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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***

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# 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

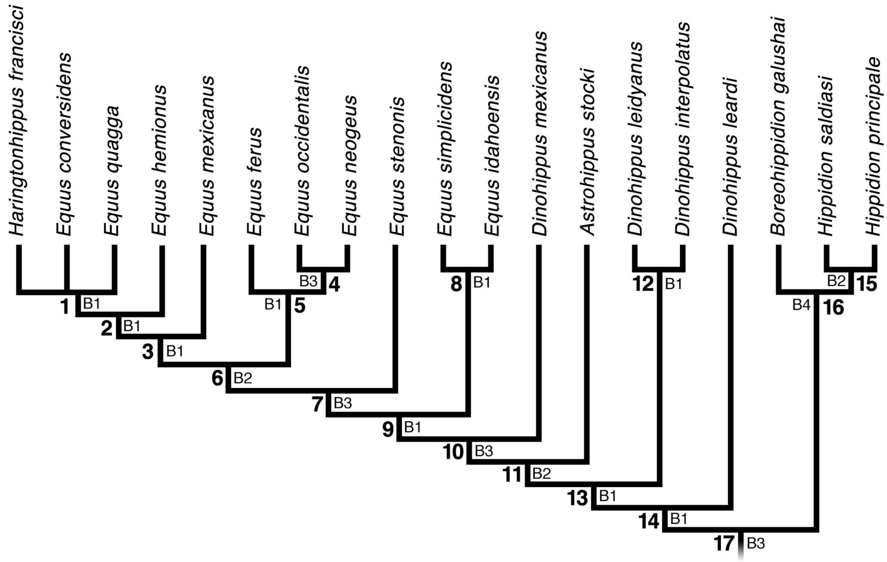

**FIGURE 1 |** Strict consensus of three equally most parsimonious cladograms of 85 steps, consistency index (CI) of 0.57 and retention index (RI) of 0.80 using a matrix of 32 morphological characters and 21 Equini taxa (**Table 1**). Numbers beside nodes indicate Bremer support values. Outgroups (*Acritohippus stylodontus* and *Pliohippus pernix*) are not shown in the figure. Characters and character states are described in the Appendix.

