]	0	1	1	1	2	1	0	1	2	?	?	?
Equus mexicanus	1	0	1	?	?	?	1	1	?	1	1	1	3	1	1	1	1	1	1	1	?	1	5	3	2	2	2	1	2	2	1	0
Equus neogeus	1	1	1	?	?	?	0	1	?	0	1	1	2	1	1	2	1	1	1	1	?	0	4	4	2	2	2	0	2	2	2	1
Equus occidentalis	1	1	1	?	?	?	0	1	?	0	1	1	2	1	1	2	1	1	1	1	?	1	4	3	2	2	2	0	2	2	2	1
Equus quagga	[01]	0	0	?	?	?	1	1	?	1	1	0	2	1	[01]	1	1	1	1	1	?	1	[45]	3	2	[12]	2	1	1	2	1	0
Equus simplicidens	1	0	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	1	[01]	0	0	1	3	2	1	0	1	2	1	1	0
Equus stenonis	1	0	1	?	?	?	0	?	?	?	1	1	?	0	1	1	1	1	1	0	1	0	2	3	2	2	2	1	2	?	?	0
Haringtonhippus francisci	1	0	1	?	?	?	1	1	?	1	1	0	2	1	1	1	1	1	1	1	?	1	5	3	2	2	2	1	0	2	?	0
Hippidion principale	2	1	0	[01]	0	0	0	1	?	0	0	0	1	1	0	2	1	1	0	0	1	0	3	2	1	1	1	0	2	0	1	1
Hippidion saldiasi	2	1	0	0	0	0	0	1	?	0	0	0	1	1	0	2	1	0	0	0	1	0	3	2	1	1	1	0	2	0	1	1

CH means character followed by the number of the character. The definitions of characters and their states are in the Appendix.

from the literature for *E. idahoensis* (Scott, 2005) and *E. stenonis* (Athanassiou, 2001; Palombo and Alberdi, 2017); all other specimens in our study were directly examined by us (**Table A1**). We analyzed the holotype and referred specimens of *E. conversidens* separately from the holotype of *Ha. francisci* (= *E. francisci*), as they are considered distinct taxa in some studies (e.g., Lundelius and Stevens, 1970; Dalquest, 1979; Scott, 1996; Azzaroli, 1998; Bravo-Cuevas et al., 2011; Barrón-Ortiz et al., 2017; Priego-Vargas et al., 2017). We note, however, that some researchers considered *E. conversidens* a senior synonym of *Ha. francisci* (= *E. francisci*) (Dalquest and Hughes, 1965), or a *nomen dubium* (e.g., Winans, 1985, 1989; Heintzman et al., 2017). *Equus ferus* is represented in our study by a sample of caballine equids of late Pleistocene age, some of which were previously referred to this taxon (Barrón-Ortiz et al., 2017). For *E. hemionus* and *E. quagga* we studied the remains of wild animals. The phylogenetic analysis was performed using TNT 1.1 (Goloboff et al., 2008) with the implicit enumeration option (exhaustive search), using equal weighting for the characters, and without a collapsing rule. We treated all characters as unordered in the analysis reported here. Two additional analyses (one without a collapsing rule and another with collapsing rule 1) that differed by including ordering of characters 1, 29, 30, and 31 break down the distinction between clades 12, 13, 14, and 17 (**Figure S1**), but leave the topology of the other clades intact (as shown in **Figures 1**, **2**). We used the strict (= Nelsen) consensus option to calculate the consensus tree.

The phylogenetic analysis resulted in three equally most parsimonious trees of 85 steps, consistency index (CI) and retention index (RI) of 0.57 and 0.80, respectively. The strict consensus tree is shown in **Figure 1**. Of particular relevance to the present study are the phylogenetic relationships among *Dinohippus mexicanus*, *Haringtonhippus francisci*, and species of *Equus*. Our phylogenetic analysis identified *Dinohippus* as a paraphyletic group, and "*D.*" *mexicanus* as the sister group to the clade including all species of *Equus* and *Ha. francisci*. The sister group relationship of "*D.*" *mexicanus* and *Equus* is consistent with some previously proposed phylogenetic hypotheses (Prado and Alberdi, 1996; Kelly, 1998). Our results also suggests that *E. idahoensis*, *E. simplicidens*, and *E. stenonis* lie outside of crown group *Equus*. This pattern is consistent with the morphometric analysis of Eisenmann and Baylac (2000), but disagrees with the phylogenetic analysis of Bennett (1980).

Haringtonhippus francisci is nested within crown group *Equus* in our phylogenetic tree, forming a polytomy with *E. conversidens* and *E. quagga* (**Figure 1**). *Haringtonhippus francisci* (= *E. francisci*) is situated in the crown group in the morphological phylogenetic analysis of Bennett (1980). A closer phylogenetic relationship of *Ha. francisci* (= *E. francisci*) to extant *Equus* than primitive species of the genus, such as *E. simplicidens* (= *E. shoshonensis*) and *E. stenonis*, is also indicated by cranial proportions (Eisenmann and Baylac, 2000). Ancient mitochondrial DNA analyses suggested that the lineage which was later named *Haringtonhippus* was the sister species to extant and fossil caballine equids (Weinstock et al., 2005; Orlando et al., 2008; Vilstrup et al., 2013; Der Sarkissian et al., 2015; Barrón-Ortiz et al., 2017). In contrast to these results, a recent genomic analysis concluded that *Ha. francisci* lies outside of crown group *Equus* (Heintzman et al., 2017), but its relationship to *E. simplicidens* and *E. stenonis* was not studied, as molecular data for these species are presently unknown. To evaluate the consistency between our phylogenetic results and the genomic study by Heintzman et al. (2017), we performed a second analysis in which *Ha. francisci* was constrained to lie outside of crown group *Equus*. This analysis resulted in eleven equally most parsimonious trees of 91 steps; 6 steps longer than the most parsimonious trees that we obtained in the unconstrained analysis. In eight of the 11 equally most parsimonious trees, *Ha. francisci* was the sister group of crown *Equus*, whereas in the three remaining trees *Ha. francisci* was the sister group of the clade formed by *E. idahoensis* + crown *Equus*. The discrepancy between the morphological and genomic analyses with regards to the phylogenetic position of *Ha. francisci* is notable, and needs to be investigated in further studies.

Extent of *Equus* Based on Four Criteria for Delimiting Genera

Phylogenetic Gaps

Application of this criterion to our phylogenetic tree (**Figure 1**) suggests that the name *Equus* best encompasses clade 6 on the basis of the number of morphological synapomorphies (**Figure 2A**). This taxonomic arrangement excludes *E. stenonis*, *E. idahoensis*, *E. simplicidens*, and "*Dinohippus*" *mexicanus* from the genus and renders *Haringtonhippus* as a junior synonym of *Equus*. There are six synapomorphies for clade 6 (**Table A2**). In contrast, clade 7 (which includes *E. stenonis* in addition to the taxa in clade 6), and clade 10 (which includes "*D.*" *mexicanus*, all taxa traditionally assigned to *Equus*, and *Haringtonhippus*) each possess five synapomorphies (**Table A2**). *Equus idahoensis* and *E. simplicidens* have at times been referred to *Plesippus*, at either the generic or subgeneric rank (Eisenmann and Baylac, 2000). Similarly, *E. stenonis* has been referred to *Allohippus* at the subgeneric rank (Eisenmann and Baylac, 2000), although we note that some researchers consider *Allohippus* a *nomen dubium* (Azzaroli, 1992). Under the phylogenetic gaps criterion, *Allohippus* and *Plesippus* should be elevated to generic rank. Furthermore, "*D.* " *mexicanus* should be assigned to a new genus, and *Haringtonhippus* synonymized with *Equus*.

Uniqueness of Adaptive Zone

An adaptive zone is defined in the literature as a particular mode of life or a unique ecological situation (e.g., Simpson, 1944, 1953; Mayr, 1950, 1969; Wood and Collard, 1999; Vences et al., 2013). This criterion has been used in the definition of our own genus, *Homo* (Wood and Collard, 1999; Collard and Wood, 2007; Holliday, 2012; Antón et al., 2014). Specializations in body size and shape, locomotor behavior, rate, and pattern of development, among other traits, are argued to have allowed *Homo* to play a unique ecological role relative to other hominins (e.g., Leakey et al., 1964; Tobias, 1991; Wood and Collard, 1999; Collard and Wood, 2007; Holliday, 2012; Antón et al., 2014). Therefore, these traits have been considered important in the delimitation of the genus *Homo* by some researchers (e.g., Leakey et al., 1964; Tobias, 1991; Wood and Collard, 1999; Collard and Wood, 2007; Antón et al., 2014; Wood, 2014), although we note that a consensus on the definition of the

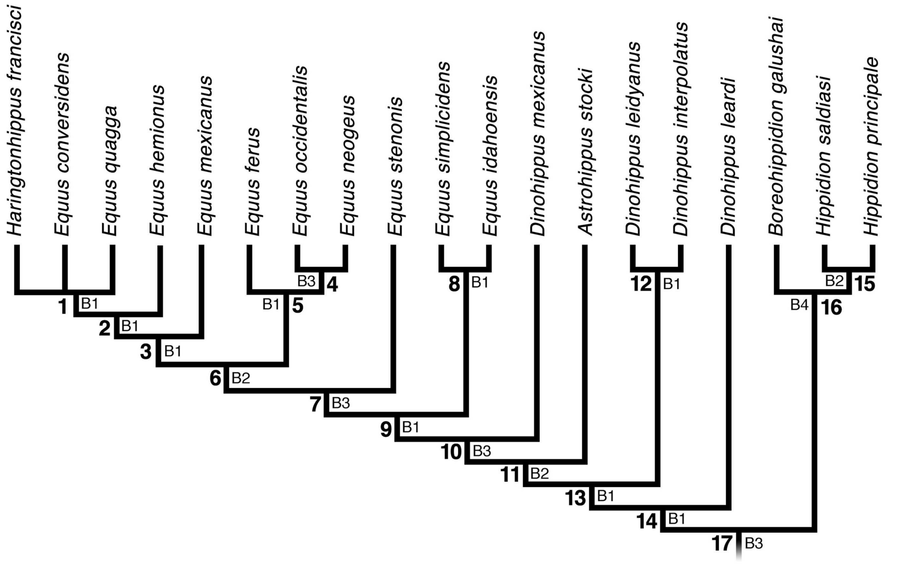

FIGURE 1 | Strict consensus of three equally most parsimonious cladograms of 85 steps, consistency index (CI) of 0.57 and retention index (RI) of 0.80 using a matrix of 32 morphological characters and 21 Equini taxa (**Table 1**). Numbers beside nodes indicate Bremer support values. Outgroups (*Acritohippus stylodontus* and *Pliohippus pernix*) are not shown in the figure. Characters and character states are described in the Appendix.

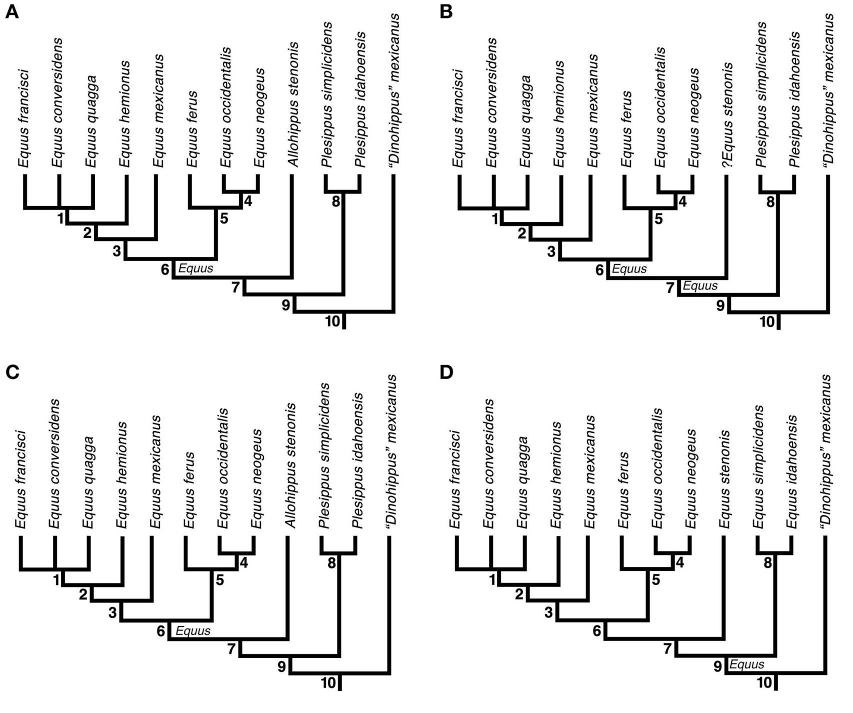

FIGURE 2 | Taxonomic position of *Equus* in the strict consensus tree (**Figure 1**) based on four explicit criteria (in addition to monophyly) previously used to delimit mammalian genera: phylogenetic gaps **(A)**, uniqueness of adaptive zone **(B)**, crown group definition **(C)**, and divergence time **(D)**.

genus has not been reached (Wood and Collard, 1999; Collard and Wood, 2007; Holliday, 2012; Antón et al., 2014; Wood, 2014).

In this context, the unique mode of life of extant equids could be defined as that of ungulate mammals that are adapted to live in generally open, arid habitats and that can thrive on low-quality, high-fiber foods such as grasses and other coarse and tough vegetation (Janis, 1976, 1988; Mihlbachler et al., 2011; Rubenstein et al., 2016; Schoenecker et al., 2016). Potential morphological adaptations for this mode of life comprise modifications of the locomotory and digestive systems. Possible locomotor adaptations to living in open habitats include the elongation of distal autopodial bones as well as the development of monodactyly and the reduction or loss of metapodials II and IV (Simpson, 1951; Shotwell, 1961; Janis and Wilhelm, 1993); however, we note that alternative explanations for digit reduction have been proposed (Thomason, 1986; Biewener, 1998; McHorse et al., 2017). The enhanced development of the stay-apparatus, which allows the individual to conserve energy while standing, is also potentially an adaptation to living in open habitats (Hermanson and MacFadden, 1992, 1996). Potential adaptations of the digestive system, particularly the dentition, to feeding on low-quality, high-fiber vegetation in open environments include increased crown-height of cheek teeth and incisors (Janis, 1976, 1988; Damuth and Janis, 2011; Mihlbachler et al., 2011; Schoenecker et al., 2016), increased enamel complexity (Famoso and Davis, 2014; including increased implications of the occlusal enamel [(Gromova, 1949; Simpson, 1951; Rensberger et al., 1984; Eisenmann and David, 1990; Kaiser, 2002)]), elongation of the protocones of the upper molars and premolars (Eisenmann, 1982; Guadelli and Prat, 1995), increased separation of the metastylid and metaconid, and enlargement of the metastylid to the point of being equal or subequal in size to the metaconid in the lower molars (MacFadden and Carranza-Castañeda, 2002).

The phylogenetic result reported here indicates that the locomotory and dental traits mentioned above did not appear at the same time. Three of these morphological traits are synapomorphies for Clade 6: oval protocone outline on P2 (character 22, state 1); oblong protocone outline on P3-P4 (character 23, state 5); and a high, well-developed intermediate tubercle, which is key in the development of the stay apparatus (character 30, state 2) (**Table A2**). Three of the remaining morphological traits are synapomorphies for Clade 7: pli-protoloph and/or pli-hypostyle common and persistent in the upper molars (character 18, state 1); oblong protocone outline on M1-2 (character 24, state 3); and metaconid and metastylid persistently well-separated from each other on p3-m3 (character 27, state 2). Metapodials II and IV reduced to less than half the length of metapodial III (character 31, state 1) is a synapomorphy for clades 10 and 16 (**Table A2**). Absence of metapodials II and IV (character 31, state 2) is a synapomorphy for clade 4 (**Table A2**). An oblong protocone outline in the M3 (character 25, state 2), and a metaconid and metastylid of equal or subequal size in the lower molars (character 28, state 1) are synapomorphies of clade 11 (**Table A2**). An unworn molar crown height > 60 mm (character 19, state 1) is a synapomorphy of clade 14 (**Table A2**). Based on the position of the majority of purported, adaptive zone-related characteristics, *Equus* is assigned in the phylogenetic tree to clade 6, or possibly clade 7, under the adaptive zone criterion (**Figure 2B**). Under this paradigm, *Haringtonhippus* is considered a synonym of *Equus*, *Plesippus* is elevated to generic rank (the same would apply to *Allohippus* if *Equus* were delimited to clade 6), and "*D." mexicanus* should be assigned to a new genus.

Crown Group Definition

Under this criterion *Equus* is defined as the most recent common ancestor of all extant species assigned to *Equus*, and all descendants of that ancestor. In our phylogenetic tree, a crown-group definition of *Equus* is constrained to clade 6 (**Figure 2C**). This clade includes the extant taxa *E. quagga*, *E. hemionus*, and *E. ferus*, which represent each lineage of extant *Equus* (zebrines, hemionines [including asses], and caballines, respectively) as well as four extinct taxa (*E. conversidens*, *E. occidentalis*, *E. neogeus*, and *Ha. francisci*). This taxonomic arrangement results in the synonymy of *Haringtonhippus* with *Equus* and excludes "*D." mexicanus* and both plesippine and stenonine equids from the genus. The latter two taxa would then be best assigned to *Plesippus* and *Allohippus*, respectively.

Divergence Time

The divergence time criterion states that species should be regarded as distinct genera if they diverged well-before the Miocene-Pliocene boundary (Groves, 2001, 2004; Groves and Grubb, 2011). Application of the time depth criterion to the time-calibrated phylogeny of Equini (**Figure 3**) retains the traditional taxonomic arrangement of *Equus*. Clade 9, which comprises *E. idahoensis, E. simplicidens*, and the remaining taxa traditionally assigned to Equus, is identified as having originated within the Pliocene (**Figure 3**). Therefore, under the divergence time criterion, taxa within clade 9 should be assigned to the same genus (i.e., *Equus*; **Figure 2D**). In contrast, "*D." mexicanus* is identified to have originated well-before the Miocene-Pliocene boundary (**Figure 3**) and should be assigned to a new genus (**Figure 2D**).

The time-calibrated phylogeny (**Figure 3**) is, of course, based on fossil occurrences. An independent assessment of divergence times for some Equini taxa, including crown group *Equus*, *Haringtonhippus*, and *Hippidion*, is provided by molecular analyses (Der Sarkissian et al., 2015; Heintzman et al., 2017). These analyses place the divergence time between the lineage leading to *Haringtonhippus* and that leading to crown group *Equus* at ∼4.1–5.7 Ma (Heintzman et al., 2017). This estimate spans the Miocene-Pliocene boundary, which is currently recognized at 5.33 Ma (Cohen et al., 2013) and is in the upper range of the cutoff interval (4–7 Ma) proposed by Groves (2001, 2004). Molecular estimates of the time of divergence between *Hippidion* and *Haringtonhippus* + *Equus* (∼5.2–7.7 Ma) overlap the lower range of the 4–7 Ma cutoff interval (Der Sarkissian et al., 2015; Heintzman et al., 2017). Based on these estimated divergence times, *Haringtonhippus* and potentially *Hippidion* should be synonymized with *Equus* under the divergence time criterion.

DISCUSSION

Delimitation of the genus *Equus* depends on at least two important factors: (1) identifying well-supported phylogenetic hypotheses, and (2) identifying which clade in a given phylogenetic tree should be considered to comprise the genus *Equus*. Our study infers the first factor and emphasizes the second by evaluating the consistency in the content of "*Equus*" across four explicit criteria (phylogenetic gaps, uniqueness of adaptive zone, crown group definition, and divergence time) previously used to delimit genera. Ideally,

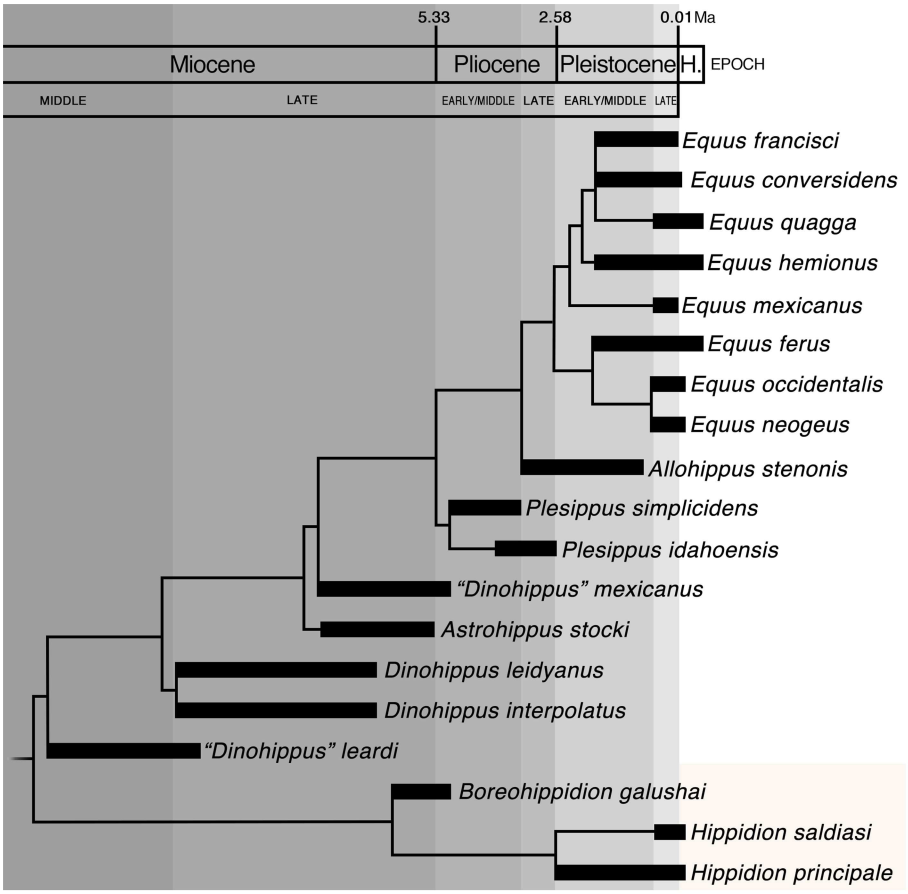

FIGURE 3 | Time-calibrated phylogeny of Equini based on fossil occurrences and the most parsimonious cladogram of 85 steps, consistency index (CI) of 0.57 and retention index (RI) of 0.80 using a matrix of 32 morphological characters and 21 Equini taxa (**Table 1**). Outgroups (*Acritohippus stylodontus* and *Pliohippus pernix*) are not shown in the figure. H., Holocene.

discussions of what "*Equus*" is should also consider taxonomic stability, except where evidence suggests that some aspect of a traditional classification is fundamentally flawed from an evolutionary perspective.

Application of the four criteria for delimiting genera results in slightly different positions for the generic name on the phylogenetic tree (**Figure 2**). Under the phylogenetic gaps criterion *Equus* should be equated with clade 6 based on the number of morphological synapomorphies (**Figure 2A**). The same is true for the crown group criterion, as extant taxa of *Equus* here analyzed (*E. ferus*, *E. hemionus*, and *E. quagga*) fall within clade 6 (**Figure 2C**). The adaptive-zone criterion places *Equus* at clade 6 or possibly clade 7, depending on how the characters are evaluated in relation to the adaptive zone (**Figure 2B**). At a minimum, clade 6 is supported by morphological synapomorphies related to the unique mode of life of extant equids, which represent adaptations for living in open, generally arid, habitats characterized by low-quality, high-fiber foods such as grasses and other coarse vegetation (Janis, 1976, 1988; Mihlbachler et al., 2011; Rubenstein et al., 2016; Schoenecker et al., 2016). The divergence time criterion suggests that *Equus* encompasses clade 9 (**Figure 2D**), based on the time-calibrated phylogeny of Equini (**Figure 3**).

With the exception of the divergence time criterion, the results of our evaluation are overall congruent in identifying clade 6 as the most suitable position of the genus *Equus*. We note that the aim of the divergence time criterion is to provide an operational definition of genera that incorporates time-depth information (Groves, 2001, 2004; Groves and Grubb, 2011). Nevertheless, whether a time interval of 4–7 Ma is a reasonable cutoff point for all taxonomic groups of mammals is debatable, given the disparate evolutionary rates for different groups of mammals (Carroll, 1998). Moreover, the objectivity of this criterion breaks down for clades that diverged very close to the Miocene-Pliocene boundary, as is potentially the case for *Haringtonhippus* and the crown group of *Equus* (Heintzman et al., 2017). In such cases, the taxonomist has to decide whether to keep the sister taxa in one genus or split them into separate genera. Another point to consider about the divergence time criterion is that it relies on the availability of either a very dense fossil record, or very precise molecular divergence estimates (often calibrated by a rather dense fossil record). The fossil record of Neogene equids is particularly dense (MacFadden, 1992). Therefore, the discrepancies between the time-calibrated phylogeny of Equini presented here (**Figure 3**) and the molecular divergence estimates for *Haringtonhippus* and *Hippidion* in two recent molecular analyses (Der Sarkissian et al., 2015; Heintzman et al., 2017) are surprising. Resolution of these differences is beyond the scope of the present study, but this is a topic that should be investigated in future studies. Lastly, the divergence time criterion is designed for extant species and is generally difficult to apply to past biodiversity.

The remaining criteria (phylogenetic gaps, adaptive zone, and crown group) consistently support a clade 6 position for the generic name, with less support for a clade 7 position (in the case of the adaptive zone criterion). We found the phylogenetic gaps and crown group criteria for delimiting genera to be more readily evaluated than the adaptive zone criterion. The broad definition of an adaptive zone implies that it consists of a hyperdimensional space, which in turn makes it difficult to consistently define and quantify. Describing the unique mode of life of extant equids as that of ungulate mammals that are adapted to live in open, generally arid, habitats, and that can thrive on low-quality, high-fiber foods such as grasses and other coarse and tough vegetation (Janis, 1976, 1988; Mihlbachler et al., 2011; Rubenstein et al., 2016; Schoenecker et al., 2016) seems reasonable, but likely captures only a small portion of the complete adaptive zone they occupy. The adaptive zone criterion may also be criticized because it looks for key (essential) traits that allow a taxon or group of taxa to occupy a unique adaptive zone. Mosaic evolution is a widespread phenomenon in vertebrate taxa, including equids (MacFadden, 1992); therefore, it is not rare for characters to have evolved at different times, raising debates about which one should be considered the "essential" character. This problem is exemplified in the present study, as both clades 6 and 7 possess synapomorphies that are relevant for the unique adaptive zone of extant equids, as defined here. Another difficulty in applying the adaptive zone criterion is that the exact ecology of extinct organisms is often hard to determine. In the particular case of equids, some aspects of their ecology, such as feeding ecology, are more readily inferred than others (e.g., MacFadden et al., 1999; Fortelius and Solounias, 2000; Solounias and Semprebon, 2002; Kaiser and Solounias, 2003; Merceron et al., 2004; Sánchez et al., 2006; Mihlbachler et al., 2011). As more complete ecological information becomes available, it will allow researchers to better define the adaptive zone or particular mode of life of extinct equid species. This is particularly relevant if researchers consider that *Equus* should have both phylogenetic and adaptive significance.

Under the phylogenetic gaps criterion *Equus* should be delimited to clade 6 in our phylogenetic tree. This is the clade that has the most synapomorphies, resulting in a "phylogenetic gap." A potential criticism of this criterion is that the positions and relative sizes of gaps among taxa may reflect not only evolutionary processes (e.g., speciation, extinction, evolutionary and adaptive radiations, and unequal rates of evolution; Mayr, 1969), but also gaps in our knowledge. As more fossils are discovered and more specimens are studied, existing gaps will be subdivided. In this regard, our phylogenetic analysis did not include taxa traditionally assigned to *Equus* of Pliocene and early Pleistocene age other than *E. idahoensis*, *E. simplicidens*, and *E. stenonis*. Inclusion of additional Plio-Pleistocene taxa could potentially make application of this taxonomic criterion more difficult, if it were to "even out" the phylogenetic gaps between clades. Nevertheless, the six currently recognized synapomorphies of clade 6 (**Table A2**), many of which are also relevant to the adaptive zone criterion, strongly suggest to us that *Equus* should encompass this clade, pending further phylogenetic analyses that include more Plio-Pleistocene equids traditionally assigned to *Equus* (e.g., *E. cumminsi*; *E. enormis*; *E. huanghoensis*; *E. koobiforensis*; *E. livenzovensis*; *E. qingyangensis*; *E. sanmeniensis*; *E. yunnanensis*; Azzaroli, 1992; Azzaroli and Voorhies, 1993; Downs and Miller, 1994; Eisenmann and Deng, 2005; Palombo and Alberdi, 2017).

As noted above, application of the crown group criterion also supports the idea that *Equus* encompasses all of clade 6 in our phylogenetic tree. These results are at odds with a recent genomic analysis that concluded *Haringtonhippus* lies outside of crown group *Equus* (Heintzman et al., 2017). The crown group criterion has been used in the literature to define genera and other higher taxonomic categories (such as *Panthera*, see King and Wallace, 2014; and *Tapirus*, see Holanda and Ferrero, 2013). Furthermore, extant taxa generally allow us to make robust inferences within a crown group about traits that generally do not fossilize. However, one criticism of the crown definition of higher taxa is that it is based on the extinction criterion (Lucas, 1992). As a result, there is great emphasis on living taxa and, instead of promoting stability, this criterion could lead to taxonomic confusion. This is especially true for relict groups, such as *Homo*. In those instances, other criteria for defining genera may be more relevant. In the case of *Homo*, the adaptive zone criterion has been used by different researchers to delimit the genus (e.g., Wood and Collard, 1999; Collard and Wood, 2007; Holliday, 2012; Antón et al., 2014).

Clade 6 also meets the three primary taxon naming criteria proposed by Vences et al. (2013) to promote economy of change in Linnaean classification schemes and reduce subjective taxonomic instability. These criteria are monophyly, clade stability, and phenotypic diagnosability (Vences et al., 2013). Clade 6 is characterized by six synapomorphies (**Table A2**), discussed above under the phylogenetic gaps criterion, and is a fairly well-supported clade (**Figure 1**). These characteristics identify clade 6 as a stable clade. Furthermore, the six synapomorphies of clade 6 also meet the phenotypic diagnosability criterion, which states that "a taxon to which a Linnaean rank is assigned should be diagnosable and identifiable phenotypically" (Vences et al., 2013, p. 228). The six synapomorphies of clade 6 are visible in both sexes and in many life-history stages of the organism; these are important requirements for this criterion (Vences et al., 2013). Equally important, considering clade 6 as encompassing the genus promotes overall taxonomic stability as traditionally considered in taxonomic treatments. Given that interpretation, our study suggests that *Haringtonhippus* should be synonymized with *Equus*, because the former is situated within clade 6.

Outside clade 6, there are some taxonomic considerations for some taxa. First, "*Dinohippus*" *mexicanus* would have to be assigned to a new genus. In our study "*D.*" *mexicanus* is identified as the sister species to the *Equus* + *Allohippus* + *Plesippus* clade. Our results contrast with previous studies that suggested including "*D.*" *mexicanus* within *Equus* (Prado and Alberdi, 1996) or even including "*Dinohippus*" s.l. within *Equus* (Hulbert, 1989), and also with studies in which "*D.*" *mexicanus* was identified as the sister species of *Equus* (Kelly, 1998). Second, by restricting *Equus* to clade 6, stenonine (i.e., akin to *E. stenonis*) and plesippine (i.e., akin to *E. simplicidens*) equids are excluded from *Equus* and would be recognized as distinct lineages. The recognition of stenonine and plesippine equids as distinct lineages from other *Equus* taxa was previously suggested by morphometric analyses of cranial proportions (Eisenmann and Baylac, 2000; Eisenmann and Deng, 2005). Based on those analyses, the extant species of *Equus* and at least some fossil taxa, such as *Ha. francisci* (= *E. francisci*) and *E. occidentalis*, are grouped under the subgenus *Equus*, whereas stenonine and plesippine equids are referred to the subgenera *Allohippus* and *Plesippus*, respectively (Eisenmann and Baylac, 2000). Based on our results, *Allohippus* and *Plesippus* should be given full generic status.

The recognition that *Ha. francisci* (= *E. francisci*) and extant species of *Equus* form a distinct clade (clade 6) from stenonine and plesippine equids is consistent with a previous morphometric study (Eisenmann and Baylac, 2000). However, this phylogenetic arrangement is not supported by some phylogenetic analyses (Bennett, 1980; Heintzman et al., 2017). In the morphological study by Bennett (1980), *E. stenonis* and *E. simplicidens* (= *E. shoshonensis*) are nested within the clade that comprises extant zebras. Moreover, *Ha. francisci* (= *E. francisci*) was found to be more closely related to *E. onager* (Bennett, 1980), whereas in our phylogenetic analysis *Ha. francisci* forms a polytomy with *E. conversidens* and *E. quagga* (**Figure 1**). In the genomic study by Heintzman et al. (2017), *Ha. francisci* lies outside the clade that comprises extant *Equus*, but its relationship to stenonine and plesippine equids was not tested because molecular data for these species are presently unknown. The discrepancies between those studies and ours emphasize that the definition of *Equus* remains a work in progress.

From the morphological side, the study of additional characters, including those relating to postcranial and cranial anatomy, will continue to refine phylogenetic hypotheses of horses. The character matrix that we used is undoubtedly biased toward dental and craniofacial characters, and incorporation of internal cranial characters and more postcranial characters may alter the resulting topology. On the molecular side, better taxonomic sampling is needed. Ultimately, using an integrative, total-evidence approach may provide a better understanding of the evolution and systematics of Plio-Pleistocene equids and a more resolved taxonomy.

As new phylogenetic datasets and hypotheses develop, we have no doubt that there will be additional discussions related to defining *Equus* and how best to reconcile taxonomy and evolutionary history. We view the deeper value of this endeavor to be stimulation of discussion around naming of genera. As long as binomial nomenclature is retained, naming of new genera (or retaining previously named genera) will almost certainly have a cascade effect, impacting how we view and discuss the evolutionary history of horses.

CONCLUSIONS

Two factors are particularly relevant in the delimitation of the genus *Equus*: (1) identifying well-supported phylogenetic hypotheses, and (2) identifying which clade in a given phylogenetic tree should be considered to comprise the genus *Equus*. In this study, we inferred a phylogenetic tree and addressed the second factor by considering the consistency in delimitation of *Equus* on our strict consensus tree across four explicit criteria previously used in combination with monophyly to delimit genera. In our phylogenetic tree, an *Equus* that encompasses clade 6 has the strongest support on the basis of the most mutually consistent criteria (i.e., phylogenetic gaps, crown group, and, to a lesser extent, adaptive zone), and results in the most taxonomically stable placement of the genus. As such, our results suggest that *Haringtonhippus* should be considered a synonym of *Equus*, *Allohippus* and *Plesippus* should be elevated to generic rank, and "*Dinohippus*" *mexicanus* assigned to a new genus.

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript and/or the **Supplementary Files**.

AUTHOR CONTRIBUTIONS

CB-O, LA, and CJ conceived the study and prepared an earlier version of the manuscript. LA, DM, HM, VB-C, and CB-O collected and analyzed the data. All authors contributed to the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00343/full#supplementary-material

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Species Diversity and Paleoecology of Late Pleistocene Horses From Southern Mexico

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Equids are among the most common mammals found in faunal assemblages of Late Pleistocene age in Mexico. Much of what is known about the *Equus* species is the result of studies conducted in central and northern Mexico; much less is known about species in lower latitudes of Mexico. Here we describe three species that inhabited Oaxaca and Chiapas states. The fossil localities are in northwestern and central Oaxaca, as well as the central part of Chiapas. In Oaxaca, the largest species, *Equus mexicanus,* and the medium-sized *Equus conversidens* are represented by mandibles, skulls, diverse isolated teeth and some postcranial bones, while the smallest species, *Haringtonhippus francisci* is represented by a skull fragment and few isolated teeth. In Chiapas, *E. mexicanus* is represented by a mandible and several isolated teeth, *E. conversidens* by several mandibles and diverse isolated teeth, and *H. francisci* by isolated teeth and two mandibles. AMS radiocarbon and uranium dating of some of the equid localities in Oaxaca and Chiapas indicate that they were at least present since ∼44,000 Cal BP years, they were common around 30,000 Cal BP years, and were still present at the end of the Pleistocene, around 12,000 years ago. The record of *H. francisci* from Chiapas is the youngest in North America. A cluster analysis of extended mesowear data and a discriminant analysis showed that *Equus conversidens* from Chiapas was obligate grazer, whilst the rest of the equids were variable grazers. Geographic distribution of localities in southern Mexico indicates that during the Pleistocene the equid species moved across the Transvolcanic Belt-Sierra Madre del Sur temperate biogeographic corridor and the Tamaulipas-Central America Gulf Lowlands tropical corridor.

Keywords: *Equus*, Pleistocene, Mexico, Oaxaca, Chiapas, paleoecology, taxonomy

INTRODUCTION

Equids are among the most common mammals in the Pleistocene Mexican faunal assemblages. Based on morphological characters, three or four Pleistocene horse species have been recently identified in Mexico. Alberdi et al. (2014) recognized *Equus conversidens, Equus mexicanus*, and *Equus cedralensis.* Priego-Vargas et al. (2017) recognized the previously mentioned species plus

Equus francisci (see their table 10). Barrón-Ortiz et al. (2017), based on linear and geometric morphometric analyses of *Equus* specimens from the western interior of North America recognized three morphological groups of *Equus* in northeastern Mexico (San Josecito Cave, Nuevo León, and Cedral localities of San Luis Potosí) and they taxonomically identify such groups as *E. ferus*, *E. conversidens* and *E. cedralensis*; additionally, based on mitochondrial DNA analyses they recognized two equid clades [Caballine and New World Stilt-legged horses (NWSL)] and they referred the NWSL clade to *E. conversidens*. By means of paleogenomic and morphometric analyses, a new genus of NWSL horse for the Pleistocene of North America was erected: *Haringtonhippus francisci*. This species was reported (as *Equus conversidens*) from San Josecito Cave, Nuevo Léon, based upon a short mitochondrial DNA sequence (Barrón-Ortiz et al., 2017); this record was subsumed into *H. francisci* by Heintzman et al. (2017). Finally, Barrón-Ortiz et al. (2019) based on a morphology-based tree, determined that *Equus* comprises eight species, including *H. francisci,* and suggested that *Haringtonhippus* should be considered a synonym of *Equus*, but the authors do not formally synonymize both taxa.

At present there are 23 main Pleistocene equid localities in Mexico (Sánchez Salinas et al., 2016; Priego-Vargas et al., 2017); of them, just five (21.73%) were previously reported from southern Mexico (Doutt and Black, 1962; Pérez Crespo et al., 2008; Priego-Vargas et al., 2017; Díaz-Sibaja et al., 2018a). In most of these reports, the equids are only mentioned or briefly described.

In Oaxaca, Doutt and Black (1962) reported a molar of *E. mexicanus* near Yolomécatl (**Figure 1**), but they did not describe it. Many years later, Pérez Crespo et al. (2008) enlisted the Pleistocene mammalian localities from Oaxaca, including the horses (*Equus mexicanus* and *E. excelsus*); Jiménez-Hidalgo et al. (2012), briefly described the horses from the Viko vijin local fauna of northwestern Oaxaca (*Equus mexicanus* and *E. conversidens*) and Viñas-Vallverdú et al. (2017) enlisted *Equus* sp. as part of the Chazumba faunal assemblage. Finally, Díaz-Sibaja et al. (2018a) described some postcranial elements that were identified as *Equus* cf. *E. conversidens* from central Oaxaca (**Figure 1**).

In Chiapas, Gómez-Pérez and Carbot-Chanona (2012) briefly described a specimen of *Equus conversidens* from the Villaflores municipality; the next year, Carbot-Chanona and Ovalles-Damián (2013) enlisted the vertebrate fossil record from Chiapas, including *E. conversidens.* Two years later, Pérez-Crespo et al. (2015) determined the dietary habits of some mammalian taxa from the Pleistocene of central Chiapas (**Figure 1**), including four specimens of *E. conversidens.* Finally, Bravo-Cuevas and Jiménez-Hidalgo (2018) enlisted the records of Pleistocene mammals from several areas of central and southern Mexico, including the equids.

This meager knowledge of southern Pleistocene horses compared to what is known from central and northern Mexico impedes our understanding of the inter-specific disparity of the recognized Mexican species, and the magnitude of the intraspecific variation along the Mexican territory. Furthermore, at present it is not possible to fully comprehend the dietary plasticity of Mexican species nor their biogeographic patterns during the Pleistocene.

Thus, the aims of this paper are: (1) to describe the equid species that inhabited northwestern and central Oaxaca, and central Chiapas during the Pleistocene; (2) to disclose the probable dietary preferences and body mass of the equids from Chiapas and Oaxaca; and (3) to comment about the geographic distribution of Mexican equids during the Pleistocene and the habitat where they roamed in southern Mexico.

MATERIALS AND METHODS

Studied Specimens

The specimens from Oaxaca are housed at Laboratorio de Paleobiología, Universidad del Mar, Campus Puerto Escondido, Oaxaca, Mexico, under the acronym UMPE. Specimens from Chiapas are housed at Colección Paleontológica of the Museo de Paleontología "Eliseo Palacios Aguilera," Tuxtla Gutiérrez, Chiapas, Mexico, under the acronym IHNFG. They were collected at some of the localities shown in **Figure 1**.

Since we evaluated morphological characters of teeth and bones of fossil horses from southern Mexico and to avoid the unnecessary proliferation of names for the Mexican equid species, we follow the taxonomic scheme of Priego-Vargas et al. (2017, table 10) that recognized four Pleistocene *Equus* species for Mexico: *Equus conversidens, E. mexicanus, E. francisci,* and *E. cedralensis.* Since Heintzman et al. (2017) transferred *E. francisci* to *Haringtonhippus*, instead of *E. francisci*, we used the name *H. francisci*.

We preferred not to synonymize *Haringtonhippus* to *Equus,* as suggested by Barrón-Ortiz et al. (2019), given the profound discrepancies between the genomic and morphologic analyses about the phylogenetic position of *H. francisci*, which reflect that the definition of *Equus* is a work still in progress (Barrón-Ortiz et al., 2019). Future analyses combining morphology and genomics will shed light about the phylogenetic relationships of *H. francisci*.

In order to disclose the taxonomic identity of the equid specimens studied, they were compared to those housed at the Colección de Macromamíferos, Museo de Paleontología, Universidad Autónoma del Estado de Hidalgo (UAHMP), the Vertebrate Paleontology Collection of the Natural History Museum of the Los Angeles County (LACM/CIT), and a cast of the holotype of *Equus mexicanus* (IGM 4009) housed at the Colección Nacional de Paleontología, Instituto de Geología, UNAM. Likewise, anatomical descriptions and illustrations of the Mexican Pleistocene species were used (Hibbard, 1955; Reynoso-Rosales and Montellano-Ballesteros, 1994; Alberdi et al., 2014; Priego-Vargas et al., 2017).

Abbreviations: Teeth abbreviations are: C/c, Canines; I/I, Incisors; P/p, Premolars; M/m, Molars upper/lower. The number indicates the position of the tooth in the tooth row. Other abbreviations are: AMS, accelerator mass spectrometry, C14 dating; Cal BP, calendar years before present; l, left; LD, linkage distance; masl, meters above sea level; perBlunt, percentage of blunt cusps; perHigh, percentage of high occlusal relief; perLow, percentage of low occlusal relief; perRound, percentage of rounded cusps; perSharp, percentage of sharp cusps; r, right.

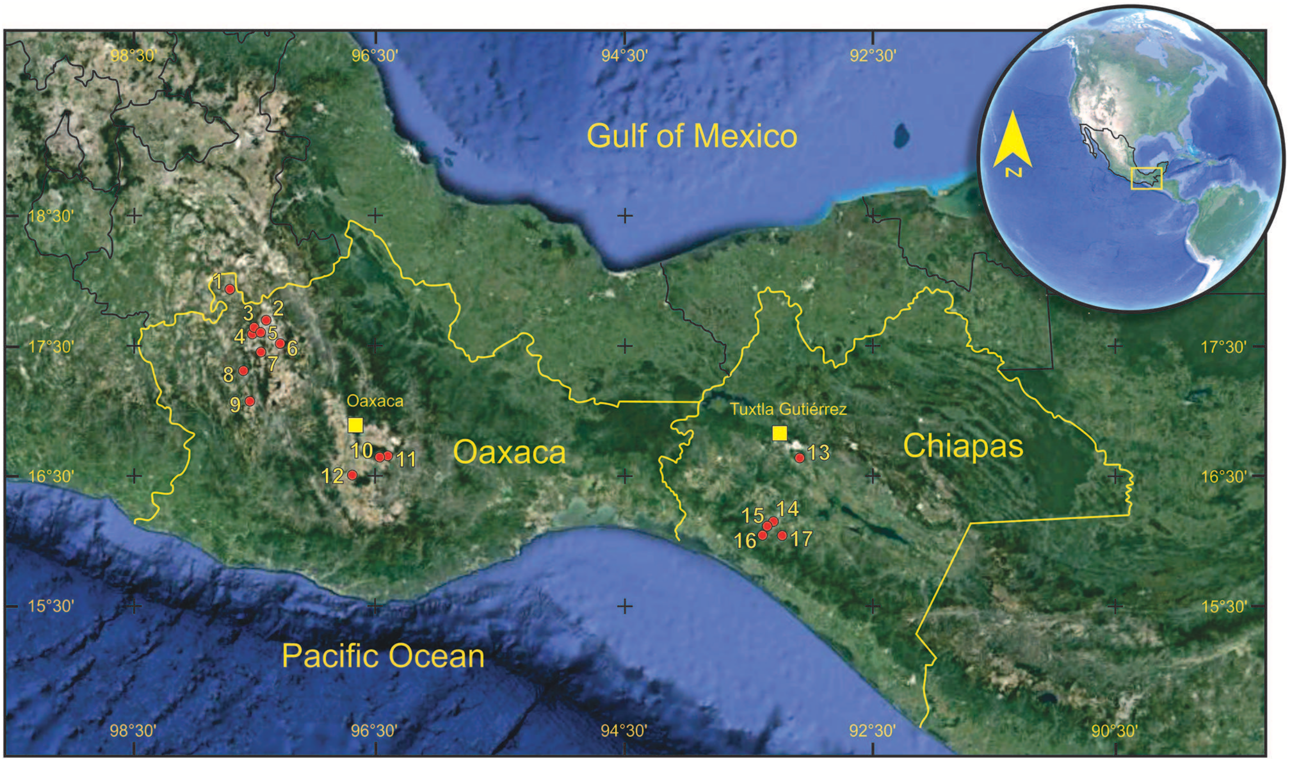

FIGURE 1 | Main Late Pleistocene equid localities from Oaxaca and Chiapas. 1. Chazumba, 2. Concepción Buenavista, 3. Río Sabinal, 4. Río Salado, 5. Cañada del Misterio, 6. Sandage, 7. Río Tejupam; 8. Yolomécatl, 9. Magdalena Peñasco, 10. Güilla, 11. San Dionisio Ocotepec, 12. San Martín de los Cansecos, 13, Nandachuquí, 14. Los Mangos, 15. Gliptodonte, 16. La Simpatía, 17. La Tejería.

Measurements and Dental Nomenclature

Mandibular and skull measurements are in mm and follow the system of measurements for *Equus* bones and teeth (Eisenmann, 2009).

Teeth measurements are in mm and were taken following Eisenmann and Mashkour (2000).

Several measurements were taken from a basicranium specimen (**Figure 2**).

All measurements were taken with digital calipers and recorded within 0.01 mm of accuracy.

Dental nomenclature follows Evander (2004), and Reynoso-Rosales and Montellano-Ballesteros (1994). The used curvature index of teeth follows MacFadden and Carranza-Castañeda (2002).

Paleoecological Aspects

Dietary Guilds

Mesowear analysis

An extended mesowear analysis was performed to include P4/p4 to M3/m3 (Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003). We excluded teeth no yet in occlusion or showing initial wear or with damage on the occlusal surface, and those with a persisting crown height of <15 mm (Fortelius and Solounias, 2000; Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003). A total of 112 cheek teeth were available for this study: 31 upper and 29 lower cheek teeth from Oaxaca (*E. mexicanus*, 13 upper, 16 lower; *E. conversidens*, 18 upper, 10 lower; *H. francisci*, three lower), and 39 upper and 13 lower cheek teeth from Chiapas (*E. mexicanus*, three upper; *E. conversidens*, 25 upper, eight lower; *H. francisci*, 11 upper, five lower). A hierarchical cluster analysis with Euclidean distance and complete linkage was performed on the mesowear variables perHigh, perSharp, perRound, perBlunt, of 35 extant species of herbivores with known dietary preferences (Fortelius and Solounias, 2000; Schulz and Kaiser, 2012) and five extinct *Equus* species (**Table S1**). The mesowear values of *Equus grevyi* and *E. burchelli* of Fortelius and Solounias (2000) were replaced by those of *E. grevyi* and *E. quagga* (= *E. burchelli*) of Schulz and Kaiser (2012).

We only coded the less-worn buccal cusp of each tooth, either the paracone or metacone in the P4-M3 and the protoconid or hypoconid in the p4-m3. The scored mesowear variables included the cusp shape (sharp, rounded, or blunt) and the occlusal relief (high or low). A sharp cusp is one that ends in a point and has no rounded area between the mesial and distal facet, a rounded cusp has a distinctly rounded apex but retains facets on the lower slopes and a blunt cusp is nearly flat and there are no facets (see Barrón-Ortiz et al., 2014). The occlusal relief depends on how high the cusp rises above the valley between paracone and metacone or protoconid and hypoconid (see Kaiser and Fortelius, 2003). All the scored data were converted to percentages, thus giving the variables perHigh, perSharp, perRound, perBlunt (**Table S1**). The dataset was analyzed with

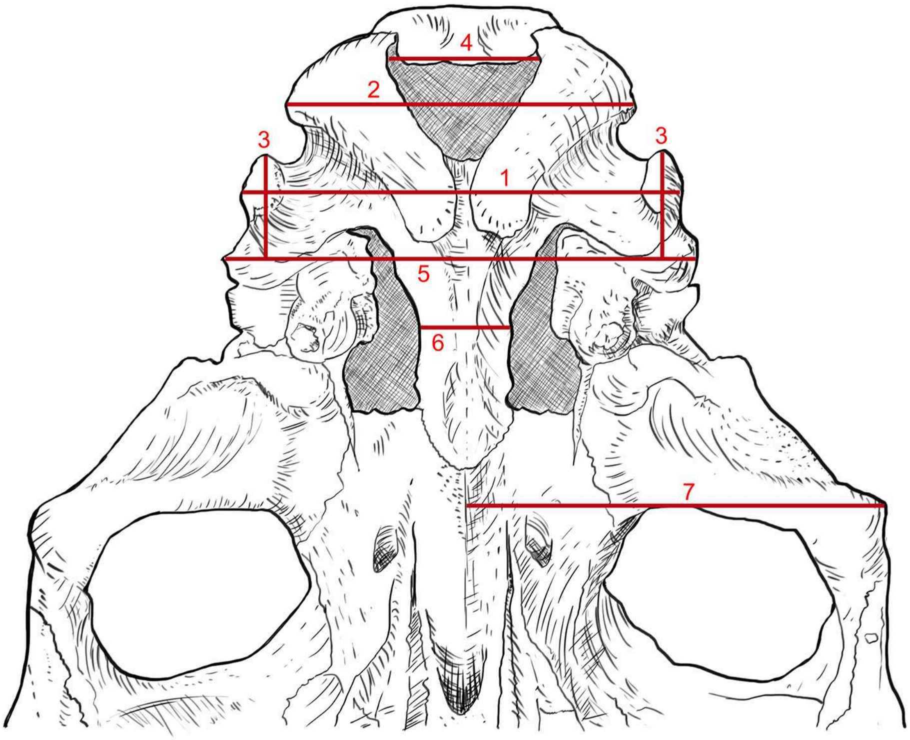

FIGURE 2 | Measurements of the basicranium of equid species. 1. Width across jugal processes. 2. Width of occipital condyles. 3. Width of jugal apophyses. 4 width of foramen magnum. 5. Width across mastoid processes. 6. Minimum width of the basilar process. 7. Width across middle line of basisphenoid to the temporal articular processes.

R software version 3.6.0 (R Core Team, 2014), using the library "fpc" (flexible procedures for clustering) version 2.2-3. Data were normalized, Euclidean distance and complete linkage were used to generate the clusters. A bootstrap analysis was performed (100 replicates) to identify how reliable were the groups (Zumel and Mount, 2014; the used script is in **Supplementary Material 1**).

Discriminant function analysis

To determine the accuracy of the classification among dietary guilds of the studied species, a discriminant function analysis was performed with the database used for the mesowear analysis, only using the dataset of extant species with known dietary habits as training set. Then, we ran a second analysis to predict the feeding group of the studied specimens. We used the linear discriminant method and common covariance as the data were of the same order of magnitude and were in covariance (Díaz-Sibaja et al., 2018b). Dietary category was the grouping variable (obligate grazer, variable grazer, mixed feeder, and browser). Posterior probabilities were calculated based on Bayes rules. We used the Wilk's lambda test ($\alpha = 0.05$) to detect statistical differences between the multivariate centroids of the dietary categories. The analyses were carried out with JMP 8.0 (SAS Institute, 2019).

The cross-validation of the discriminant model was performed with the R library "flipMultivariates" version 0.1, using leave-one-out cross-validation.

Body Mass Estimation

To estimate the probable body mass of the fossil horses from southern Mexico, we used the predictive equations of Janis (1990) for perissodactyls and hyracoids only:

1. Log mass = (2.887 × log second upper molar width) + 1.345 ($r^2 = 0.993$).
2. Log mass = (3.010 × log second lower molar length) + 1.216 ($r^2 = 0.986$).
3. Log mass = (3.090 × log fourth lower premolar length) + 1.290 ($r^2 = 0.986$).

In order to adhere to the equation specifications, the measurements of the teeth were converted to cm, and the estimated body mass to kg.

To detect if the estimated mean body mass of the identified species was statistically different, we used the Mann-Whitney *U*-test.

The datasets generated for this study can be found in the accompanying tables and in the **Supplementary Materials** and can be freely downloaded.

STRATIGRAPHY OF FOSSIL LOCALITIES

Stratigraphic information is available for some of the studied fossil localities. In the Sandage locality, municipality of Coixtlahuaca, northwestern Oaxaca (**Figure 1**), an *Equus* *mexicanus* maxillary fragment with teeth was discovered within an A horizon of a paleosol. The A horizon is thick (> 1 m), dark, organic rich, having a silty loam texture, a prismatic structure and evidence for slickensides. The enamel of one molar was dated by AMS, offering an age of 29,426–30,123 Cal BP. The paleosol is covered by several meters of alluvial sediments.

Also, in northwestern Oaxaca, in the Mixteca region, there are two fossil localities within the municipality of San Antonio Acutla. In the Cañada del Misterio locality (**Figure 1**), diverse *E. conversidens* and *E. mexicanus* specimens were collected from a medium-grained pinkish sand measuring 40 cm thick, which gradually changes from fine-grained sand to a microconglomerate with clasts measuring up to 3.0 cm in diameter. The fossiliferous bed is unconformably underlain by a succession of light brown silty and clayey beds. Organic sediment and a snail shell of the fossiliferous bed were dated by AMS, returning ages of 43,030–44,510 Cal BP and 43,120–44,830 Cal BP, respectively. At another site in Cañada del Misterio, an *Equus* mandible was collected on the top of an 11.0 cm thick microconglomerate containing clasts of up to 3.0 cm in diameter, which was covered by 25 cm of dark gray fine silt with abundant charcoal fragments. One of these fragments was dated by AMS, giving an age of 29,320–29,765 Cal BP.

In the Llano de Hueso locality, also in the municipality of San Antonio Acutla, an *Equus conversidens* skull and some *E. mexicanus* isolated teeth were recovered in the top of a poorly sorted fine- to medium- grained sand, 30 cm of thick, with medium-grained sand of paleochannels. The sand bed gradually becomes siltier toward the top. The *E. conversidens* skull was dated by means of uranium series, offering an age of 24,650–27,305 Cal BP (Ordoñez-Regil et al., 2016).

In the Río Salado locality (**Figure 1**), within Santiago Teotongo and San Antonio Acutla municipalities, several isolated teeth and some postcranial bones of *E. conversidens, H. francisci*, and *E. mexicanus* has been collected from fine-grained silty sand. A tooth of *E. conversidens* collected from the top of the stratigraphic sequence was dated by uranium series, giving an age of 11,380–12,620 Cal BP (Ordoñez-Regil et al., 2016).

In the Río Tejupam locality (**Figure 1**), within the Tejupam municipality, an *H. francisci* basicranium, as well as several *E. conversidens* and *E. mexicanus* specimens were collected from fine-grained silty sand and silty clay beds 25 cm thick (Jiménez-Hidalgo et al., 2011). Organic matter from the silty clayey sediments was dated by AMS returning an age of 19,584–20,180 Cal BP. The deposit of silty-clay is unconformably overlain by a 30 cm thick silty clay bed with dissecation marks. A massive fine-grained sand that interbeds with silty sediments with abundant charcoal overlays the previous bed. One charcoal piece was dated by AMS and showed an age of 6,880–7,005 Cal BP.

In the Güilla locality of central Oaxaca (**Figure 1**), an *E. mexicanus* upper teeth series were collected from the bottom of a well-rounded, imbricated alluvial and fluvial conglomerate of andesite and limestone clasts ranging 6.0–8.0 cm in diameter and of 4.0 m in thickness.

In Los Mangos locality of central Chiapas (**Figure 1**), several teeth and some mandibles of *H. francisci, E. conversidens,* and *E. mexicanus* were collected from a 75 cm thick deposit of silty sediments which was overlaid with coarse sand lenses in a silty matrix. Organic sediment from the top of the fossiliferous sediment was dated through AMS, showing an age of 12,720–12,820 Cal BP.

Associated Fauna

In the Acutla localities the associated fauna consists of gastropods of the families Physidae and Succineidae, *Coelocentrum, Polygyra couloni, Mesomphix (Omphalina) lucubratus* and *Gyraulus parvus,* the bivalve *Pisidium*, the lizard *Sceloporus,* the ground sloth *Nothrotheriops*, the lagomorph *Sylvilagus floridanus,* the rodents *Microtus mexicanus*, *Peromyscus difficilis,* and *Reithrodontomys* cf. *R. megalotis*, the tapir *Tapirus*, the cervid *Odocoileus virginianus,* the bovid *Bison antiquus* and the proboscideans *Cuvieronius hyodon* and *Mammuthus columbi* (Jiménez-Hidalgo et al., 2011, 2013).

In the Río Salado locality, the *Equus* specimens are associated with *Glyptotherium cylindricum* and the camels *Hemiauchenia macrocephala* and *Camelops hesternus*. The mammals *Bison antiquus* and *M. columbi* are also associated with the equids in the Acutla, Río Salado and Río Tejupam localities. Additional taxa from Río Tejupam include the ostracod *Candona*, the gastropods *G. parvus, Planorbella trivolvis*, Lymnaeidae and Poligyridae gastropods, the bivalve *Pisidium casertanum,* the salamander *Ambystoma,* and the rodents *M. mexicanus*, *Neotoma mexicana, Neotomodon alstoni, Peromyscus difficilis,* and the rabbit *S. floridanus* (Jiménez-Hidalgo et al., 2011, 2013; Guerrero-Arenas and Jiménez-Hidalgo, 2015).

The associated fauna collected from Los Mangos locality include the glyptodont *Glyptotherium cylindricum*, the deer *Odocoileus virginianus*, the capybara *Neochoerus aesopi* and the bovid *Bison* sp. (Gómez-Pérez and Carbot-Chanona, 2012; Carbot-Chanona et al., in press).

RESULTS

Systematic Paleontology

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Tribe Equini Gray, 1821
Equus Linnaeus, 1758
Equus conversidens Owen, 1869

Referred Material

Chiapas state: locality Los Mangos. IHNFG-5351, rM2. locality Gliptodonte. IHNFG-2683, lP3-M3 teeth series, lM1-M3 teeth series, lm3, lm1, or lm2; IHNFG-2856, left mandible with p2, p4-m3; IHNFG-2685, lP2-M3 and rP2-M3 teeth series, rp2-m1 teeth series; IHNFG-4148, lp2-m3 and rp2-m3 teeth series, IHNFG-4162, lp4; IHNFG-5762, lP4; IHNFG-5803, lm1-m3 teeth series. locality La Tejería 2. IHNFG-5758, lP3-M3 and rP2-M3 teeth series, lp3-m3 teeth series and rm3. locality La Simpatía. IHNFG-5789, rP4; IHNFG-5804, rp3. Oaxaca state: Locality Oax-4 Río Salado. UMPE 014, lM3; UMPE 448, lm3; UMPE 450, lP4-M1, p3; UMPE 452, lM1; UMPE 470, rP4; UMPE 472 rm2; UMPE 484, rm3; locality Oax-5 Llano de Hueso. UMPE 077, skull; UMPE 476, lm3; UMPE 477 rm1;

UMPE 479 lm3; UMPE 481, lM2; UMPE 535, rM1. Locality Oax-6 Cañada del Misterio. UMPE 453, rm1; UMPE 454, rm3; UMPE 478, lM3; UMPE 482, lm3; UMPE 508, rP4; UMPE 542, rp3 UMPE 625, P2-M3 and rostral fragment. Locality Oax-7 Río Tejupam. UMPE 008 left maxillary fragment with DP4-M3; UMPE 539 lM1; UMPE 569, rP3; UMPE 620, left mandible with p2-m3 and incisors; UMPE 898, lm3. Locality Oax-8 Magdalena Peñasco. UMPE 455 rM2; UMPE 457, rm2; UMPE 458, rm2. Locality Oax-17 Río Sabinal. UMPE 531, rM2. Locality San Martin de los Cansecos. UMPE 911, cast of lm3.

DESCRIPTION

Skull

The specimen UMPE 077 is somewhat dorsoventrally crushed (**Figure 3**). The skull is broken behind the retro-articular processes of the temporal bones. The nasal notch is retracted to a position that lies dorsal to the mesostyle of P2. The rostrum is deep and the facial crest begins at the level of the mesostyle of P4. Compared to extant *Equus*, the muzzle is short. The infraorbital foramen is located dorsal to the metastyle of P3. Measurements of the skull are in **Table 1**.

The palatine is lateromedially concave and narrow; the major palatine foramina and the rostral margin of the choanae are located at the level of the M2's protocone. The teeth series converge rostrally, especially the right one (**Figure 3**). The mandibular fossa is shallow.

Mandible

The mandibles are somewhat stout (**Figure 3**), increasing in height from the premolars to the molars (**Table 2**). The mental foramen is ovoid in outline and well-developed, and it is below the diastema, which is short. The incisor's arcade is quadrangular in outline. The symphysis is relatively slender (**Table S2**).

Upper Teeth

The P2 is triangular in outline, rostro-caudally short (L/B mean ratio of 1.398), the anterior accessory rib is slightly developed, the parastyle is rounded to slightly acute on its rostral portion; the mesostyle is rectangular in outline and the metastyle is slightly developed. The pli protoloph and the pli protoconule are deep; the pli postfossette and pli hypostyle are also deep. The protocone varies from long to rounded. The plicaballine is moderately developed (**Figure 3**).

The P3 and P4 are quadrangular (**Table S2**), with quadrangular or rounded parastyle and mesostyle, the metastyle is slightly developed; there are 2 or 3 folds in the caudal part of the prefossette, the pli protoloph is deep and the pli protoconule could be shallow or deep. The pli postfossette is deep and the pli hypostyle is shallow or deep. The protocone is elongated and slightly curved on its lingual side, and its length represents around 50% the total tooth length (**Table S2**).

The M1 and M2 are quadrangular (**Table S2**), the parastyle is rounded, the mesostyle is quadrangular to rounded and the metastyle is slightly developed; there are three or no folds in the caudal part of the prefossette, the pli protoloph is shallow to absent; the pli protoconule is deep; the pli postfossette generally is deep, but it is absent in one specimen; the pli hypostyle is shallow or absent. The protocone is elongated and usually flat, but in few specimens, it is slightly curved in its lingual part (**Figure 3**), its length represents slightly less than the 50% of the total tooth length. There is no pli caballine in these molars.

The M3 is triangular in outline and small (**Table S2**), its parastyle and mesostyle are rounded, and the metastyle is not present. There are 1–3 folds in the caudal part of the prefossette, the pli protoloph is absent, the pli protoconule can be shallow or deep. The pli postfossette is shallow to absent; the pli hypostyle is deep or absent. The protocone is long, flat, slightly curved or sinuous in its labial side (**Figure 3**). The M3's have a curvature index of 40.

Lower Teeth

The incisors lack infundibula; the i3 is separated by the canine by a short diastema (**Figure 3**). In males the canine is well-developed and bears a crest that runs all along the crown height.

The p2 is triangular in outline (**Table S3**), the metaconid is rounded and the metastylid has an acute tip, the linguaflexid is "U"-shaped, there is a rounded entoconid; the postflexid is very long. The ectoflexid is shallow and does not penetrate the isthmus. There is a faint pli caballinid.

The p3 and p4 are rectangular, the metaconid is rounded and the metastylid is triangular (**Figure 3**), the linguaflexid is "V"-shaped; the postflexid is long and with a somewhat sinuous labial margin; usually, the ectoflexid is moderately deep and does not penetrate the isthmus; the pli caballinid is slightly developed.

The m1 and m2 are also rectangular (**Table S3**) and the m3 is triangular in outline. They have a rounded metaconid and a triangular metastylid; the linguaflexid is "V" or "U"-shaped (**Figure 3**); the postflexid is long and less sinuous than in the premolars or almost flat; the entoflexid is moderately deep or deep and can or cannot penetrate the isthmus. The pli caballinid can be present or absent.

DISCUSSION

The studied specimens have a close morphology and dimensions when compared to fossil material of *Equus conversidens* from central and northern Mexico. In this species the muzzle is short and tapers rostrally, the infraorbital foramen is set high, the facial crest extends anteriorly to a position dorsal to P4, and the teeth series converge rostrally, as in UMPE 077 (**Figure 3**; **Table 1**). The studied upper teeth from Oaxaca and Chiapas are of medium size compared to the other Mexican Pleistocene species (**Table S2**), the P2 is rostro-caudally short and the M3 is small. The mandible is stout and has a similar size to those identified as *E. conversidens* (**Table 2**); the lower teeth have an elongated protocone that is slightly curved on its lingual side, the premolars and molars have few folds in the inner side of the fossettes, they have V-shaped linguaflexids and moderately deep ectoflexids; the size of the teeth is similar to those of

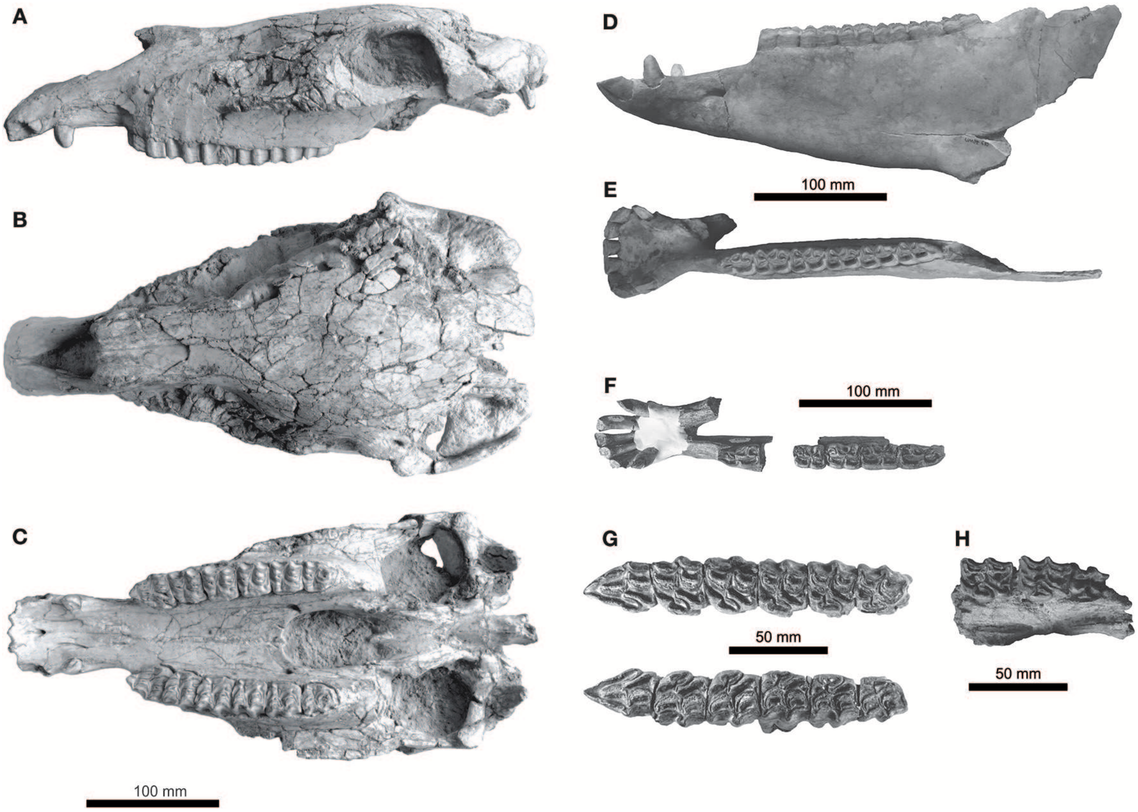

FIGURE 3 | *Equus conversidens* from southern Mexico. UMPE 077, skull in **(A)** lateral, **(B)** dorsal, and **(C)** palatal views. UMPE 620, left mandible in **(D)** lateral and **(E)** dorsal views. IHNFG-2856, left mandible in **(F)** dorsal view. IHNFG-2685, upper teeth series in **(G)** occlusal view. UMPE 008, left maxillary with DP4- M2 in **(H)** occlusal view.

TABLE 1 | Skull measurements of the equids from the Pleistocene of southern Mexico and other selected specimens from North America.

E. conversidens	2	2-5	3	5	6	7	7 bis	9	10	10bis	17	17bis	21	22
CIT 3229*	240	113		127	94	84	45				70	52	53	49
CIT 3163*	247	126		121	92	90	70				72	51	63	54
CIT 3928*				122		83	68				64	52		
UAHMP-509	240	119	111	120.6	94.1	88.5	70.8	74.2	47.5	34.8	77.2	45.0	60.5	50
UAHMP-1116	244	128.8		114.9	93.6	88.9	74.9				77.8	35.8	51.4	47.2
UMPE 077	227	122	116.4	104	75	72.4	72.4	79	46.4	42.1	66.6	44.4	62.9	37.3
E. mexicanus														
IGM 4009	264	169	127.4	124.5	99	101.3	86.5	105.9	50.0	43.0	87.9	47.9	74.2	61.5
UMPE 521	273	140	136.1	132	95	98.2	80.7			42.7	86.0	46	67.6	43.9

Data from Eisenmann (2009). Description of each measurement is in **Supplementary Material 2.*

E. conversidens (**Table S3**) and intermediate in size between *E. mexicanus, E. cedralensis,* and *H. francisci* (Azzaroli, 1998; Bravo-Cuevas et al., 2011; Alberdi et al., 2014; Priego-Vargas et al., 2017).

The above described combination of characters identifies the studied specimens as *Equus conversidens*.

In the studied sample, the M3 of *E. conversidens* has the lowest curvature index (40 vs. 70 and 50 in the other species). If this curvature value is also present in specimens from other localities, it could be useful to identify isolated M3 of this species.

On the other hand, the presence/absence of incisors' infundibula is very variable within horse species, and it also changes with tooth wear (Barrón-Ortiz et al., 2017). Thus, we do not consider it as a useful taxonomic character, but we believe it is important to describe the character state of the sample from southern Mexico.

Equus mexicanus (Hibbard, 1955)

TABLE 2 | Measurements of equid mandibles from the Pleistocene of southern Mexico and other selected specimens from North America.

E. conversidens	3	12	4	4b	9	10	11
UAHMP-386	80.0	108.7	87.3	79.2	54.6		
UAHMP-504			84.6	77.2	57.6	81.4	110.4
UAHMP-s/n				73.3		92.9	121.9
LACM 17968*	88		77	72	65	80	
LACM 120754*	86		83	75	67	87	
UMPE 610	84	105.2	85.3	78.5	70.1	92.3	118.6
E. mexicanus							
LACM 123901	99	130.2	96	93	63	100.5	138
UMPE 554				84.2		97.2	134.3
UMPE 643	82	106.5	88.2	79.1	65.54	90.7	113.6
IHNFG-4872		100	120	82.4	64.6	87.2	
Haringtonhippus francisci							
TAMU 2518		98	88.1	66.3	55.8	72.7	94.6
IHNFG 4211		90	73.6	72.8	55.43	70.4	68.35

Data from Eisenmann (2009). Description of each measurement is in* ***Supplementary Material 3**.*

Referred Material

Chiapas state: locality Los Mangos. IHNFG-4872, mandible with both series of DP2-M2, the left incisors and both canine roots; IHNFG-4886, lP3 or lP4; IHNFG-5660 rP4. Locality Nandachuqui. IHNFG-694, rP2; IHNFG-691, rM1 or rM2. Locality La Simpatía. IHNFG-5352, rM3. Locality La Tejería. IHNFG-4700, Mx. Oaxaca state: Locality Sandage. UMPE 908, lP4-M3 and rM1-M3 teeth series. Locality Oax-4 Río Salado. UMPE 011, lM1; UMPE 900 rm3; UMPE 447, calcaneum; UMPE 489, left metatarsal III. Locality Oax-5 Llano de Hueso. UMPE lP4; UMPE 474, P3; UMPE 480, Mx; UMPE 490, right mandible with p2-m2; UMPE 903, rP4. Locality Oax-6 Cañada del Misterio. UMPE 546, rp3; UMPE 643, dentary with both p2-m3 teeth series, the canines and incisors; UMPE 897, lM2; UMPE 901, lP2; UMPE 902, rm2. Locality Oax-7 Río Tejupam. UMPE 505, rM2. Locality Oax-17 Río Sabinal. UMPE 521, skull; UMPE 554, left mandible with p3-m3; UMPE 567, lP2; UMPE 611, lm2. Locality Güilla. UMPE 907, lP2-M3 and rP2-Px-M2.

DESCRIPTION

Skull

The specimen UMPE 521 is dorsally crushed, so, it is not possible to observe any undistorted feature. It is large, caudally, the skull preserves the left temporal articular tubercle and the retro-articular process (**Figure 4**). The premaxillaries are stout. The nasal notch is retracted to a position that lies dorsal to the mesostyle of P2. Rostrally, the facial crest ends between the P4 and the M1. The muzzle is short (**Table 1**), as in the skull of *E. conversidens*.

The palatine is wide (**Table 1**); the anterior margin of choanae is immediately behind M2's protocone (**Figure 4**). The upper teeth series seems straight. The mandibular fossa is shallow.

Mandible

The mandible is somewhat stout, its height increases caudally along the teeth series (**Table 2**). The diastema is short. The incisor's arcade has a "U" outline. The symphysis is somewhat slender. The articular process is very similar to extant *Equus*.

Upper Teeth

The P2 is long and triangular in outline (**Table S2**), the anterior accessory rib is slightly developed, the parastyle is acute to slightly rounded, the mesostyle is rectangular in outline (**Figure 4**), there is a deep pli protoloph and pli protoconule; the pli postfossette and pli hypostyle are also deep. The protocone is subrounded with a wide isthmus. The plicaballine is moderately to well-developed.

The P3 and P4 are quadrangular, with quadrangular parastyle and mesostyle, there are 4–5 folds in the caudal part of the prefossette, and the pli protoloph and the pli protoconule are deep. The pli postfossette and pli hypostyle are also deep. The protocone is elongated and slightly curved on its lingual side, its length represents around 2.41 of the total length of these premolars. The plicaballine is single and moderately developed.

The M1 and M2 are quadrangular, the parastyle is rounded to quadrangular, the mesostyle is rectangular in outline, there is 1–3 folds in the caudal part of the prefossette, the pli protoloph is very variable, it can be absent, be moderately deep or deep; the pli protoconule can be shallow to deep. The pli postfossette varies from moderately deep to very deep; the pli hypostyle varies from shallow to deep. The protocone is elongated and can be slightly curved to flat on its lingual side; its length represents around 2.14 of the total teeth length. The pli caballine is faint to absent, only in the M2 UMPE 505 it is well-developed.

The M3 is triangular in outline (**Table S2**); it has a rounded parastyle, a rounded to slightly quadrangular mesostyle and there is no metastyle (**Figure 4**). There are one to four shallow folds in the caudal part of the prefossette, the pli protoloph is shallow, the pli protoconule can be shallow or deep. The pli postfossete is faint to absent, the pli hypostyle is deep. The protocone is long and flat to slightly curved lingually. The M3's have a curvature index of 50.

Lower Teeth

The incisors lack infundibula; the i3 is separated by the canine by a very short diastema. In females the canine is a very small conical tooth.

The p2 is triangular in outline (**Table S3**), the metaconid is rounded and the metastylid has an acute tip, the linguaflexid is "V"-shaped, there is a rounded entoconid; the postflexid is very long. The ectoflexid is shallow and does not penetrate the isthmus.

The p3 and p4 are rectangular (**Table S3**), the metaconid is rounded and the metastylid is triangular to ovoid with an acute tip in outline, the linguaflexid is variable, can have a "V" shape, or is "U"-shaped; the postflexid is very long and with a sinuous labial margin; the ectoflexid is moderately deep and does not penetrate the isthmus; the pli caballinid can be present or absent.

The deciduous premolars of IHNFG-4872 are large and their morphology is very similar to those of the permanent premolars

FIGURE 4 | *Equus mexicanus* from southern Mexico. UMPE 521, skull in **(A)** palatal view. UMPE 554, left mandible in **(B)** lateral and **(C)** occlusal views. **(D)** IHNFG-4886, M1; **(E)** IHNFG-5660, P4, and **(F)** UMPE 908, P4 in occlusal views. UMPE 643, mandible in **(G)** lateral and **(H)** dorsal views. IHNFG-4872, mandible in **(I)** lateral and **(J)** dorsal views. UMPE 489, left metatarsal in **(K)** cranial view.

(**Figure 4**), the ectoflexid is deep and penetrates the isthmus. Their measurements are in **Table S4**.

The m1 and m2 are almost quadrangular and the m3 is triangular in outline. They have a rounded metaconid and a triangular to slightly rounded metastylid; the linguaflexid is "V" or "U"-shaped, the postflexid is long and less sinuous than in the premolars; the ectoflexid is deep and penetrates the isthmus. The pli caballinid is present to slightly developed.

Postcranial Bones

The partial left calcaneus UMPE 447 is large, stout and with a quadrangular outline; the sustentaculum is broken. The left metatarsal UMPE 489 is stout and dorsoventrally short (**Figure 4**); its length is 263.1 mm, the proximal width is 55.3 mm, diaphysis width at middle is 34.49 mm; distal width is 52 mm.

DISCUSSION

The skull UMPE 521 shares with the holotype of *Equus mexicanus* its large size, a nasal notch that is retracted to a position that lies dorsal to the P2 and a facial crest that ends between the P4 and the M1 (Hibbard, 1955); the mandibles from Chiapas and Oaxaca share their large size (**Table 2**) and robustness with this species (Azzaroli, 1998).

The upper teeth from southern Mexico have a large size with moderately to complexly plicated enamel on fossettes, long, flat to somewhat curved protocones, a deep pli protoloph and pli hypostyle on premolars and a long P2; these features are present in *E. mexicanus*, as are those of the lower molars, such as a large size, a predominantly triangular metastylid, and deep to moderately deep ectoflexids.

The limbs bones are large and stout, as those of *E. mexicanus* from Cedral, San Luis Potosí (Alberdi et al., 2014).

The P2s of *E. mexicanus* and *H. francisci* are longer than those of *E. conversidens*; by the same token, the occlusal area of the M3 in these species is comparatively larger than that of *E. conversidens* (**Table S2**) and its curvature index is higher.

The above described combination of characters allows this sample to be identified as *Equus mexicanus*.

Haringtonhippus (Heintzman et al., 2017)

Haringtonhippus francisci (Hay, 1915)

Referred Material

Chiapas state: locality Los Mangos. IHNFG-4211, dentary with both p2-m3 teeth series, the canines and incisors; IHNFG-4698, lP2-M3 and rP2-M2 teeth series; IHNFG-4700, rP2; IHNFG-4211, mandible with lp3-m1, rp2-m3, i1-2 and the canines; IHNFG-4699, mandible with lp2-m3, incisive fragments, and canines. Locality Gliptodonte. IHNFG-4155, lP2-M1 teeth series and rP4, rM2; IHNFG-2708, Mx. Oaxaca state: locality Oax-5 Llano de Hueso. UMPE 906, rP4. Locality Oax-6 Cañada del Misterio. UMPE 905, lP3. Locality Oax-7 Río Tejupam. UMPE 561, basicranium. Oax-17 Río Sabinal. UMPE 904, lP4.

DESCRIPTION

Skull

The available skull is broken, only the basicranium is preserved (**Figure 5**); the left bones are slightly distorted; the bones seem somewhat slender. The zygomatic arches are missing. The caudal part of the frontal is present, it is flat as in extant *Equus*; the parietals are somewhat bulbous, and the median sagittal crest is slightly developed. The foramina that are present at the base of the temporal crest are large. Measurements of the basicranium are in **Table 3**.

The external auditory meatus is faintly ovoid in outline; the mastoid process is triangular in outline as in extant *Equus*.

The nuchal crest is missing, the occipital condyles are very similar to the ones of extant *Equus*, the jugal processes are dorsoventrally short; the basioccipital bone is slender, as is the preserved portion of the basisphenoid. The retroarticular processes are also dorsoventrally short. The preserved part of the mandibular fossa is deeper than in *E. conversidens* and *E. mexicanus* specimens from Oaxaca.

Mandible

There are two mandible fragments in the sample (**Figure 5**). They are small and somewhat stout; they increase in height from the premolars to molars (**Table 2**). The mental foramen is ovoid in outline and well-developed.

Upper Teeth

The P2 is triangular in outline and long (**Table S2**), the anterior accessory rib is slightly developed, the parastyle is rounded, the mesostyle is rectangular to slightly rounded and the metastyle is poorly developed (**Figure 5**). The pli protoloph and the pli protoconule are moderately deep; the pli posftossette and pli hypostyle are also moderately deep. The protocone is short. The plicaballine is well-developed in IHNFG-4698, but is absent in IHNFG-4155, which has more worn teeth.

The P3 and P4 are quadrangular, with quadrangular to subrounded parastyle and mesostyle; the metastyle is slightly developed (**Figure 5**). There are 2 or 3 folds in the caudal part of the prefossette, the pli protoloph is deep to shallow, the pli protoconule is deep. The pli posfossette is deep to moderately deep and the pli hypostyle is shallow. The protocone is elongated and slightly curved on its lingual side, and its length represents around 43.3% of the total length of these premolars (**Table S2**); the pli caballine is absent.

The M1 and M2 are quadrangular (**Table S2**), the parastyle is rounded, the mesostyle is quadrangular and the metastyle is slightly developed. There are two or no folds on the caudal portion of the prefossete, the pli protoloph is deep to shallow, the pli protoconule, the pli postfossete and the pli hypostyle are shallow. The protocone is elongated and flat to slightly concave in its lingual part; it represents around 45% of the total tooth length. The pli caballine is absent.

The M3 is triangular in outline, the parastyle and mesostyle are quadrangular in outline, the metastyle is absent. There is 1-fold in the caudal part of the prefossette, the pli protoloph is somewhat deep, the pli protoconule is very deep; the pli postfossette is absent and the pli hypostyle is deep. The protocone is very long and flat. The M3 has a curvature index of 70.

Lower Teeth

The incisors lack infundibula. In males the canine is well-developed and bears a crest that runs all along the crown.

The p2 is triangular in outline (**Table S3**), the metaconid is rounded and the metastylid has a sub-acute tip; the linguaflexid has an open "V" shape, the entoconid is rounded and the postflexid is long. The ectoflexid is moderately deep and does not penetrate the isthmus. There is not pli caballinid.

The p3 and p4 are rectangular (**Table S3**), the metaconid is rounded and the metastylid is triangular, the linguaflexid is predominantly "V"-shaped, but few are "U"-shaped; the postflexid is relatively long and almost flat; the ectoflexid is moderately deep and does not penetrate the isthmus. There is no pli caballinid.

The m1 and m2 also are rectangular (**Table S3**) and the m3 is very elongated and triangular in outline. These molars have a rounded or sub-acute metaconid and a triangular to subrounded metastylid; the linguaflexid is "V" or slightly "U"-shaped; the postflexid is somewhat long and flat or slightly concave; the ectoflexid is deep and penetrate the isthmus. The pli caballinid is absent.

DISCUSSION

The basicranium from Oaxaca is most similar in size to a skull identified as *H. francisci* (LACM(CIT) 109/156450) from the Pleistocene of Nevada (Heintzman et al., 2017); UMPE 561 is smaller than those of *E. conversidens* and *E. mexicanus* (**Table 3**). The mandible measurements of IHNFG-4211 are like those of the mandible TAMU 2518, which is part of the holotype of *H. francisci* (**Table 2**).

The upper molars from Chiapas and Oaxaca share with *E. cedralensis* and *H. francisci* their small size (**Table S2**), their flat or somewhat curved and elongated protocone, the few plications on the fossettes, the absence of plicaballine and the very elongated protocone of M3. The lower molars are also of small size (**Table S3**) and share with the small equid species a rounded metaconid and a predominantly acute metastylid, and a lack of pli caballinid (Hay, 1915; Lundelius and Stevens, 1970; Alberdi et al., 2014; Priego-Vargas et al., 2017).

Teeth of *H. francisci* and *E. cedralensis* have a very similar occlusal pattern and size (Barrón-Ortiz et al., 2017; Priego-Vargas et al., 2017), but according to Alberdi et al. (2014), *E. cedralensis* does not possess slender metapodials as *H. francisci*, but shorter and stouter ones. The studied sample of small

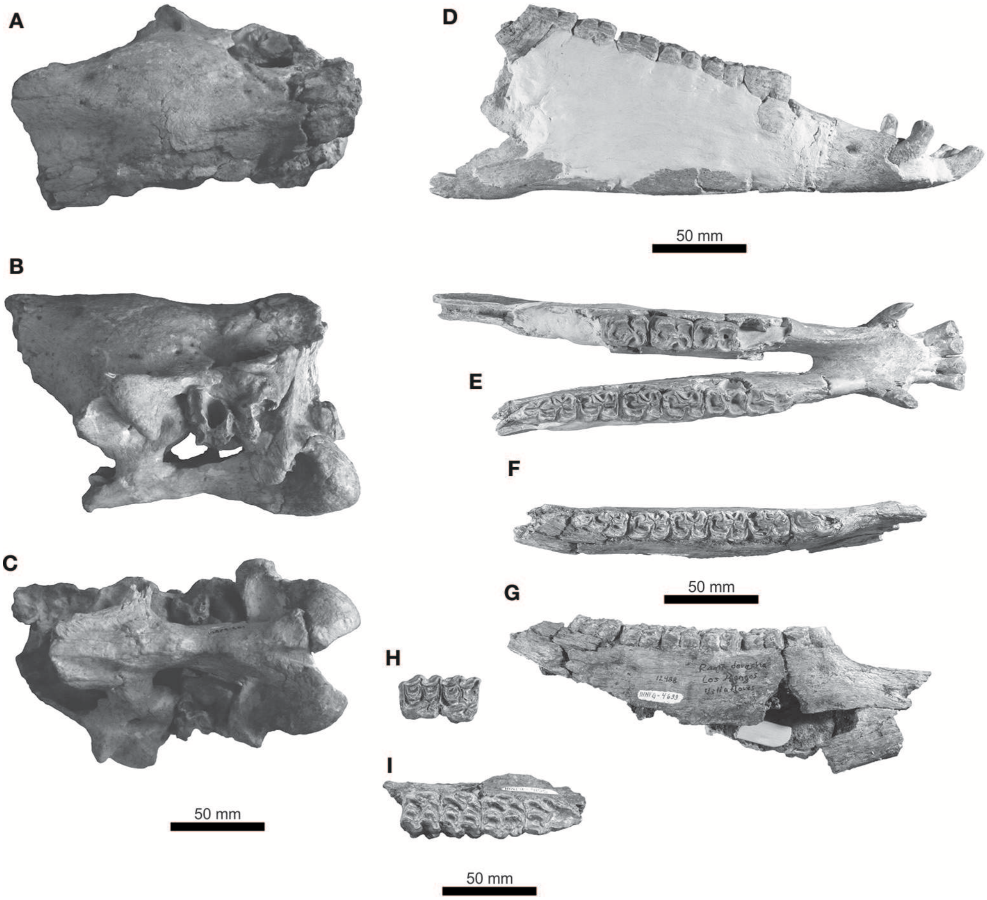

FIGURE 5 | *Haringtonhippus francisci* from southern Mexico. UMPE 561, basicranium in **(A)** dorsal, **(B)** lateral, and **(C)** ventral views. IHNFG-4211, mandible in **(D)** lateral and **(E)** dorsal views. IHNFG-4699, mandible in **(F)** lateral and **(G)** dorsal views. IHNFG-4155, right P4-M1 in **(H)** occlusal view and left P2-M1 in **(I)** occlusal view.

TABLE 3 | Basicranium measurements of Pleistocene equid species present in Mexico.

E. conversidens	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
UAHMP-509	144.3	93.4	23	36	133	30.6	116	95
LACM 3929	116	85	25	43	124	30	115.5	80
F:AM 42810*	100	77.6	23.1	38	114.3	27	93	103
Haringtonhippus francisci								
LACM 156450	94.6	71.5	23	34.7	98.5	24	65.7	60
UMPE 561	95	79.8	24	32.3	88.5	23.5	82.8	60
E. mexicanus								
IGM 4009	139	101	31	46	137.5	31.1	115.7	111

*Number of measurements as in **Figure 2**. Measurement 8 is the width between beginning of the sagittal crest to the external part of the temporal articular tubercle.*
**Measurements taken from the image of Eisenmann (2009).*

teeth was not associated with any metapodial; nonetheless, the basicranium and the mandible are morphologically similar and about the same size as those of *H. francisci,* and giving that this small species was the first erected (Hay, 1915), we identify the small specimens from southern Mexico as *H. francisci*.

PALEOECOLOGICAL ASPECTS OF EQUID SPECIES FROM SOUTHERN MEXICO

Dietary Guilds

The cluster of the mesowear analysis shows five main groups (**Figure 6**); one containing the hypergrazer *Bison bison* and *Equus conversidens* from Hidalgo (LD = 0.86), one with obligate grazers and variable grazer species (LD = 3.3), one with exclusively variable grazers (LD = 3.3), another with variable grazers and mixed feeder species (LD = 2.4), and a cluster with browser species (LD = 2.0). The bootstrap nodal support of these five main clusters range from 0.70 to 0.95, meanwhile the support of the equid species from southern Mexico ranges from 0.62 to 0.97 and those of the Pleistocene equids from other regions of Mexico varies from 0.68 to 0.93 (**Figure 6**).

Most of the studied samples are distributed in the clusters of variable grazers, except for the sample of *Equus conversidens* from Chiapas that is in the cluster of obligate grazers. None of

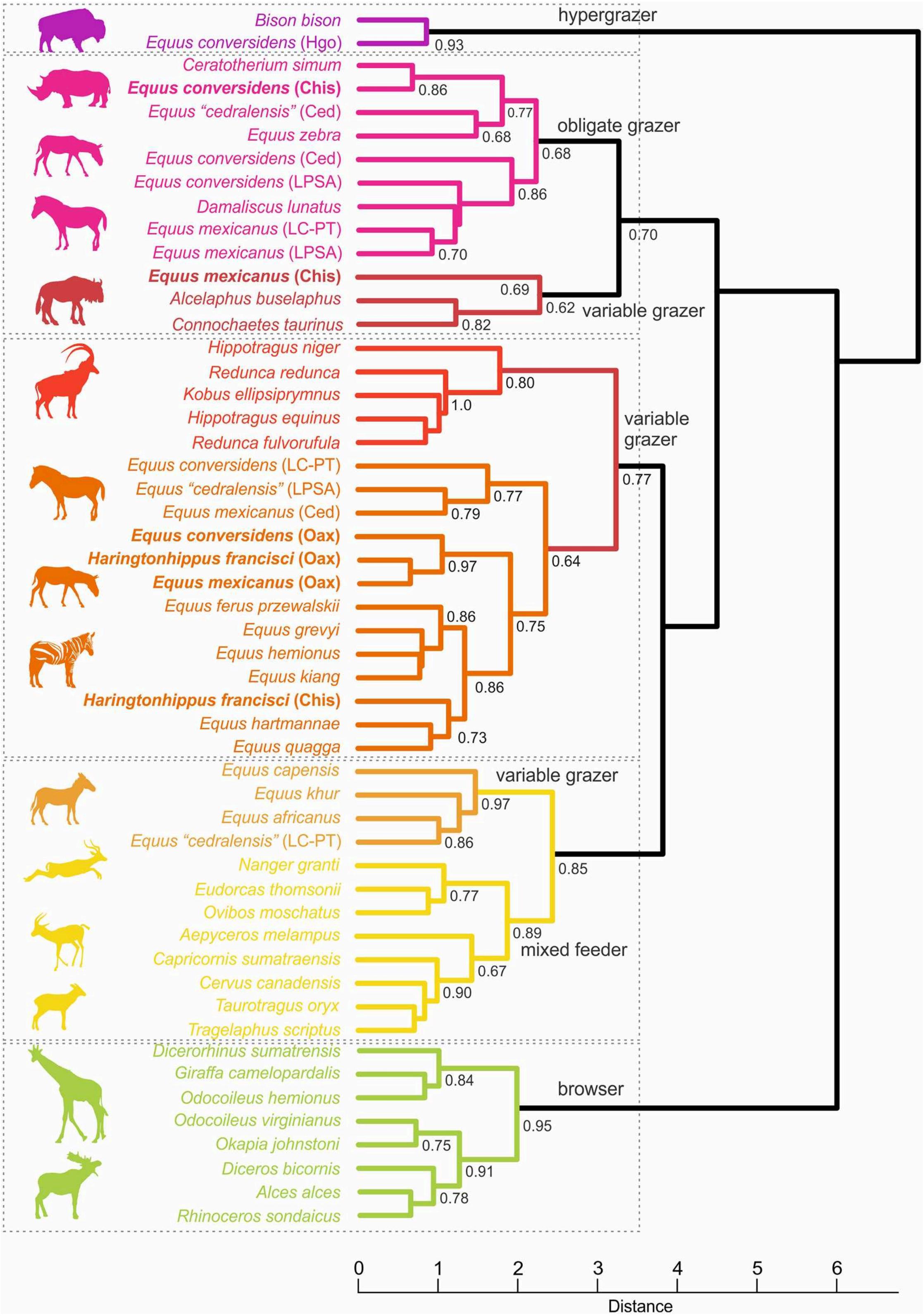

FIGURE 6 | Hierarchical cluster of the mesowear analysis of diverse extant and extinct equid species and other extant herbivorous mammals. The equid species of this study are in bold. Hgo, Hidalgo; Chis, Chiapas; Ced, Cedral locality in San Luis Potosí; LPSA, La Piedad de Santana locality in Michoacán; LC-PT, La Cinta-Portalitos locality in Michoacán; Oax, Oaxaca.

the samples are in the cluster of the extant mixed-feeders or typical browsers.

The Oaxacan samples of *Equus mexicanus, E. conversidens* and *H. francisci*, showed a comparable occlusal relief and commonly have rounded cusps. These samples are joined in a group (LD = 1.0), which in turn integrates a subcluster with the Przewalski's wild horse *E. ferus przewalskii*, the giant wild ass *E. kiang*, the onager *E. hemionus*, and the zebras *E. grevyi, E. hartmannae*, and *E. quagga* (LD = 28); in this subcluster is *H. francisci* from Chiapas (LD = 1.2) (**Figure 6**).

The sample of *Equus conversidens* from Chiapas is in the cluster of the obligate grazers. It is grouped with the white rhinoceros *Ceratotherium simum* (LD = 0.73), integrating a subcluster that includes *E. zebra* and *E. cedralensis* from Cedral in north-central Mexico. The sample of *Equus mexicanus* from Chiapas is grouped with the variable grazers *Alcelaphus buselaphus* and *Connochaetes taurinus* (**Figure 6**).

It is important to note that given the small teeth samples (n = 3) of *E. mexicanus* from Chiapas and *H. francisci* from Oaxaca, these results are preliminary.

In the discriminant function analysis, the sample of *E. conversidens* from Chiapas was classified as obligate grazer with a posterior probability of 100%, meanwhile that from Oaxaca was classified as variable grazer with a probability of 99% (**Figure 7**). *Haringtonhippus francisci* from Chiapas was classified as variable grazer with a probability of 90% and that from Oaxaca was classified in the same guild with 99%. The samples of *E. mexicanus* from Chiapas and Oaxaca were classified as variable grazers with a posterior probability of 60 and 99%, respectively (**Figure 7**).

The centroids of each dietary category showed statistically significant differences between groups (prob $> F \leq 0.0001$).

Estimated Body Mass

The estimated body masses of the equid species from Chiapas and Oaxaca are found in **Table S5**. The highest estimations are those based on the length of p4, whereas similar body mass estimations resulted with the measurements of the second upper and lower molar.

The lowest body mass estimations are those of *H. francisci* (167–251 kg) and the highest are those of *E. mexicanus* (305–458.21 kg); *E. conversidens* has intermediate mass estimations (242.71–326.48 kg). There is a difference of 75.8–193 kg between the body mass estimations of *E. mexicanus* and *E. conversidens*, and of 51.6–75.5 kg between the estimations of *E. conversidens* and *H. francisci* (**Table S5**).

DISCUSSION

Species Richness and Geochronology

Three horse species inhabited the territory that now constitutes the states of Chiapas and Oaxaca during the Late Pleistocene: the largest is *Equus mexicanus*, the medium-sized is *E. conversidens,* and the smallest is *H. francisci*.

The dating of several of the fossiliferous localities indicate that in Oaxaca, *E. conversidens* and *E. mexicanus* were present since at least 44,510–43,030 Cal BP, they were common between 30,123 and 19,584 Cal BP, and that *E. conversidens* persisted until 12,620–11,380 years BP. *Haringtonhippus francisci* was present in the Mixteca region of Oaxaca between 19,584 and 20,180 Cal BP. By the same token, the three identified equid species were present in Chiapas at least until 12,720 Cal BP.

The equids *E. conversidens* and *E. mexicanus* from Oaxaca are the oldest dated records in Mexico. Previously, both species were recovered from sediments that are around five meters above a 49,724 ± 2,074 Cal BP dated bed in Huexoyucán, Tlaxcala, in central Mexico (Tovar et al., 2013; Sánchez Salinas et al., 2016). *Equus conversidens, E. mexicanus*, and *E. cedralensis* have been recorded in sediments of around 24,000 Cal BP in La Cinta-Portalitos, west-central Mexico (Marín-Leyva et al., 2016; Díaz-Sibaja et al., 2018b), and they were also collected in beds bracketed by dates of 37,694 ± 1,963 years BP and 21,468 ± 458 Cal BP in Cedral, northern Mexico (Alberdi et al., 2014). Additionally, *E. conversidens* was recorded in strata having an age between 11,000 and 27,000 Cal BP in San Josecito Cave in northern Mexico (Arroyo-Cabrales et al., 1995; Arroyo Cabrales and Johnson, 2003), and it also has been collected in sediments that are three meters above a bed dated in 34,512 ± 220 Cal BP from Santa Cruz Nuevo, Puebla state, central Mexico (Tovar et al., 2014).

The dated record of *H. francisci* from Chiapas is the youngest in North America, since the Last Appearing Datum (LAD) from Eastern Beringia is 14.4 ^{14}C ka BP, the LAD in Gypsum Cave, Nevada is 13.1 ^{14}C ka BP (Heintzman et al., 2017).

Paleoecological Aspects

Dietary Guilds

The bootstrap values of the five main recovered clusters (hypergrazer, obligate grazer/variable grazer, variable grazer, variable grazer/mixed feeder, and browser) range from 0.70 to 0.95, whilst those for the Pleistocene equids from southern Mexico ranges from 0.62 to 0.97 (**Figure 6**); these values indicate a good nodal support for the recovered clusters, with the exception of 0.62, which can be considered as moderate (Zumel and Mount, 2014). Probably, the lower nodal support of 0.62 of *E. mexicanus* from Chiapas and the variable grazers is related to its small teeth sample (n = 3).

The Oaxacan samples of *Equus mexicanus, E. conversidens,* and *H. francisci* are clustered together and they integrate a subcluster with *E. ferus przewalskii, E. kiang*, *E. hemionus*, and the zebras *E. grevyi, E. hartmannae*, and *E. quagga*; in this subcluster also is *H. francisci* from Chiapas. The extant horses clustered with the Oaxacan samples are almost exclusively grazers, although the wild horse, the giant ass, and the onager can browse, whereas the zebras consume a wide variety of grasses (Kingdon, 2015; King et al., 2015). In the mesowear analysis of Schulz and Kaiser (2012), these extant equids cluster with the variable grazers *Alcelaphus buselaphus* and *Connochaetes taurinus,* but in our analysis both bovids formed a cluster with *E. mexicanus* from Chiapas; both bovids shows seasonal and geographical variability in their diet (Gagnon and Chew, 2000).

The sample of *E. conversidens* from Chiapas clusters in the obligate grazers (**Figure 6**), with the white rhinoceros *Ceratotherium simum*, integrating a subcluster that also includes

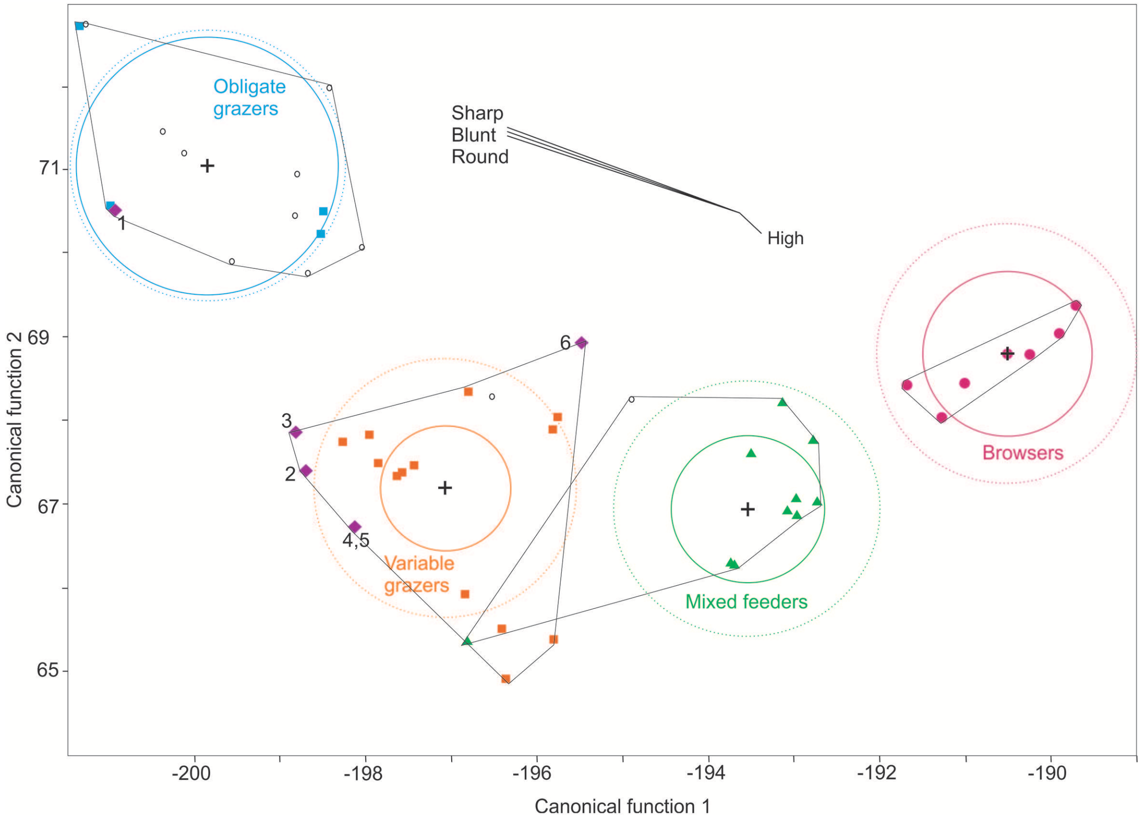

FIGURE 7 | Canonical plot of the discriminant analysis of the mesowear data used in this paper. Chiapas: 1. *Equus conversidens*, 3. *Haringtonippus francisci*, 6. *E. mexicanus*. Oaxaca: 2. *E. conversidens*, 4. *H. francisci*, 5. *E. mexicanus*. Obligate grazers, blue squares; variable grazers, orange squares; mixed feeders, green triangles; browsers, fuchsia dots. Open circles are the *Equus* species from central and northern Mexico. Crosses show the centroid of each dietary group. In each dietary category, the inner circle represents the 95% confident region that contain the true mean of the group; the exterior dotted circle represents the region estimated to contain the 50% of the population for that group. The biplot lines (High, Sharp, Blunt, Round) indicate the coordinate directions in canonical space. Convex hulls for each diet category are outlined. Canonical function 1 explains 84.88% of the variation and canonical function 2 explains 14.99%.

E. cedralensis from Cedral. In the contiguous cluster is *E. conversidens* from Cedral, *E. conversidens* from La Piedad-Santa Ana, *E. mexicanus* from La Cinta-Portalitos and *E. mexicanus* from La Piedad-Santa Ana. The white rhinoceros is a typical pure grazer that consumes short and tall grasses depending on the season (Macdonald, 2006).

In our cluster analysis, the extant abrasion-dominated grazer species are at one end of the dendogram and the attrition-dominated browsers are at the other end; two extant variable grazer species (*Equus africanus* and *E. khur*) clusters with the mixed-feeders and two other species (*Alcelaphus buselaphus* and *Connochaetes taurinus*) cluster with the obligate grazers; in between there is a cluster composed of exclusively variable grazers (**Figure 6**). *E africanus* and *E. khur* have a higher proportion of high valleys and sharp edges compared to *A. buselaphus* and *C. taurinus* (**Table S1**); this indicates that these *Equus* species have a less abrasive diet than the bovids.

The topology of our dendrogram seems to reflect how abrasive are the dietary resources taken by the considered ungulate species. Thus, *E. conversidens* from Chiapas should had a more abrasive diet that *E. mexicanus* from Chiapas, and both should have a more abrasive diet than the Pleistocene equids from Oaxaca; *H. francisci* from Chiapas should had the least abrasive diet (**Figure 6**).

As can be observed, the four Pleistocene equid species from Mexico show a dietary plasticity, they can be an obligate grazer in some regions of the country, or variable grazer in another regions (**Figure 6**).

Regarding the discriminant analysis, the results showed a high percentage of correct classification within dietary guilds (97.1%). After performing the cross-validation analysis this high percentage of correct classification persist (94%) (**Table S5**). Except for *E. conversidens* from Chiapas, the rest of the samples were classified as variable grazers (**Figure 7**), and as was previously mentioned, there are statistically significant differences between the centroids of each guild. *Equus mexicanus* from Chiapas was classified as a variable grazer with a probability of 60% and as mixed feeder with a probability of 40%. The mesowear signal of *E. conversidens* from Chiapas as an obligate grazer is consistent with the results obtained by stable isotopes (Pérez-Crespo et al., 2015).

The extinct species *Equus capensis* was classified as a mixed-feeder with a probability of 80%. Regarding the species from central Mexico, *E. cedralensis* from La Cinta-Portalitos was classified as a variable grazer (99% of probability), *E. conversidens* from La Cinta-Portalitos was classified as a grazer (77% of probability) or variable grazer (23% of probability). The rest of the species were classified as obligate grazers (probability of 92–100%). This is in accordance to what has been previously published of these species in other regions of Mexico (see **Table S1** for references).

Estimated Body Masses

The estimated body mass of *Equus mexicanus* from southern Mexico ranged from 305 to 458.21 kg, that for *E. conversidens* is 242.71–326.48 kg and the body mass of *H. francisci* ranged from 167 to 251 kg (**Table S6**). The estimated mean body size differences of these species are statistically significant for the M2 and p4 estimations (**Table S7**); the Mann-Whitney *U*-test could not be calculated with equation (2) given the small sample of m2's for *H. francisci* and *E. mexicanus*.

The mean estimated body mass based on M2 of *E. conversidens* is 23.52% less compared to that of *E. mexicanus*, and the estimated body mass of *H. francisci* is around 21% less than that of *E. conversidens*; for the mean body masses based on m2, the body mass of *E. conversidens* is 28.70% less than that of *E. mexicanus* and the one of *H. francisci* is 23% less than the one of *E. conversidens.*

Body mass is highly linked with the ecological adaptations such as diet of the herbivorous mammals (Maiorama, 1990); hence, the estimated body mass differences between the identified equid species from the Late Pleistocene of Chiapas and Oaxaca, probable diminished the resources competition between them, allowing to inhabit common areas, at least during some periods of time.

Here, estimated body masses values are like those previously reported for *E. conversidens* of 229.5 kg from La Piedad-Santana and 307.9 kg from La Cinta-Portalitos, and the body mass of *E. mexicanus* (476.7 kg) from La Piedad-Santana, in west-central Mexico, all based on measurements of postcranial bones (Marín-Leyva et al., 2016). These authors also reported a body mass of 126 and 145.5 kg for *E. cedralensis*, the other small-sized equid.

The body masses of the equids from Oaxaca and Chiapas are also like the previous estimations derived from Cedral specimens of northern Mexico: 354.33–532.28 kg for *E. mexicanus*, 215.63–282.52 kg for *E. conversidens,* and 91.83–169.59 kg for *E. cedralensis* (Alberdi et al., 2014).

Paleoenvironments and Habitats of Pleistocene Equids From Southern Mexico

Evidence for slickensides in the A horizon of Sandage locality of Coixtlahuaca, suggests that dry-wet seasonality was important around 30,000 CAL BP. A thick A horizon may reflect fast turnover typical of grasslands or result from a cumuli environment. Thick, dark A horizons with slickensides are characteristic of some Mollisols, which typically develop under grasslands, although in some cases they have been observed forming in marshes or under forests (Soil Survey Staff, 1999).

The textural features of the fossiliferous sediments from San Antonio Acutla, Santiago Teotongo and the sandy sediments of Tejupam, indicate that they were deposited as part of a perennial, very low energy fluvial system during some time; additionally, the presence of caliche or nodular calcretes in some beds suggests low humidity or precipitation during other times. By the same token, the silty clayey beds of Tejupam indicate the presence of some perennial water bodies (marshes) during some time intervals.

The associated fauna of San Antonio Acutla, Río Salado, and Tejupam localities of Oaxaca, include extant ostracod, charophyte and gastropod species that now live in quiet and shallow water, litter and deciduous forests (Pilsbry, 1946; Turthill et al., 1964; Schultz and Cheatum, 1970), salamanders that live in shallow ponds, with abundant aquatic vegetation (Duellman and Trueb, 1994); rodents that inhabit dry, semiarid hills to montane forests or deserts, salt marshes, and pine-oak forests (Davis and Follansbee, 1945; Webster and Knox, 1982; Fernández et al., 2010), open woodland or shrub vegetation types (Cornely and Baker, 1986).

This associated fauna suggests that in these Oaxacan fossil localities there were patchy habitats with grasses and weedy habitats, and temperate forests composed by conifer species with shrubs and grasses. Leaf litter allowed the conditions for terrestrial gastropods. Perennial or intermittent water bodies provided the habitat for the freshwater mollusks, which is also indicated by the stratigraphy. These heterogeneous habitats allowed the maintenance of diverse herbivore mammals, including the equids.

In Chiapas, the fine-grained fossil sediments of Los Mangos locality indicate that they were deposited in a water pond that later changed to a low flow fluvial regime. The associated *Glyptotherium* and *Neochoerus* suggest a perennial body water with subaqueous vegetation.

Geographic Distribution of Mexican Equids During the Late Pleistocene

The described equid species had a wide geographic distribution in Mexico during the Late Pleistocene, with most of the localities above 1,000 masl, in the Mexican highlands (**Figure 8**).

The climatic oscillations of the Late Pleistocene, as well as the rugged terrain of the Mexican highlands, generated heterogeneous habitats all along the country (Mastretta-Yanes et al., 2015); which, as was described before, in Chiapas and Oaxaca consisted of some areas with grasses, woodlands and forests, with fluvial systems and permanent water bodies during the last 44,000 years. These patchy habitats allowed a rich array of herbivorous and carnivorous mammals to inhabit in Mexico during the Pleistocene.

The geographic distribution of the Late Pleistocene equid fossil localities indicate that *Equus mexicanus*, *E. conversidens* and *H. francisci* could move across Mexico by the Rocky Mountains—Sierra Madre Occidental and the Transvolcanic Belt—Sierra Madre del Sur temperate corridors, and the Sonora—Central America Pacific lowlands and the Tamaulipas—Central America Gulf Lowlands tropical corridors (see Ceballos et al., 2010).

CONCLUSIONS

Three Pleistocene equid species were identified in southern Mexico, the largest is *Equus mexicanus*, the medium-sized is *E. conversidens* and the smallest is *H. francisci*. In Oaxaca

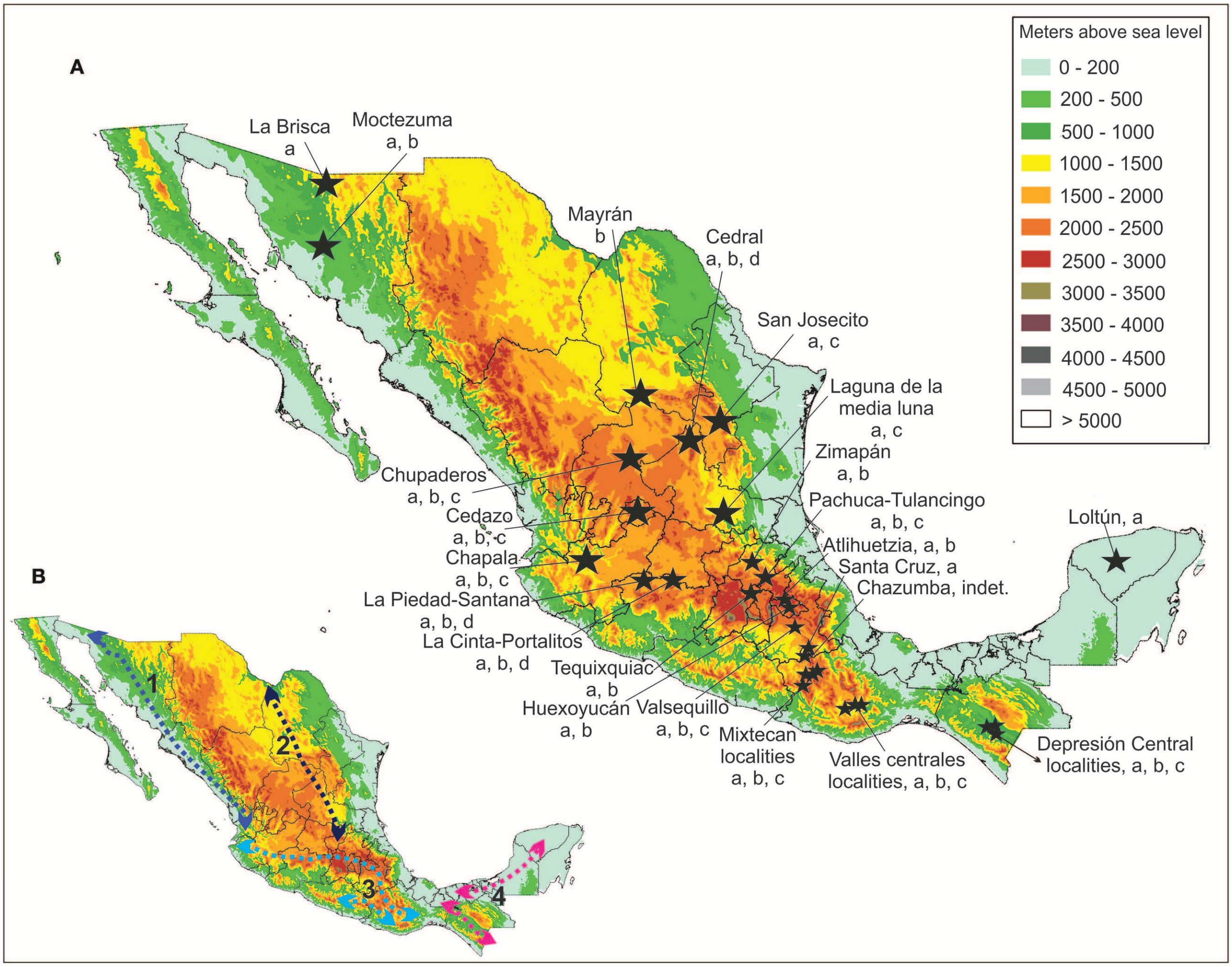

FIGURE 8 | (A) Main Late Pleistocene Mexican equid localities. a, *Equus conversidens*; b, *E. mexicanus*; c, *Haringtonhippus francisci*; d, *E. cedralensis*. Data from Priego-Vargas et al. (2017). **(B)** Mexican biogeographic corridors used by Pleistocene equids. 1. Sonora, Central America Pacific lowlands; 2. Rocky Mountains, Sierra Madre Occidental; 3. Transvolcanic Belt, Sierra Madre del Sur; 4. Tamaulipas, Central America Gulf Lowlands.

E. conversidens and *E. mexicanus* were present since at least 43,000 Cal BP years and *E. conversidens* persisted until 12,620–11,380 years BP. These three identified equid species were present in Chiapas at least until 12,720 Cal BP. The record of *H. francisci* from Chiapas is the youngest in North America.

The studied equid specimens from Chiapas and Oaxaca were mainly variable grazers, meanwhile those from central or northern Mexico were mainly obligate grazers. This indicates a dietary plasticity for *Equus mexicanus*, *E. conversidens,* and *H. francisci;* this plasticity has already been observed for the first two species in central and northern Mexico. In our analysis *H. francisci* from southern Mexico and *E. cedralensis* from Michoacan had similar dietary habits.

In southern Mexico, the identified equid species could move across the Transvolcanic Belt—Sierra Madre del Sur temperate corridor and the Tamaulipas—Central America Gulf Lowlands tropical corridor during the Late Pleistocene.

As in other regions of Mexico, these equids species were a common component of the Late Pleistocene landscapes of southern Mexico.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the manuscript/**Supplementary Files**.

AUTHOR CONTRIBUTIONS

EJ-H and GC-C conceived the study. EJ-H wrote the manuscript with the input of all the authors. RG-A, GC-C, EJ-H, produced the figures. EJ-H and GC-C measured the specimens. II-A and GH described the stratigraphy of the fossil localities and dated some localities. RG-A described the associated fauna and their habitat preferences. VB-C, GC-C, and EJ-H described and interpreted the mesowear cluster. EJ-H performed the discriminant analysis. All authors contributed to the interpretations of results and to editing of the text.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00394/full#supplementary-material

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The *Equus* Datum and the Early Radiation of *Equus* in China

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To approach a comprehensive understanding of the *Equus* Datum, we summarize the history of the study of Chinese fossil equids, from the "dragon bones" stage to scientific investigation, by Chinese, European and American people, and then review the stenonid species in China and discuss the phylogenetic relationships of early *Equus*. We conclude that there were at least two dispersal waves of *Equus* into the Old World from North America, and the second wave led to a radiation of the genus *Equus* in China. In China, the ages of the lower boundaries of the fossiliferous layers in classical Early Pleistocene faunal localities are all around 2.5 Ma (close to the age of the lower boundary of the Quaternary) according to magnetostratigraphic and biostratigraphic analyses. All of the geochronological results reveal China as an evolutionary center of *Equus* in Eurasia. In the late Neogene, the dominant equid lineage in China was Hipparionini. Even in the Pliocene, when hipparionines were not as widespread as before, there were still 5 genera and 7 species. In the Early Pleistocene, the hipparionines included only 2 genera and 2 species. In the meantime, global cooling caused Arctic ice sheets to form, lowering the sea level so that the Bering land bridge fell dry and allowed *Equus* to disperse into China. The rise of *Equus* was accompanied by the recession of hipparionines. The dispersal and radiation of *Equus* in China were not a coincidence, but a complicated process of adaptation and competition, and a comprehensive outcome of significant climatic, tectonic and biotic events.

Keywords: *Equus* Datum, stenonid, evolution, environment change, paleozoogeography

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INTRODUCTION

The *Equus* Datum, the first appearance of *Equus* in the Old World, was a remarkable biotic event in the Quaternary. It has often been used as a marker of the lower boundary of the Quaternary. This biotic event was contemporary with other important geologic and environmental events. *Equus* fossils are critical research material for studies on evolutionary, climatic, and environmental changes during the Quaternary in Eurasia (Deng and Xue, 1999a). Therefore, fossil *Equus* are essential for elucidating the Pleistocene paleobiology and paleoenvironment in Eurasia.

Chinese people were the first to obtain and utilize *Equus* fossils. Since historical times in China, vertebrate fossils, which were called "dragon bones," have been used as pharmaceutical material. The "dragon bones" include *Equus* skeleton fossils. Fossil teeth of *Equus* are also regarded as pharmaceutical material and called "dragon teeth." To review the history of paleontological research in Yushe Basin, Shanxi Province, Qiu and Tedford (2013) investigated historical records of "dragon bones" in the Shanxi area from ancient Chinese literature.

They consulted Li Shizhen's famous "Compendium of Materia Medica" and found that the first reliable record of "dragon bones" as pharmaceutical material was in a lost medical book written by Lei Xue, who lived in the Song Dynasty (420–479 A.D.) of the Southern Dynasties. According to Tao Hongjing (456–536 A.D.), who lived in the Liang Dynasty of the Southern Dynasties, the Shanxi area was listed as the only place of origin for "dragon bones." Finally, they concluded that the earliest reliable history of "dragon bones" can probably be traced to the fifth century, at least for Shanxi Province.

However, actual recognition of fossil *Equus* still depends on scientific observations and descriptions, which were initiated hundreds of years later by Western scholars. Matsumoto (1915) erected a new species, *E. leptostylus*, based on an isolated upper premolar from the Yinxu site, although this species was soon after considered invalid. However, the critical specimens for the *Equus* Datum date to the Early Pleistocene, which is when *Equus* invaded Eurasia. Later, they were called stenonid horses (see below). Vertebrate paleontologists from Europe and the United States began to study early *Equus* from China in the early twentieth century. Teilhard de Chardin and Piveteau (1930) reported the classic Pleistocene mammalian fauna, the Nihewan Fauna from Yangyuan, Hebei Province, and erected *Equus sanmeniensis*, which was the first named Chinese stenonid species. Zdansky (1935) first published a monograph of *Equus* in China based on the abundant specimens of the Lagrelius Collection housed in Uppsala, which were collected from Hebei, Henan, Shanxi, and Shandong by Andersson. Zdansky identified all stenonid specimens in this fossil series as *Equus* cf. *sanmeniensis*. Hopwood (1936) divided Eurasian *Equus* into caballines and zebrines. Early *Equus* species were considered zebrines, because they had a V-shaped linguaflexid like extant zebras. Colbert (1940) studied the *Equus* specimens collected from Yuanmou, Yunnan, by the Central Asiatic Expeditions research team of the American Museum of Natural History and erected *Equus yunnanensis*. He concluded that this new species was identical to the Pleistocene *Equus* from the upper Irrawaddy of Myanmar and was similar to the Pleistocene *Equus* of India in certain features. Eisenmann (1975) rediscovered *E. sanmeniensis* specimens in the Nihewan Fauna, which was divided into two different forms based on size by Teilhard de Chardin and Piveteau (1930). She erected a new species, *Equus teilhardi*, for the small form, and argued that in addition to its small size, its lack of an incisor cup distinguished it from other *Equus* species.

After 1949, as the economy was rebuilt and science progressed, Chinese scholars began to research early *Equus*. Chow and Liu (1959) described cheek tooth specimens of *Equus* collected from Pinglu, Shanxi Province, and erected a new species, *Equus huanghoensis*. Pei (1961) reported new specimens of *E. yunnanensis* collected from Yuanmou, Yunnan Province, and *Gigantopithecus* Cave in Liucheng, Guangxi Province. Liu (1973) reported a mandible specimen of *Equus* in Locality 1 of Zhoukoudian; he identified it as *E. sanmeniensis* and thus extended the last occurrence of this species to the Middle Pleistocene. Liu and You (1974) described much better specimens of *E. yunnanensis* than previously discovered, which included a skull and mandible. Forsten (1984) proposed a "stenonid pattern" to describe the V-shaped linguaflexid when she discussed the supraspecific classification of the Old World hipparionines. The term "stenonid" references *E. stenonis*, which was the first erected species among early *Equus*, and gradually came to be used as a generic term for early *Equus*, especially by the authors of certain extensive review publications (Alberdi et al., 1998; Deng and Xue, 1999a).

Deng and Xue (1999b,c), respectively, erected two new species, *Equus qingyangensis* and *Equus wangi*, based on the specimens collected from Bajiazui, Qingyang, Gansu. In the same year, they also published the most comprehensive review of early *Equus*, or stenonids: the monograph Chinese Fossil Horse of *Equus* and Their Environment (Deng and Xue, 1999a). Qiu et al. (2004) reported a new Pleistocene mammalian fauna, the Longdan Fauna, from Dongxiang, Gansu Province. They erected *Equus eisenmannae* based on the large equid form in this fauna. Dong and Fang (2005) reported some fragmented cranial specimens of *E. huanghoensis* found from Tangshan, Nanjing, Jiangsu Province, and supplied some important features of *E. huanghoensis*. Li et al. (2016) reported the most complete fossil record yet known of *E. huanghoensis*, which included a skull associated with a mandible from Yangshuizhan in Yangyuan, Hebei Province. Sun et al. (2017) rediscovered a skull and mandible in the Lagrelius Collection from Qixian, Shanxi Province, which was previously identified as *E.* cf. *sanmeniensis* by Zdansky (1935). They identified the skull and mandible, respectively, as *E. teilhardi* and *E. qingyangensis*.

In this article, we will review all the known stenonid species on the robust basis of our predecessors. We will reorganize all important information about these species, explore their early evolution, and further elucidate the *Equus* Datum.

MATERIALS AND METHODS

For phylogenetic analysis, we reorganized the data matrices from previous publications and summarized them in a new data matrix, which includes 16 taxa, and 53 characters. The phylogenetic analysis were performed using TNT 1.1 with a traditional search method (Goloboff et al., 2008), 1,000 replications and the trees-bisection-reconnection branch-swapping algorithm (TBR) applied in our analysis. All characters are equally weighted and additive. Gaps are treated as "missing" and multistate taxa interpreted as polymorphism. The resulting strict consensus tree is presented in **Figure 1**. Character list and data matrix are presented in the **Supplementary Information**.

Abbreviations: IGF, Instituto geologico di Firenze, Florence, Italy; IVPP V, vertebrate paleontology collection of Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NHMUK PV M, cast at the Natural History Museum, London, UK; NIH, Nihewan collection of the Muséum national d'Histoire naturelle, Paris, France; NWUV, Institute of Cenozoic Geology and Environment, Northwest University, Xi'an, China; PMU M, Museum of Evolution of Uppsala University, Uppsala, Sweden; THP, Tianjin Natural History Museum, Tianjin, China.

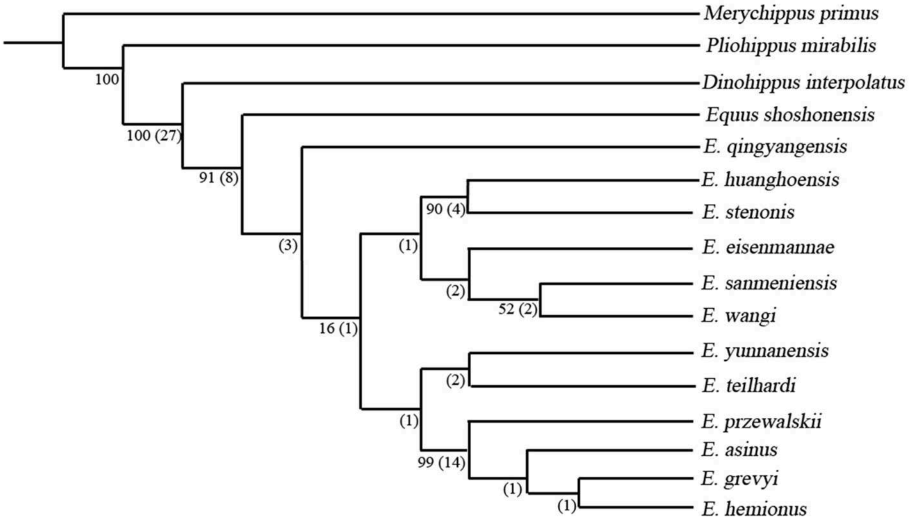

FIGURE 1 | Most parsimonious tree (MPT) obtained from phylogenetic analysis, Tree length = 148, consistency index = 0.635, retention index = 0.768. Numbers by the nodes denote the Bootstrap (outside brackets, not shown if value < 50) and Bremer values (in brackets, not shown if value < 1).

SYSTEMATIC PALEONTOLOGY OF STENONIDS IN CHINA

We review all of the stenonids species in China in the order in which they were erected. All discussions are based on the classical descriptions and the most recent reports. The main localities of stenonids are shown in **Figure 2**.

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Genus *Equus* Linnaeus, 1758
Equus stenonis Cocchi, 1867

Holotype: IGF—560, adult skull with mandible, collected from the Lower Pleistocene of the upper Arno valley in Italy.

Diagnosis (following Deng and Xue, 1999a): large size, facial angle is very narrow, well-developed preorbital pit retained, deep groove along nasal suture, lateral outline of skull undulated, domed parietal, frontal also undulated laterally. DP1 present, diastema elongated, protocone short, hypocone extends lingually, plications complex. Linguaflexid sharply V-shaped, cup on lower incisor developed. Snout elongated, nasal notch very deep, its posterior margin is at the level of mesostyle or even the posterior margin of P3, and the anterior foramen of the palatine canal is open to the level of M3.

Age: Nihewanian, Early Pleistocene.

Distribution: Eurasia and North America.

Remarks: *Equus stenonis* was the first erected stenonid species (**Figure 3**). This species has been studied for a long time, and there is an abundance of specimens. Its fossil record is widespread in Eurasia, and there are many recognized subspecies, although some of them have been upgraded to species, such as *E. livenzovensis* (Alberdi et al., 1998). However, a definite record of *E. stenonis* in China was obtained late.

Azzaroli (1982) observed a skull collected from Taigu, Shanxi Province, that is housed in the Frick Collection in the AMNH. He identified this skull as *E. stenonis*. This is the earliest formal report of *E. stenonis* in China. Forsten (1986) studied the specimens collected from Taigu that are housed in the Licent Collection in the THP. She argued that the protocones of the Taigu specimens were longer than *E. stenonis* material from any locality in Europe, so the Frick specimen should not be considered this species. Azzaroli (1987) argued that the locality information of the Licent specimens was not clear and not comparable to the Frick specimen. Deng and Xue (1999a) observed the Frick specimen based on plate published by Azzaroli (1982) and recognized that many features indeed belonged to *E. stenonis*.

Azzaroli et al. (1988) proposed that *E. stenonis* dispersed into Europe about 2 Ma and survived until the end of the Early Pleistocene at 1 Ma. Deng and Xue (1999a) considered *E. stenonis* to be the probable ancestor of *E. stehlini* and *E. bressanus*, which are both common fossil equids found in Europe. Deng and Xue (1999a) described a molar of *E. stenonis* from Xinyaozi Fauna in Tianzhen, Shanxi and they noted that the age of the Xinyaozi Fauna was older than that of the Nihewan Fauna s. s. Azzaroli and Voorhies (1993) proposed that the North American subspecies *E. stenonis anguinus* occurred about 2 Ma. Therefore, the earliest record of *E. stenonis* known so far is in China, which was probably the center of origin of this species.

Equus sanmeniensis Teilhard de Chardin and Piveteau, 1930

Lectotype: NIH 002 (**Figure 4**), aged adult skull with mandible, collected from Nihewan, Yangyuan, Hebei Province, formally assigned by Eisenmann (1975).

Diagnosis (following Deng and Xue, 1999a): giant build, skull elongated, basal narrow and short so it shown an elongated snout with narrow frontal, DP1 stably present. Protocone elongated

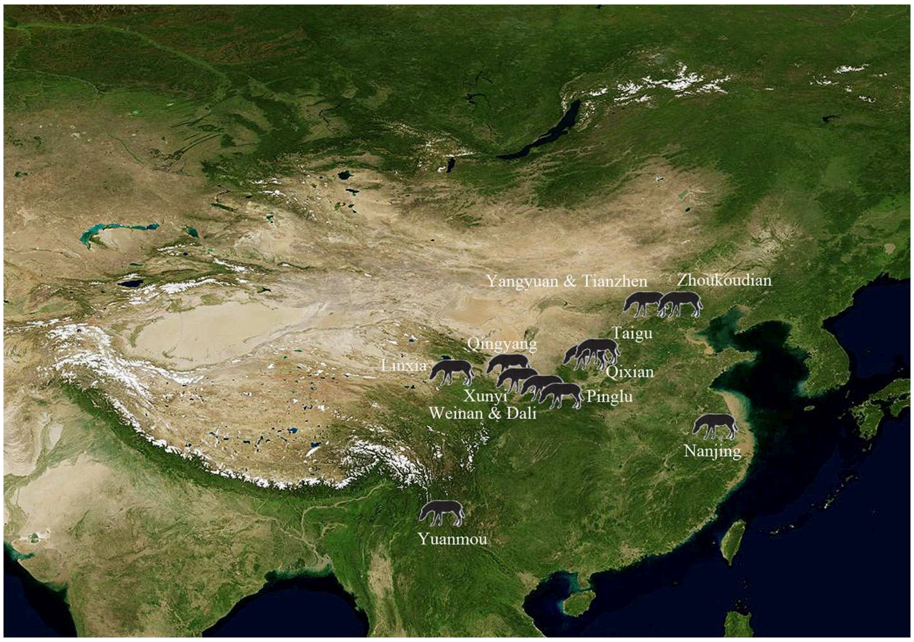

FIGURE 2 | Main localities of stenonids in China.

FIGURE 3 | Right lateral view of cast of holotype skull with mandible of *E. stenonis*, NHMUK PV M 29511.

FIGURE 4 | Right lateral view of lectotype skull of *E. sanmeniensis*, NIH 002, collected from Nihewan Basin.

and concave lingually, labial margins of para- and mesostyle often concave, pli caballine strong, but often diminished to absent by wear, M3 has isolated enamel ring and double-angled occlusal surface. Linguaflexid V-shaped, ectoflexid deep, penetrating into the isthmus, even touching the linguaflexid on lower molars, making lingual margin of linguaflexid and labial margin of ectoflexid flat. Plications complex, but often diminished to absent by wear.

Age: Nihewanian–Zhoukoudianian, Early to Middle Pleistocene.

Distribution: North and Northwest China, Siberia, probably Tajikistan.

Remarks: Teilhard de Chardin and Piveteau (1930) erected the first stenonid species in China, *E. sanmeniensis*. This species was distributed in northern China, Siberia, and Tajikistan from the Early to Middle Pleistocene (Deng and Xue, 1999a). This species evolved early, and was an outcome of the diversification of *Equus* that dispersed into Eurasia approximately 2.5 Ma (see below). *Equus sanmeniensis* has primitive features similar to the earliest *Equus* species in North America, *E. shoshonensis*, such as a transversely undulated lateral outline of skull, groove along the nasal suture, elongated facial part, and obvious preorbital pits. However, *E. sanmeniensis* differs from *E. stenonis* by having a less deep nasal notch and an elongated protocone. All of these features indicate that *E. sanmeniensis* and *E. stenonis* share derived features inherited from some common ancestor type, which most likely lived in North America, but they evolved along different trajectories. Therefore, we conclude that *E. sanmeniensis* and *E. stenonis* underwent parallel evolution, and they have a close but not an ancestor-descendant relationship. Early on, authors tended to identify more stenonid specimens as *E. sanmeniensis*. Teilhard de Chardin and Piveteau (1930) described all *Equus* species they found in the Nihewan Fauna as *E. sanmeniensis*, even though they noticed that there were two different types of specimens. Zdansky (1935) identified all of the stenonid specimens in his study as *E.* cf. *sanmeniensis*. Some of these have been revised (Eisenmann, 1975; Sun et al., 2017); however, we believe that lots of specimens of other stenonid species are still considered *E. sanmeniensis*.

Equus yunnanensis Colbert, 1940

Lectotype (assigned by Deng and Xue, 1999a): IVPP V 4250.1, female skull, about 7–8 years old, extrusion-deformed, well-preserved except for a little damage.

Paralectotype: IVPP V 4251, senile male mandible, coronoid process damaged. All of type specimens are collected from Madahaixigou, Youmou, Yunnan.

Diagnosis (following Deng and Xue, 1999a): Medium size, skull relatively large, frontal narrow, snout elongated. Lingual margin of I3 not enclosed, size of cheek teeth and length of protocone medium, enamel plications usually strong, linguaflexid V-shaped, metaconid and metastylid very rounded, ectoflexid shallow, rarely penetrates into the isthmus even on lower molars, pli caballinid not strong, posterior tip of m3 halberd-shaped. Distal limb robust.

Age: Nihewanian to Salawusuan, Early to Late Pleistocene.

Distribution: Yuanmou, Yunnan; Liucheng, Guangxi; Jianshi and Enshi, Hubei; Hanzhong, Shaanxi; Huili, Sichuan; Irawaddy, Myanmar.

Remarks: Colbert (1940) erected *E. yunnanensis* based only on isolated cheek teeth. Therefore, it was difficult for researchers to conduct enough work on morphology of this species. Fortunately, Liu and You (1974) discovered and reported well-preserved cranial and limb specimens from Yuanmou Basin. They observed much more morphological information than Colbert (1940) and further discussed the relationships of Asian *Equus*. They argued that *E. yunnanensis* should be considered a separate lineage distinct from other species in South Asia. They suggested that *Equus* sp. found in Huili, Sichuan Province, was likely derived from *E. yunnanensis*. Therefore, this lineage seemed to have dispersed to the north. Deng and Xue (1999a) thought that *E. yunnanensis* and *E. wangi* were closely related because they shared similar derived features, such as rounded double-knots and short ectoflexids. Pei (1961) noted that *E. yunnanensis* was an equid species similar to asses and horses based on its short ectoflexid. Deng and Xue (1999a) argued that short ectoflexids should not be thought to be particular to asses, because other equids, such as *E. wangi* and *E. przewalskii*, also have this feature. Based mainly on rounded double-knots and short ectoflexids, Deng and Xue (1999a) considered these species sister-groups. Gromova (1949) and Deng and Xue (1999a) both suggested that the different dental features, such as the morphology of enamel plications on the upper cheek teeth, were adaptations to different environments. As an increasing number of specimens have been discovered, the arguments regarding phylogenetic relationships were revised in recent years. We propose some new ideas about the relationship between *E. yunnanensis* and other stenonid species below.

Equus huanghoensis Chow and Liu, 1959

Holotype: IVPP V 2385–2389, three upper premolars and two upper molars, collected from bank of Yellow River (Huanghe) in Sanmenxia, Pinglu, Shanxi Province.

Diagnosis (following Li et al., 2016): Large skull with elongated face and snout; outline of parietal part undulated as seen in lateral view. Nasal-frontal-parietal part with hollow in middle part and upturned anterior end, middle groove of nasal bone narrow. Nasal notch deepens to reach level of boundary of P3/P4. Orbit posterior of cheek teeth row, anterior foramen of palatine canal opens posteriorly; interalveolar margin long. Occipital plane pentagonal, and supramagnum protuber strong. Protocone shortened, mesostyle robust, pli caballine very weak, and plication simple. Mandible elongated. Condyle of mandible elongated transversely with rounded anterior margin and cupped internally posterior margin. Cups of lower i3 enclosed, pli caballinid weak to absent, enamel plication of post-flexid strong, and linguaflexid V-shaped. **Locality and age:** Nihewanian, Early Pleistocene. **Distribution:** Nihewan, Hebei; Linyi, Shanxi; Sanmenxia, Pinglu, Shanxi; Xunyi, Shaanxi; Nanjing, Jiangsu.

Remarks: Chow and Liu (1959) erected *Equus huanghoensis* based on five isolated upper cheek teeth collected from Sanmenxia, Pinglu, Shanxi Province. Forsten (1986) reviewed numerous classical specimens of Chinese fossil *Equus*. She identified a skull from the Lagrelius Collection in the Museum of Evolution, Uppsala University, as? *Equus huanghoensis* based on the very short protocone of this specimen. Deng and Xue (1999a) described *E. huanghoensis* specimens from Xunyi, Shaanxi Province, and stated that *E. huanghoensis* is primitive because of its very short protocone, and further identified this species as a stenonid. Dong and Fang (2005) reported some fragmented cranial material of *E. huanghoensis* from Tangshan, Nanjing, Jiangsu Province. Li et al. (2016) reported the most complete material ever known of *E. huanghoensis* from Nihewan, Yangyuan, Hebei Province, which included a complete skull with a broken mandible, and described all of the critical features of this species (**Figure 5**). *Equus huanghoensis* is a very large stenonid species with deep nasal notch, lower cranial proportion, elongated snout and facial part, and V-shaped linguaflexid. All of these features supported Deng and Xue's argument that *E. huanghoensis* is a stenonid species. Based on the measurements of Nihewan material, *E. huanghoensis* is one of the *Equus* species with the largest absolute and relative palatal lengths, and is similar to *E. eisenmannae*, which was the largest *Equus* species in China (Qiu et al., 2004; **Figure 6**). Deng and Xue (1999a) suggested that the age of *E. huanghoensis* was in the Early Nihewanian (2.5–1.8 Ma). Ao et al. (2013b) suggested that the age of the *E. huanghoensis* specimens from Nihewan was around 1.7 Ma. This is the youngest record of *E. huanghoensis* ever known in China. In addition, the Nihewan material is smaller compared with the holotype from Sanmenxia. Li et al. (2016) indicated that the P4 and M2 lengths of the holotype are around 1.16 times larger than those of the Nihewan specimen. The ratio between the length of the basilar and cheek tooth row is generally stable in *Equus* (**Figure 7**). Based on this ratio, the holotype teeth should belong to a very large individual whose basilar length was 647.28 mm, in contrast with that of *E. eisenmannae* (625 mm, Qiu et al., 2004).

Equus teilhardi Eisenmann, 1975

Holotype: NIH 001, a broken mandible with symphysis and left ramus.

Diagnosis (following Sun et al., 2017): Middle size. The nasal notch extends above the mid-P2 to the boundary of P2/P3. Snout short, preorbital fossa shallow with indistinct border, lateral outline is undulated, deep groove along nasal suture. Cups of incisors possibly incomplete or even lacking. The upper cheek teeth have simple fossettes, short protocones and weak plis caballines. The lower cheek teeth have V-shaped linguaflexids and deep ectoflexids on molar that penetrate into the isthmuses, even touching the linguaflexids on the lower molars. The limb bones are short and robust. **Distribution:** Northwestern and northern China. **Age:** Nihewanian, Early Pleistocene.

FIGURE 5 | Left lateral view of skull of *E. huanghoensis*, NWUV 1403.1, collected from Yangshuizhan Locality, Nihewan Basin. Scale bar = 5 cm.

Remarks: When Teilhard de Chardin and Piveteau (1930) erected *E. sanmeniensis*, they recognized two forms of Nihewan specimens with different body sizes. However, they did not resolve this issue and still identified all specimens as *E. sanmeniensis*. In Zdansky's study on Chinese fossil *Equus*, he described many specimens with different features and from different localities as *Equus* cf. *sanmeniensis*. Later, when Eisenmann studied Nihewan equids housed in Paris, she erected *E. teilhardi* based on a broken mandible. Eisenmann (1975) only listed two features in the diagnosis: small size and lack of lower incisor cup. Forsten (1986) studied the equid materials of the Nihewan fauna collected by Licent and identified two fragmented cranial specimens (THP 00150, 00151) as *E. teilhardi*. She proposed many important features for cranial and dental morphology. Deng and Xue (1999a) described a left ramus fragment (NWUV 1243) from Bajiazui, Qingyang, Gansu Province. They focused on the absence of a cup on the lower incisor of *E. teilhardi* and argued that this species should be regarded as a lineage distinct from other Eurasian stenonids. Sun et al. (2017) reviewed the equid specimens in the Lagrelius Collection described by Zdansky (1935) and recognized a skull from Qixian, Shanxi Province, as *E. teilhardi* (**Figure 8**). The features of this skull are basically identical to those described by Forsten. Based on measurements of Qixian material, Sun et al. (2017) noted that *E. teilhardi* had relatively shorter distal limbs

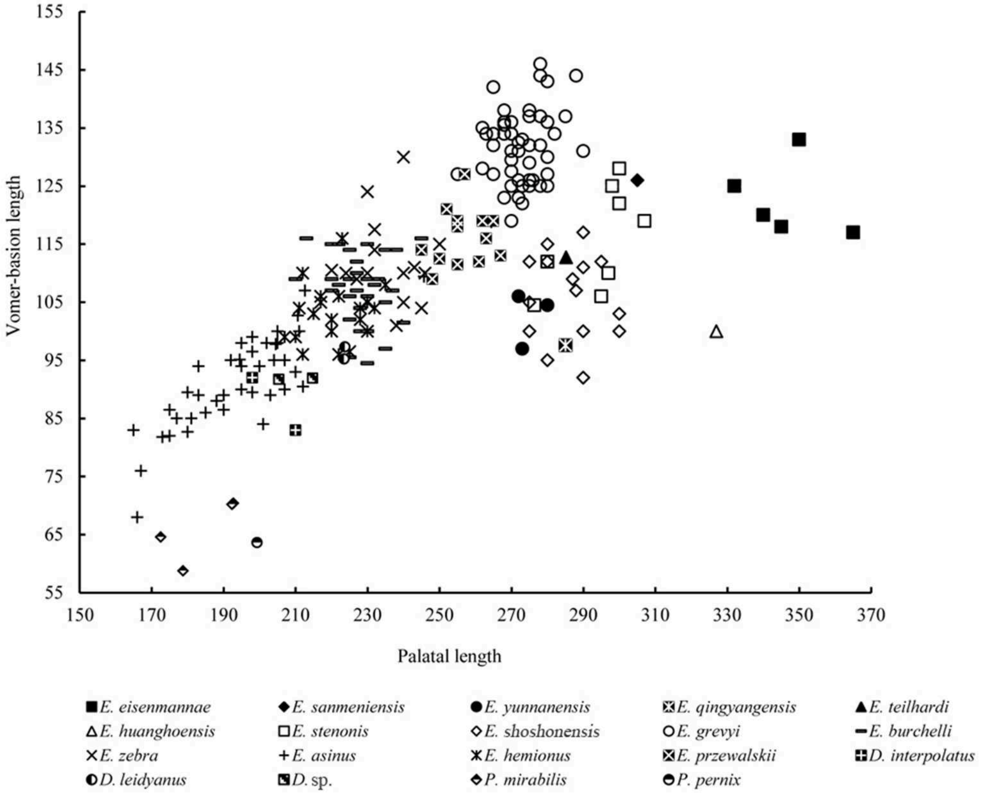

FIGURE 6 | Comparison of lengths of palatine and basicranial in several extinct and extant species of Equidae. Abbreviations of genera: *E*, *Equus*; *D*, *Dinohippus*; *P*, *Pliohippus* (same in below).

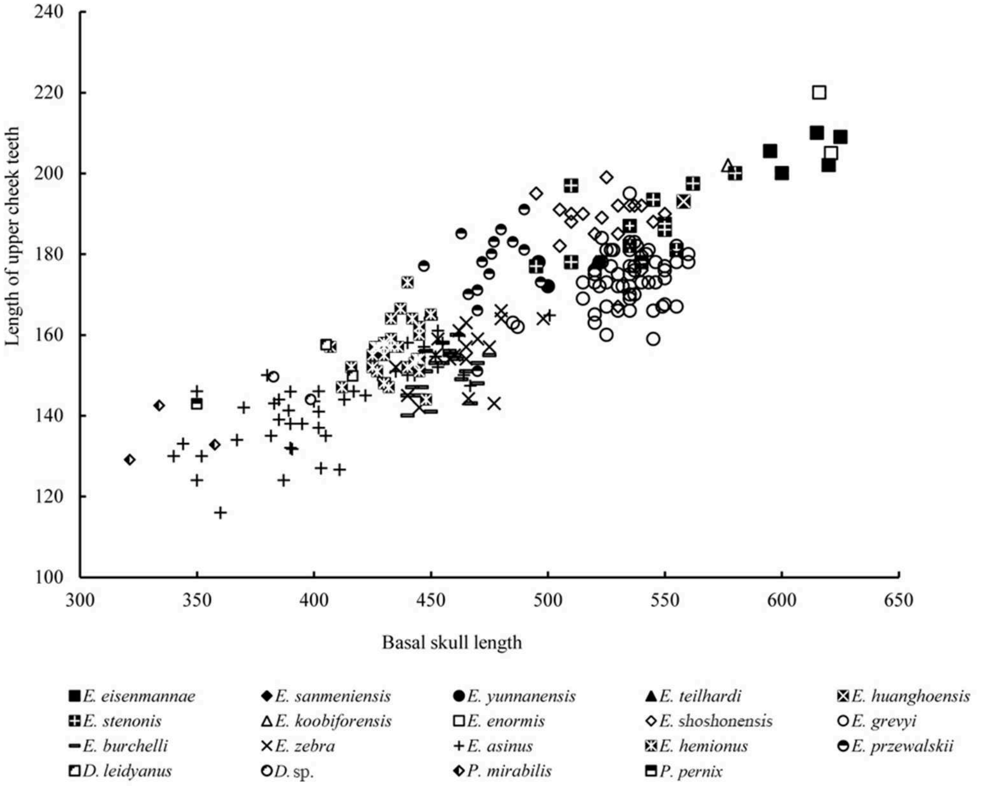

FIGURE 7 | Comparison of cheek tooth row length and basilar length in several extinct and extant species of Equidae.

FIGURE 8 | Left lateral view of skull of *E. teilhardi*, PMU M 1321, collected from Qixian, Shanxi, housed in Museum of Evolution, Uppsala University. Scale bar = 5 cm.

than most Eurasian stenonids. Additionally, based on the I3 character of Qixian material and observation of other early *Equus* specimens, such as *E. shoshonensis* in the Hagerman Collection, Sun et al. (2017) argued that the lack of a lower incisor cup of *E. teilhardi* was due to variation. Some European stenonid horses, such as *E. stehlini*, also have incomplete lower incisor cups (Azzaroli, 1965, 1982). Based on skull and post-cranial morphology, Sun et al. (2017) hypothesized that *E. teilhardi* and *E. yunnanensis* were probably closely related.

Equus qingyangensis Deng and Xue, 1999b

Holotype: NWUV 1128, the middle and back of a skull with all cheek teeth, about 12 years. **Diagnosis:** Medium size. Nasal notch extends above back of P2, preorbital pit is shallow with indistinct border, deep groove along the nasal suture. The upper teeth have long protocones and weak plis caballines. The lower teeth have typical V-shaped linguaflexids and deep ectoflexids that penetrate into the isthmuses or even touch the linguaflexids on the lower molars. The limb bones are slender. The metacarpal middle shaft index is smaller than 13.5 and the metatarsal smaller than 12.0. It was the early species of *Equus* with the most slender limb bones in Eurasia. **Distribution:** Northwestern and northern China. **Age:** Nihewanian, Early Pleistocene.

Remarks: Deng and Xue (1999b) erected a new stenonid species, *E. qingyangensis*. According to their description, although *E. qingyangensis* is morphologically similar to *E. sanmeniensis*, except for the large body size of the latter, *E. qingyangensis* has some impressive features that have never been found in known stenonid horses in China. For example, its skull has about a 12 mm distance between the temporal condyle and the posterior margin of the orbital bar (Deng and Xue, 1999a). This is a primitive feature because of its presence in the hipparionine genus *Proboscidipparion* (Qiu et al., 1987), and in some primitive equid species, based on our observation, such as *Pliohippus*. In contrast, these two constructs are adjacent in most extinct and extant *Equus* species. The Mc III of *E. qingyangensis* is more slender than those of all known stenonid horses, with a middle shaft index of 13.3 (Deng and Xue, 1999a). Eisenmann and Deng (2005) collected measurements of *E. qingyangensis*, other Eurasian stenonids, and North American early *Equus*, and conducted a series of statistical analyses. They concluded that *E. qingyangensis* are similar to *E. shoshonensis* but different from *E. stenonis* based on cranial and post-cranial proportions. Our plot also shows that *E. qingyangensis* has very low ratio of cranial part (**Figure 9**), which has been regarded as a primitive feature (Qiu et al., 2004). Sun et al. (2017) found a similar phenomenon. Based on observation of the Hagerman Collection, they indicated that *E. shoshonensis* also have about a 10–12 mm distance between the temporal condyle and the posterior margin of the orbital bar, which is identical to that of *E. qingyangensis*. Eisenmann and Deng (2005) argued that *E. shoshonensis* and *E. qingyangensis* probably have a direct ancestor-descendant relationship and represent a lineage that is distinct from the Eurasian species *E. stenonis*. Sun et al. (2017) also hypothesized that *E. qingyangensis* may be a direct descendant of *E. shoshonensis* and the earliest and most primitive stenonid species in Eurasia.

Equus wangi Deng and Xue, 1999c

Holotype: NWUV 1170, complete upper and lower cheek tooth rows that belong to an individual, and the upper tooth rows go with the remains of the maxillae, about 5 years.

Diagnosis: Teeth are very large. DP1 present. Protocones long, narrow and middle-grooved. Mesostyles flat or lightly middle-grooved. Enamel plications strong, especially on the premolars. Hypoconal grooves on premolars with flat bottoms. The m3 has a double-angled back margin and an enamel lake within its hypocone. The double–knots are very circular so that their metastylids do not have posterior angles. Linguaflexids wide and sharply V-shaped. Ectoflexids shallow so that they never penetrate into isthmuses even on molars, and post-flexids correspondingly long. Plis caballinid much developed. Enamel plications of post-flexids strong. Entoconids on premolars with sharp beak-shaped ends. Hypoconulid on m3 like a short dagger with a wide and round end.

Distribution: Qingyang, Gansu.

Age: Nihewanian, Early Pleistocene.

Remarks: Deng and Xue (1999c) erected a new species, *E. wangi*, based on cheek tooth rows and a cranial fragment from Bajiazui, Qingyang, Gansu Province. They estimated that this species has a deep mid-nasal groove and preorbital pit based on the broken skull. The cheek tooth size of *E. wangi* is very large, similar to *E. sanmeniensis*, *E. huanghoensis*, and *E. eisenmannae*. However, *E. wangi* has obvious morphological differences from *E. sanmeniensis* and *E. huanghoensis*. *Equus wangi* has features in common with *E. yunnanensis*, such as circular metastylids and shallow ectoflexids (Deng and Xue, 1999a). Qiu et al. (2004) noted that *E. eisenmannae* has many characters in common with *E. wangi*, including large cheek teeth, short plis caballine, simple mesostyles, strong enamel plications, rounded double-knots, shallow ectoflexids, and elongated post-flexids. Another unusual feature of *E. wangi* is its beak-shaped entoconid. According to Qiu et al. (2004) and Wang and Deng (2011), *E. eisenmannae* also has similar lower premolar structures. Therefore, *E. wangi* is probably more closely related to *E. eisenmannae* than other stenonid species. In addition, *E. wangi* is similar to *E. shoshonensis* from Hagerman, Idaho, USA based on its very circular double-knot, beak-shaped premolar, and sharp V-shaped linguaflexid (Deng and Xue, 1999a). *Equus shoshonensis* was the earliest *Equus* species, whereas *E. yunnanensis* and *E. eisenmannae* occurred during the beginning of the Quaternary in China. Consequently, *E. wangi* should be a very primitive lineage. Deng and Xue suggested that first occurrence of *E. wangi* was between 2.5 and 2.4 Ma.

Equus eisenmannae Qiu et al., 2004

Holotype: IVPP V13552, a complete adult and male skull (**Figure 10**) with its mandible, about 12 years old.

Diagnosis: (1) giant size with a basal skull length of 613.8 mm on average; (2) longer face than in any known horses; (3) shallow preorbital fossa; (4) high vomer index (111.2–133.9); (5) long distance between orbit and third molar; (6) rounded double-knots of lower cheek teeth; (7) shallow labial valleys on lower molars. Character states 2–6 are primitive within horses; character states 1 and 7 are considered derived.

Distribution: Longdan, Dongxiang County, Gansu Province.

Age: Nihewanian, Early Pleistocene.

Remarks: *Equus eisenmannae* was the most recently erected stenonid species in China. This species is very interesting. Based on measurement and comparison, Qiu et al. (2004) noted that *E. eisenmannae* was one of the largest *Equus* species (**Figure 7**). Furthermore, facial and snout lengths, and absolute and relative palatal lengths, were all larger than those of any other known *Equus* species (**Figures 6**, **11**, **12**). However, based on the method proposed by Eisenmann and Karchoud (1982), Qiu et al. (2004), and Sun et al. (2017) compared the Mc III and cranial basilar lengths among all Chinese stenonid horses and determined that *E. eisenmannae* has the largest relative robustness of Mc III. *Equus eisenmannae* also has the most abundant cranial material record among Chinese stenonids, including several complete skulls from different fossiliferous levels. Qiu et al. (2004) noticed that individuals from different levels have morphologic differences; for example, individuals from the upper level have larger cranial proportions, deeper ectoflexids in the lower molars, and sharper post-erolingual angles of the metastylid. Wang and Deng (2011) performed univariate and multivariate analyses on all specimens from different levels in the locality where *E. eisenmannae* was recovered. They concluded that the differences between *E. eisenmannae* samples across the two stratigraphic intervals were not significant enough to warrant recognizing two species. They also discussed some critical trends in equid evolution based on their comparison between *E. eisenmannae* and modern horses (Forsten, 1988; Azzaroli, 1992; Eisenmann, 1996; Prado and Alberdi, 1996; Eisenmann and Baylac, 2000). Qiu et al. (2004) summarized the important features of *E. eisenmannae* and indicated that its beak-shaped entoconids on the lower premolars and rounded double-knots were similar to those of *E. wangi*, and its oval entoconids on the lower molars and shallow labial valley not reaching the isthmus were similar to those of *E. yunnanensis* and *E. wangi*. They also argued that *E. eisenmannae* is a transitional form between North American plesippines and Eurasian allohippines (i.e., stenonids).

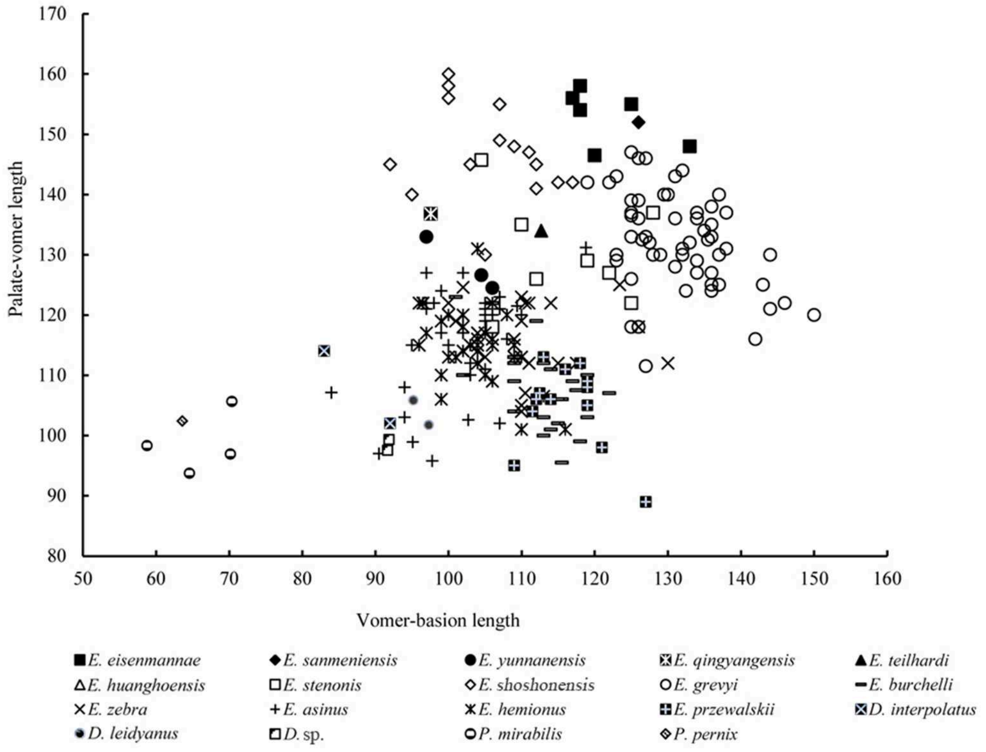

FIGURE 9 | Comparison of basicranial proportion in several extinct and extant species of Equidea.

FIGURE 10 | Right lateral view of holotype skull of *E. eisenmannae*, IVPP V 13552, collected from Longdan Locality, Linxia Basin. Scale bar = 5 cm.

SUMMARY OF CHINESE STENONID PHYLOGENETIC RELATIONSHIPS

Deng and Xue (1999d) reviewed all of the fossil equids in China and summarized their relationships in a phylogenetic tree. They proposed that *E. teilhardi* and *E. huanghoensis* are two independent lineages alone and traced these two species directly back to *E. shoshonensis*. They could not recognize diagnostic properties of these two species because of lack of complete material. Deng and Xue (1999a) considered the other stenonid species they reviewed to be a clade, within which *E. qingyangensis* was a separate lineage that they suggested directly dispersed into Eurasia as a New World origin. *Equus wangi* and *E. yunnanensis* are sister groups, as were *E. stenonis* and *E. sanmeniensis*. The establishment of these groups was also based on the morphological similarities we discussed above. As new lineages are discovered and more complete material of known species reported, it is necessary to perform a new review of the stenonid horses in China.

Some authors have suggested that *Equus* originated within genus *Dinohippus*, a large monodactyl form constrained to the New World (Bennett, 1980; Dalquest, 1988; MacFadden, 2005, 2006; Pagnac, 2006). In the current research, we try to figure out the origin of *Equus* in different method and then obtain different conclusions. In our plots, stenonids are more similar to *Pliohippus* in cranial proportion rather than to *Dinohippus*, caballoids, hemiones, asinines, and zebrines (**Figures 6**, **9**, **11**, **12**). On the other hand, we perform a phylogenetic analysis. The analysis yield one parsimonious tree, shows a new phylogenetic relation between primitive monodactyl equids, stenonids, and some extant species (**Figures 1**, **13**). In this phylogenetic tree, a monophyletic clade consists of species of *Equus* forms sister groups with species of *Dinohippus*. Moreover, the clade consists of *Equus* and *Dinohippus* forms sister groups with species of *Pliohippus*.

Eisenmann and Deng (2005) agreed with Deng and Xue's argument regarding the phylogenetic position of *E. qingyangensis*. Consequently, there were likely at least two dispersal waves of *Equus* into the Old World, with one wave represented by *E. qingyangensis*. Eisenmann and Deng (2005) argued that *E. shoshonensis* may be the direct ancestor of *E. qingyangensis*. In our result of new phylogenetic analysis, *E. qingyangensis* is attributed in a clade distinguished from all other species. This probably represents an independent dispersal event,

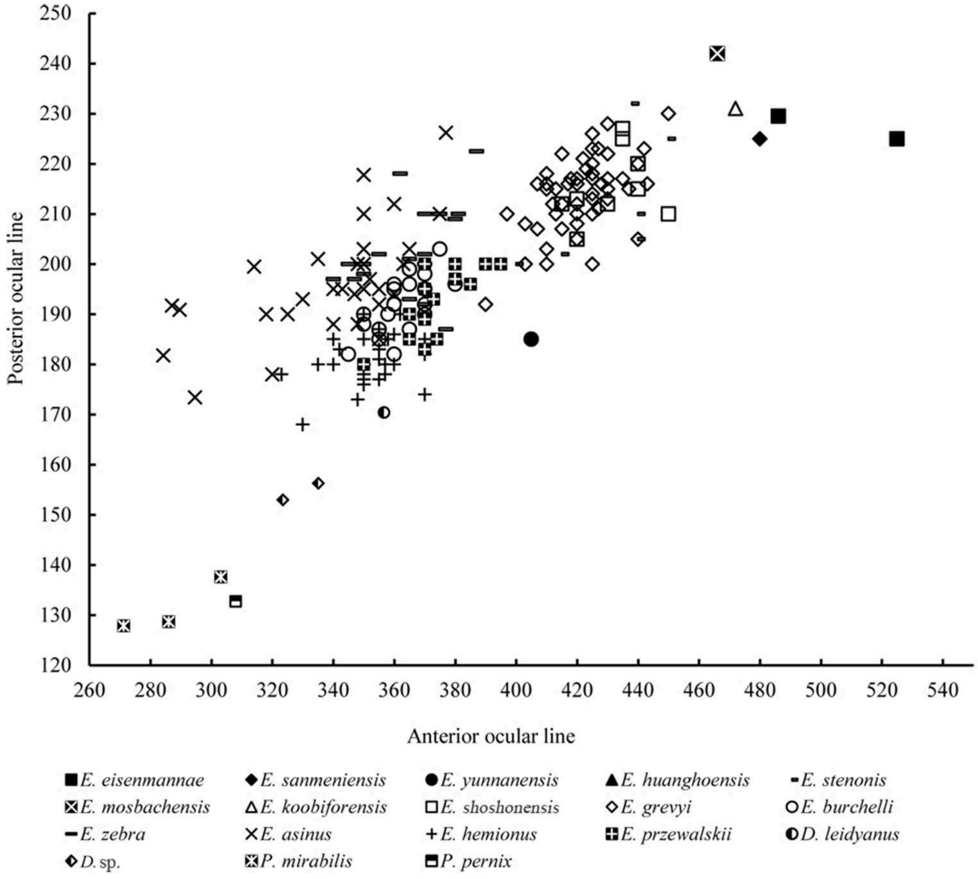

FIGURE 11 | Comparison of anterior and posterior ocular lengths in several extinct and extant species of Equidae.

and accords with the arguments of Deng and Xue (1999a) and Eisenmann and Deng (2005).

In the new phylogenetic tree, large-sized stenonid species form a clade. Large body size is a primitive character. Body size decrease was an important trend in equid evolution (Eisenmann and Baylac, 2000; Wang and Deng, 2011). The earliest *Equus* species in Europe, *E. livenzovensis*, is also very large, and is thought to have lived 2.5 Ma in Italy, Spain, and Russia. According to geochronological data, the first occurrences of *E. huanghoensis* and *E. eisenmannae* were close to the lower boundary of the Quaternary (see below). Although these huge species of Chinese stenonid have primitive body size and early geohistorical distribution, their features are derived. This probably suggested that the differentiation of early *Equus* was significantly earlier than 2.58 Ma. Qiu et al. (2004) considered *E. eisenmannae* to be the ancestor of *E. sanmeniensis* and *E. stenonis*. Based on morphology of cranial and dental features, *E. eisenmannae* is more closely related to *E. sanmeniensis* than *E. stenonis*. They share some morphological similarities, such as extremely large body size (basilar length of type skull of *E. sanmeniensis* is 585 mm, this length of *E. eisenmannae* is 613 mm), shallow nasal notch, elongated protocone, and strong enamel plications on upper cheek teeth. In addition, based on morphological features, *E. wangi*, *E. sanmeniensis* and *E. eisenmannae* probably have the closest relationship, fits the result of our phylogenetic analysis. *Equus wangi* and *E. sanmeniensis* formed a lineage as sister groups, which form a group with *E. eisenmannae*. *Equus huanghoensis* and *E. stenonis* shared features such as a transversely undulated forehead, very deep nasal notch, short protocone, and very weak enamel plications on upper cheek teeth. These similarities also fit the result of our phylogenetic analysis, in which *Equus huanghoensis* and *E. stenonis* form sister groups.

Previously, due to poor material, it was difficult to recognize the phylogenetic position of *E. teilhardi* (Eisenmann, 1975; Forsten, 1986). Recently, a report on a nearly complete skull of *E. teilhardi* provided a perfect opportunity to discuss this species (Sun et al., 2017). Most stenonid species have large body size, elongated facial part and limbs. In contrast, *E. teilhardi* has medium body size, a short snout and robust metapodials (Sun et al., 2017). *E. yunnanensis* has similar cranial and post-cranial features as *E. teilhardi*, such as body size, cranial proportions and limb shape. In the result of our phylogenetic analysis, *E. teilhardi* forms sister groups with *E. yunnanensis*. This result fits the similarities above in morphology feature. Due to the introduction of extant species (caballoid,

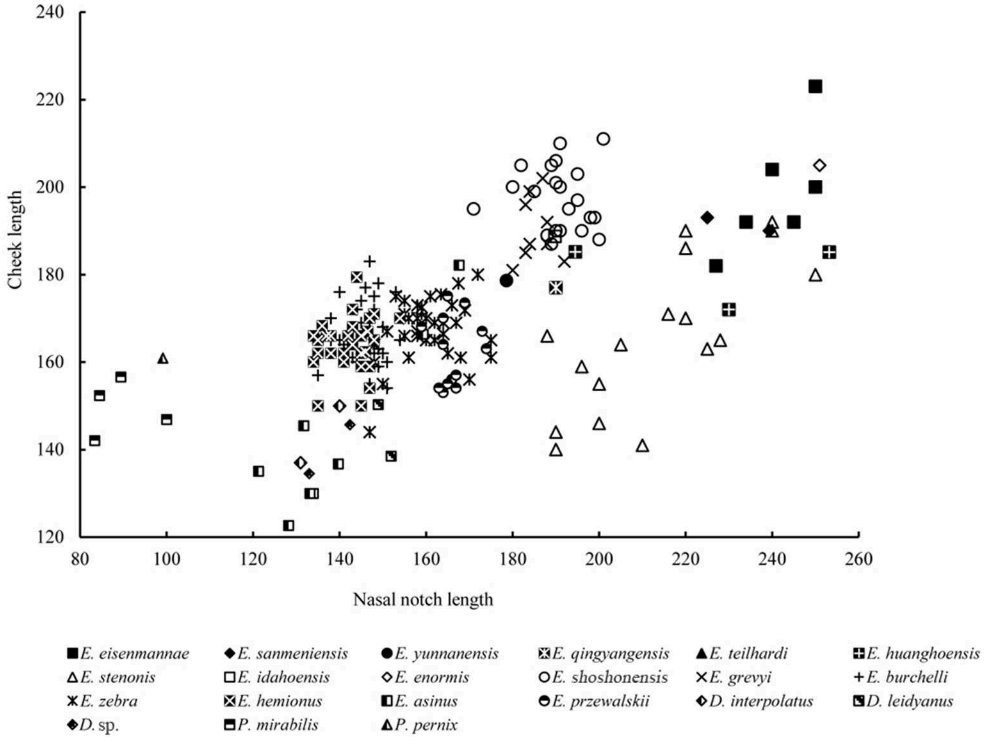

FIGURE 12 | Comparison of lengths of nasal notch and cheek in several extinct and extant species of Equidae.

hemione, asinine, and zebrine), we achieve a completely new pattern of early evolution of *Equus*. The clade consisting of *E. teilhardi* and *E. yunnanensis* forms sister groups with all extant species, distinct from the clade that consists of all other stenonid species. Based on this result, probably the "stenonids" are not a phylogenetic unit any more, but just a morphologic concept. *E. teilhardi* and *E. yunnanensis* are not typical stenonid species, they both have relatively short facial part and robust limbs, which are more similar to most extant species. Probably these two species are closer to extant forms rather than other stenonid species.

THE *EQUUS* DATUM IN CHINA AND THE LOWER BOUNDARY OF THE QUATERNARY

Deng and Xue (1997) demonstrated once again the significance of the *Equus* Datum. They argued that the first appearance of *Equus* can be considered an easily recognized sign of the lower boundary of the Quaternary in Eurasia. Indeed, the first appearance of *Equus* was roughly contemporary with many important geological events around 2.5 Ma, such as the Matsuyama/Gauss boundary as determined by magnetostratigraphy, the beginning of loess accumulation in China, the appearance of the ice cap in the Arctic (Backman, 1979) and the first strengthening of neotectonism (Zhu et al., 1994). In recent decades, we put substantial effort into describing the classical localities of the Early Pleistocene in China to correlate the Quaternary mammalian paleontology in China relative to that throughout Eurasia.

Nihewan Basin

In 1924, Barbour observed the strata of Nihewan, Yangyuan, Hebei Province (**Figure 2**) and established a stratigraphic unit, the Nihewan Beds. Afterwards, Barbour, Licent, Teilhard de Chardin, and Piveteau further studied the Nihewan Beds and their mammalian fossils. In 1948, IGC (International Geology Congress) regarded the Villafranchian as the lower boundary of the terrestrial Pleistocene in Europe, which suggested that the Nihewan Beds represented the lower boundary of the Pleistocene in China. The suggestion was formally approved and used by Chinese geologists in 1954.

Along with research progress, a lot of different viewpoints about the Nihewan Beds have emerged, the main three of which are: (1) the Nihewan Beds are assigned to the Lower Pleistocene; (2) the Nihewan Beds consist of the Lower Pleistocene and Middle Pleistocene; and (3) the Nihewan Beds may include Lower–Middle Pleistocene and Upper Pleistocene, and even Pliocene (Wei and Xie, 1989).

Tang and Ji (1983) established the Dongyaozitou Formation and its accompanying Dongyaozitou Fauna on the basis of the Dongyaozitou section in Yuxian, Hebei Province. Based on the components of this fauna, Deng and Xue (1999a) assigned it to the Pliocene.

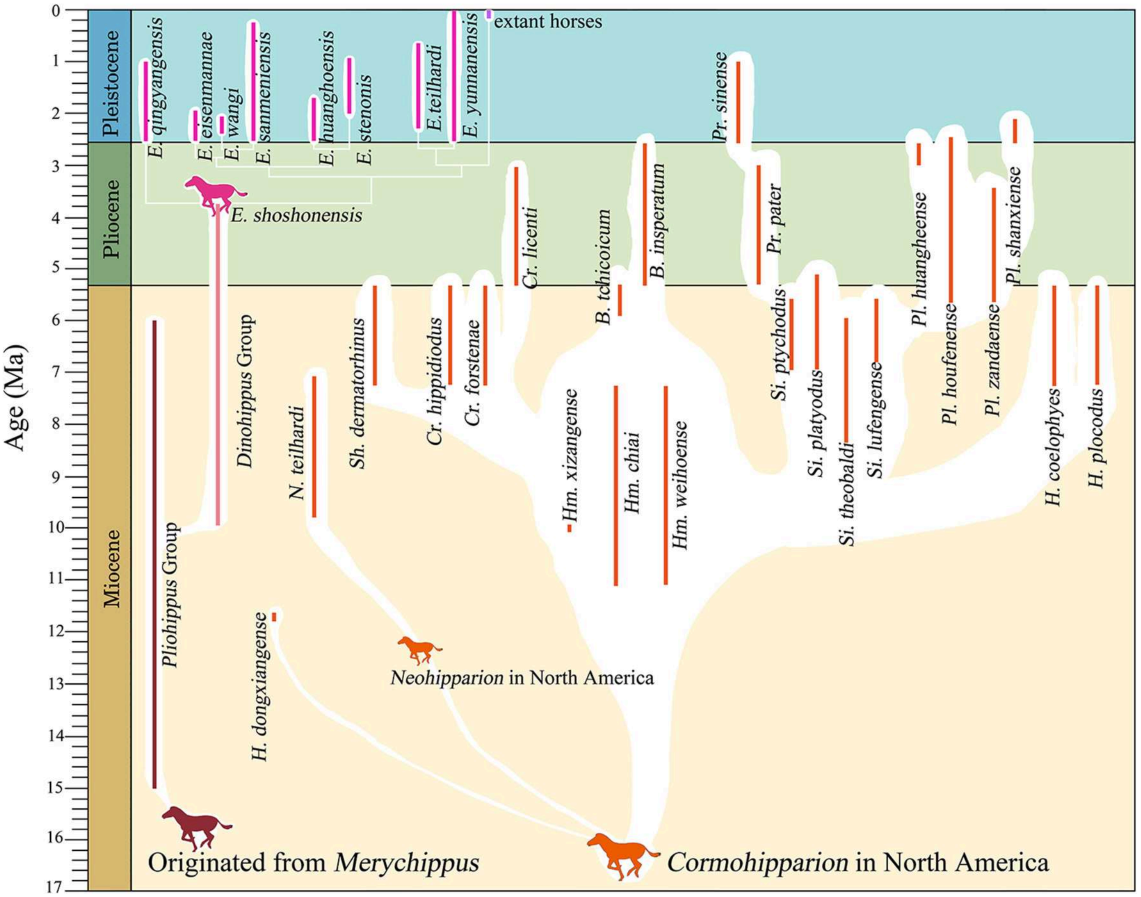

FIGURE 13 | Proposed phylogenetic interrelationships of species of hipparionine and genus *Equus* in China, based on Qiu et al. (1987), Li and Li (1990), Deng and Xue (1999a), MacFadden (2005), Sun (2013), Wolf et al. (2013), Deng et al. (2016), Bernor et al. (2018), and Sun et al. (2018). Abbreviations of genera: H, *Hipparion* (a polyphyletic group including all the species with undefined attribution); N, *Neohipparion*; Sh, *Shanxihippus*; Cr, *Cremohipparion*; Hm, *Hippotherium*; B, *Baryhipparion*; Pr, *Proboscidipparion*; Si, *Sivalhippus*; Pl, *Pliohipparion*; E, *Equus*.

Li (1984) discovered typical Nihewan Fauna in the Danangou section above the Dongyaozitou Formation in Yuxian. Most of the fossils are the main members of the Nihewan Fauna. Based on the primitive features of the micromammals, this section was shown to represent the earliest horizon of the Pleistocene (i.e., the Nihewan Formation) (Zheng, 1981). Because the Nihewan Fauna is located between the two formations in Danangou, Yuxian, the first appearance of *Equus* corresponds to their boundary.

Wu et al. (1995) studied the age of the Nihewan Beds, especially the lower boundary of the Quaternary, by amino acid dating. The dating samples are bones collected from a grayish-white gravel bed in the lower part of the Dongyaozitou Formation in Yuxian, which is 2.78 Ma old. Wu et al. thought that the lower boundary of the Quaternary in this region should be the lower boundary of the Nihewan Formation but above the Dongyaozitou Formation in the Danangou section, and that it was about 2.5 Ma old.

Cai et al. (2004) chose the Danangou section as the type section of Nihewan Formation. They divided this section into four informal lithological members. They noted that *Equus* was accompanied by hipparionines in member 2. They suggested that the base of member 2 corresponded to the lower boundary of the Quaternary (about 2.58 Ma) based on the micromammalian fossil assemblage. Recently, an increasing number of studies on magnetostratigraphy suggested that the oldest sediments of the Nihewan beds date back to about 2.5 Ma, which is roughly corresponds to the Plio-Pleistocene boundary (Zhu et al., 2007; Deng et al., 2008; Gibbard and Head, 2010; Liu et al., 2012, 2018; Ao et al., 2013a).

Yuanmou Basin

The Yuanmou Basin in Yunnan Province has been the type region of the Early Pleistocene strata in South China (**Figure 2**), and it has been researched for as long as the Nihewan region. In the 1920s–1930s, Walter Granger collected mammalian fossils from the Yuanmou Basin. In the 1940s, Colbert (1940) studied these fossils and named a fossil horse among them *E. yunnanensis*. He thought that these fossils corresponded to the fauna of the Upper Irrawaddy in Myanmar and the Early

Pleistocene Nihewan Beds in North China based on the horse's small size and some primitive features of its teeth.

Pei (1961) suggested that the Early Pleistocene strata, which had yielded *E. yunnanensis*, should correspond to the Pinjor and Tatrot Beds of the Upper Siwalik in the Indo-Pakistani subcontinent, and its geological age should correspond to the Villafranchian in Europe. After discovering human fossils in 1965, a lot of researchers began to study this region and proposed some different viewpoints.

The fossiliferous beds in the Yuanmou Basin are included in the Yuanmou Formation, which is subdivided into four members. Li (1981) thought the fossils that were collected from the Yuanmou Basin could be divided into two groups: one group at Members 1–2, which contains Late Pliocene forest mammals, and another group at Members 3–4, which contains some surviving Neogene mammals. The latter's extinction rate was rather high, but there are also some Quaternary mammals that were widespread in North and South China, such as *E. yunnanensis*. Members 3–4 do not contain forms of the *Ailuropoda-Stegodon* Fauna; therefore, it should be assigned to the Early Pleistocene.

Qian and Zhou (1991) separated the fossils from Members 1–2 of the Yuanmou Formation from the previously confused "Yuanmou Fauna" and named them the Shagou Fauna. Chow (1961) first thought that this fauna corresponded to that of the Dhok Pathan Beds of the Middle Siwalik in India, which have yielded a similar fauna and date to the Late Pliocene. The Shagou Fauna does not contain *Equus*. The Xiaohe Fauna is under the Shagou Fauna. Qian et al. thought that the Xiaohe Fauna corresponded to the Middle Siwalik Fauna in South Asia, the Baode Fauna in North China, and the Lufeng Fauna in Yunnan, so it should undoubtedly be assigned to the Pliocene. Qian et al. had a different viewpoint from Chow (1961), but Zhang et al. (1978) and some other authors thought that the Xiaohe Fauna is actually included in the Shagou Formation and this formation belongs to the Pliocene.

The Yuanmou Fauna is located above the Shagou Fauna and collected from Members 3–4 of the Yuanmou Formation. The Yuanmou Fauna contains rich mammalian fossils, including *Homo erectus yuanmouensis*, which is famous in Chinese paleoanthropology research, in its upper part, mammalian survivors of the Neogene, of which the extinction rate was 93%, and Early Pleistocene mammals. Deng and Xue (1999a) indicated that firstly Yuanmou Fauna contains Early Pleistocene mammal such as *E. yunnanensis*, *Canis yuanmouensis*, *Hyaena licenti*, *Stegodon elephantoides*, *Axis shansius*, *Axis* cf. *rugosus*, *Rusa yunnanensis*, etc.; there are also some survivors of the Neogene mammals; and the members which commonly occur in the *Ailuropoda-Stegodon* fauna in the Pleistocene in south China such as *Ailuropoda*, *Tapirus*, *Ursus*, *Pongo,* and *Macaca*. They concluded that Yuanmou Fauna has been shown to be the earliest Early Pleistocene fauna.

Because *Equus* is absent from the Shagou Fauna, *E. yunnanensis* is the first appearance of *Equus* in the Yuanmou Fauna and its earliest appearance was in Member 3 of the Yuanmou Formation. Paleomagnetic dating revealed that the Matsuyama/Gauss boundary, which is located on the bottom of Member 3 (Qian and Zhou, 1991), dates to about 2.58 Ma. Moreover, according to the fission track dating performed by Qian and Zhou (1991), the age of the upper section of Shagou Formation was 2.59 Ma. *Equus yunnanensis* happens to appear at this boundary, which thus corresponds well with the lower boundary of the Quaternary.

According to a highly resolved magnetostratigraphic analysis performed by Zhu et al. (2008), the sediments of the Yuanmou Basin, which were divided into 17 polarity units, should be grouped into three distinct directional intervals. The base of Group I, which represented the lower boundary of the Quaternary, dates to 2.58 Ma.

Linxia Basin

The Linxia Basin is located in the east of Gansu Province (**Figure 2**). Since the end of the 1980s, the Linxia Basin has been famous for its wealth of fossil mammals. In May of 1999, while identifying the "dragon bones" obtained by a local "dragon bone" dealer, Zhanxiang Qiu noticed some canid fossils from loess deposits. Based on the dealer's information, Qiu found a very fossiliferous locality in Longdan Village, Dongxiang Autonomous County. After about 1 year, Qiu and his colleagues collected more than 100 specimens, mainly skulls and mandibles. Consequently, the Longdan Fauna became one of the most important Early Pleistocene mammalian faunas in China.

The Longdan Fauna described by Qiu et al. (2004) includes 31 species of 29 genera. The presence of *Equus* and the absence of Middle Pleistocene species indicates that the age of the Longdan Fauna is Early Pleistocene. Additionally, Wang (2005), Qiu et al. (2009), and Deng (2012), respectively, reported specimens of *Castor anderssoni*, *Ursus yinanensis*, and *Proboscidipparion sinense* from Longdan. Qiu et al. noted that the Longdan Fauna and the Nihewan Fauna shared only eight species. They determined that the Simpson similarity index (i.e., the number of common taxa divided by the number of total taxa of the fauna with fewer taxa) was only 25.8%. The number of genera commonly shared by the two faunas is 17, and the similarity index at the generic level is thus 58.6%.

Qiu et al. (2004) suggested that differences in composition between the Longdan and Nihewan Faunas may reflect differences in geologic ages and paleoenvironments. The Longdan Fauna was slightly older than the Nihewan Fauna based on the observation that the Longdan Fauna contains some primitive forms and the Nihewan Fauna includes a large number of advanced forms. For example, the extremely large horse *E. eisenmannae* represented a very primitive lineage that was similar to the earliest horse in Europe, *E. livenzovensis*.

Although no agreement has been reached regarding the geologic age of the Nihewan Fauna, many paleontologists consider it to be around 1.8 Ma (Liu and Liu, 2000; Qiu, 2000). Previous paleomagnetic data indicated that the Longdan is 2.55–2.16 Ma old (Qiu et al., 2004). The results of paleoenvironmental and chronological analysis performed by Zan et al. (2016) demonstrated that the age of the Longdan Fauna was 2.5–2.2 Ma.

Other Sections

The loess in southeastern Shanxi Province is, from bottom to top, divided into Old Red Loam, New Red Loam, Lishi Loess, Malan Loess, and Holocene Loess. The Old Red Loam is distributed in the eastern Yushe Basin. Cao et al. (1995) discovered a lot of mammalian fossils in the basal conglomerate bed of the Old Red Loam. Most of these fossils are teeth of *Equus* sp., and they are intact and not abraded, which means that they are probably not reworked and most likely represent the true horizon at which *Equus* appears. Under the Old Red Loam, the Yushe Group contains hipparionines but not *Equus*. According to paleomagnetic studies (Shi, 1994; Shi et al., 1994), the Old Red Loam was deposited 2.5–1.5 Ma; therefore, its lower boundary was 2.5 Ma. The *Equus* fossils were collected from the basal conglomerate bed of this boundary.

In the Youhe District in Weinan, Shaanxi Province (**Figure 2**), the strata that contained the Early Pleistocene Nihewan Fauna are yellowish-brown coarse deposits, and they are informally called "Yellow Sanmen"; the strata that contained the Pliocene Youhe Fauna are green or grayish-green mudstones or marls, and are called "Green Sanmen." In the Youhe section, *Equus first* appears in the Yellow Sanmen, under which the Green Sanmen is only observed from Borehole W7 in Yancun, Weinan, which indicates that the Matsuyama Chron is recorded in the Yellow Sanmen, which dates to approximately 3.0–2.58 Ma. Zhu et al. (1995) conducted a paleomagnetic study on the Songjiabeigou section in Youhe, Weinan, and they also found that the Matsuyama/Gauss boundary is located between the Sanmen Formation (i.e., the Yellow Sanmen) and the Youhe Formation (i.e., the Green Sanmen). Consequently, the sections in the Youhe District demonstrate that the first appearance of *Equus* was at the Matsuyama/Gauss boundary at 2.58 Ma. Tang et al. (1983) described the Linyi Fauna, which included *E. huanghoensis* reported by Chow and Chow (1965). Based on the composition, Tang et al. (1983) stated that the age of the Linyi Fauna corresponded to the middle to late Villafranchian, which is the same as the Sanmen Formation. Therefore, the first occurrence of *E. huanghoensis* should be about 2.58 Ma at the lower boundary of the Quaternary.

In 1961, Xue and Wang collected plenty of mammalian fossils from Bajiazui, Qingyang, Gansu Province (Deng and Xue, 1999a; **Figure 2**). These fossils were obtained from sandstone at the base of the section, the age of which was identified as Early Pleistocene (Wang et al., 1966; Wang and Xue, 1982). Deng and Xue (1999a,b,c) studied the *Equus* specimens of this mammalian fauna and erected two new species, *E. qingyangensis* and *E. wangi*, and identified a known species, *E. teilhardi*. Deng and Xue (1999a) indicated that *E. qingyangensis* occurred around 2.5 Ma based on the position of fossils and loess between fluvial-lacustrine deposits. As we discussed above, *E. qingyangensis* was very primitive, especially on its very low cranial proportions, which are similar to those of the earliest *Equus* in the world, *E. shoshonensis* (**Figure 12**).

SCENARIO OF *EQUUS* DATUM AND EARLY EVOLUTION

Based on the information detailed above, we can describe the pattern of the early evolution of stenonids in China. There is no doubt that stenonids first arrived in China at the lower boundary of the Quaternary. It also can be confirmed that at least five stenonid species simultaneously appeared in China about 2.5 Ma (**Figure 14**). This is not strange. Equids are all highly cursorial and able to migrate very long distances in a relatively short time. When stenonids arrived in Eurasia and dispersed, the time difference of their dispersal was negligible on a geochronological scale. But why could stenonids radiate and produce high diversity as soon as they appeared in Eurasia, even only in China? Was that a coincidence?

Equidae originated in North America 56 Ma and was restricted to this continent from the Eocene to the Oligocene (MacFadden, 2005; Bai et al., 2018). Since the Early Miocene, there have been several migrations of Equidae to the Old World (MacFadden, 2005). This is probably related to the Mi-1 glaciation (Zachos et al., 2001). Based on diversity, geographic distribution, and population, Anchitheriinae was not a prosperous lineage in Eurasia. For example, only two genera with four species of Anchitheriinae have been found in China (Hou et al., 2007). In the beginning of the Late Miocene, a much more successful clade, Hipparionini, appeared in Eurasia. The earliest species was *Hipparion dongxiangense*, which was found in Guonigou, Dongxiang, Gansu Province; the first occurrence of *H. dongxiangense* was 11.5 Ma (Fang et al., 2016). Throughout the Late Miocene, hipparionine originated and diversified into a successful taxon in China, with 8 genera and 17 species. In the Pliocene, four genera with three species of hipparionine survived, and one new genus and three new species originated (Qiu et al., 1987; Li and Li, 1990; Sun, 2013; Deng et al., 2016; Bernor et al., 2018; Sun et al., 2018; **Figure 13**). Although the diversity decreased significantly, Hipparionini was still the main member of the mammalian fauna in the Pliocene. In the Pliocene, the first appearance of *Equus* was in North America (3.5 Ma, Winans, 1989). According to O'Regan et al. (2010), the Bering Strait was likely exposed about 3.3 Ma, which allowed the North American *Equus* species to invade Eurasia (**Figure 15**). However, they likely did not migrate until later because hipparionine species were still the dominant equids in Eurasia, at least in East Asia (**Figure 13**).

Stable carbon isotopic analysis performed by Hou et al. (2006) indicated that the habitats in western China were steppes dominated by C3 grasses during the Late Miocene and Early Pliocene instead of savannas dominated by C4 plants. They suggested that C4 plants dispersed into northern China in the Pliocene along with the strengthening of the East Asian summer monsoon. Simultaneously, the diversity of the *Hipparion* fauna in East Asia gradually declined. They also suggested that Miocene equids in North America faced a similar crisis because of C4 plant dispersal 7–5 Ma. The dispersal of C4 plants has been explained to be correlated with a decrease in atmospheric CO_2 (Cerling et al., 1993, 1997; Wang et al., 1994). Janis et al. (2000) suggested that the observed decline in species

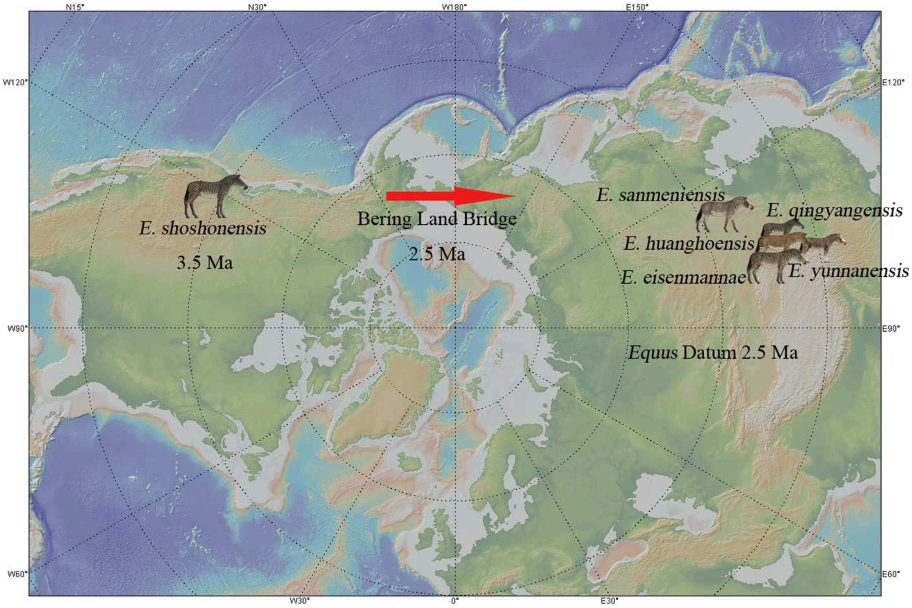

FIGURE 14 | Origin of *Equus* in North America and the *Equus* Datum in China.

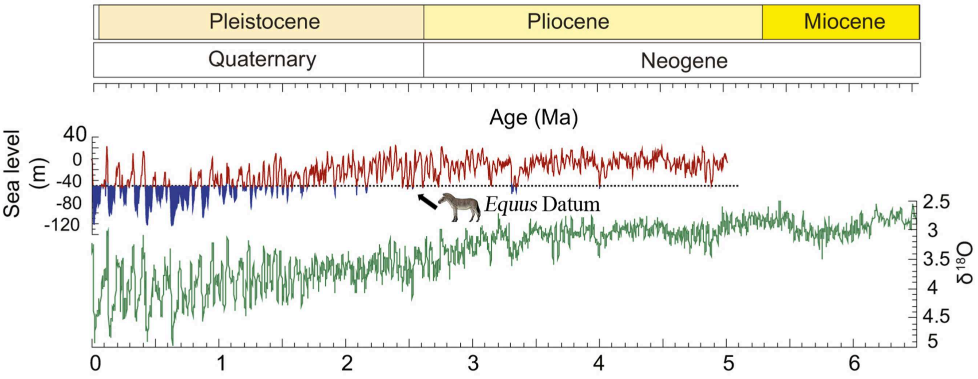

FIGURE 15 | *Equus* Datum, global sea-level and global benthic $\delta^{18}O$ compilation. Blue shading of the sea-level curve indicates times when global sea-level dropped below 50 m and the Bering Strait was likely exposed (modified after O'Regan et al., 2010).

richness of North American horses may represent a gradual decline in primary productivity, which would be consistent with a decrease in atmospheric CO_2. In summary, we propose that, after the Early Pliocene, hipparionine species declined as a result of decreased primary productivity of vegetation in their habitats.

The massive recession of *Hipparion* was initiated in the Early Pleistocene, by which only two genera and two species survived (Qiu et al., 1987; Deng, 2012; Bernor et al., 2015). This recession was mostly the result of accumulation and aggravation of the constant decline of primary productivity of the vegetation and partly influenced by climate change. The beginning of the Pleistocene was when *Equus* first immigrated into Eurasia. As described in our discussion above, at least five stenonid species (*E. qingyangensis*, *E. eisenmannae*, *E. sanmeniensis*, *E. huanghoensis*, and *E. yunnanensis*) simultaneously appeared in China at the very beginning of the Pleistocene. Compared with hipparionine, stenonids had obvious advantages. First, monodactyl feet adapted to vertical standing made *Equus* the perfect steppe runner. In addition, the V-scars of *Equus* are developed on the first phalanx of both fore and hind digit III, and are much wider and flatter than those of hipparionines (Deng et al., 2012). Additionally, all stenonid species have very elongated face. Qiu et al. (2004) indicated that the elongated jaw could accommodate a larger cheek tooth row, which would be a powerful adaptation for chewing coarse food, like dry grass. In contrast, hipparionines in the Early Pleistocene, such as *Proboscidipparion sinense*, had relatively small cheek teeth. Moreover, the global climate became colder in the Early Pleistocene, and the animals with larger body sizes were better adapted to the cold environment according to Bergmann's rule (Qiu et al., 2004). The famous Early Pleistocene fauna, the Nihewan Fauna, consisted of large animals, such as, *Coelodonta nihowanensis*, *Elasmotherium* sp., *Paracamelus gigas*, and *Bison palaeosinensis* (Cai et al., 2013). The stenonid horses, especially *E. eisenmannae*, are very large. Only very large hipparionine species, including *Proboscidipparion sinense* and *Plesiohipparion shanxiense*, survived in the beginning of the Pleistocene in China (Qiu et al., 1987; Deng, 2012; Bernor et al., 2015); consequently, plenty of open habitats and ecological niches were available for the new incoming lineages. As *Equus* arrived in Eurasia, its adaptations to this new situation helped it radiate and disperse rapidly. Deng et al. (1999, 2002) performed carbon isotopic analysis on mammalian fossils in the Quaternary in China and revealed an environment dominated by C3 plants in northern China in the Early Pleistocene that was led by strengthening of the East Asian winter monsoon along with Quaternary glaciation. Therefore, the primary productivity of vegetation likely increased significantly, and stenonid horses, which had been widespread in northern China, faced an opportunity for further evolution.

Equus shoshonensis has often been regarded as ancestral to all stenonids and even all *Equus* species (Deng and Xue, 1999a). Skinner and Hibbard (1972) argued that there were marked similarities between the skulls and dentitions of the extinct North American *E. shoshonensis* (his *E. simplicidens*) and the living Grévy's zebra, *E. grevyi*. Based on our observation and comparison of *E. shoshonensis* fossils and specimens of extant *E. grevyi* housed in several museums, these two species are similar in absolute size, and in cranial and distal limb proportions. However, our phylogenetic analysis places *E. grevyi* in the smallest clade formed by extant horses (**Figures 1**, **13**). The similarities discussed above, which are referred to functional morphology, should relate to similar habitat. *E. grevyi* lives in a semi-desert environment in northern East Africa with negative mean annual climatic water balance (Schulz and Kaiser, 2013). *Equus shoshonensis* probably lived in a similar environment to that of modern *E. grevyi*. Therefore, *Equus* was probably adapted to arid environments from the very beginning. When the Bering land bridge opened at the beginning of the Pleistocene (**Figures 14**, **15**), *Equus* immigrated into Eurasia from North America, where it first stopped in East Asia. Since 2.5 Ma, a stronger winter monsoon system and higher continental desiccation occurred in China, most probably due to strong uplift of the Tibetan Plateau (An et al., 2001). *Equus* was well-adapted to this climate and rapidly radiated into a considerably dominant member of the Early Pleistocene mammalian fauna, the *Equus* Fauna.

DATA AVAILABILITY STATEMENT

All datasets for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

BS and TD designed the conceptual model and contributed equally to the writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00429/full#supplementary-material

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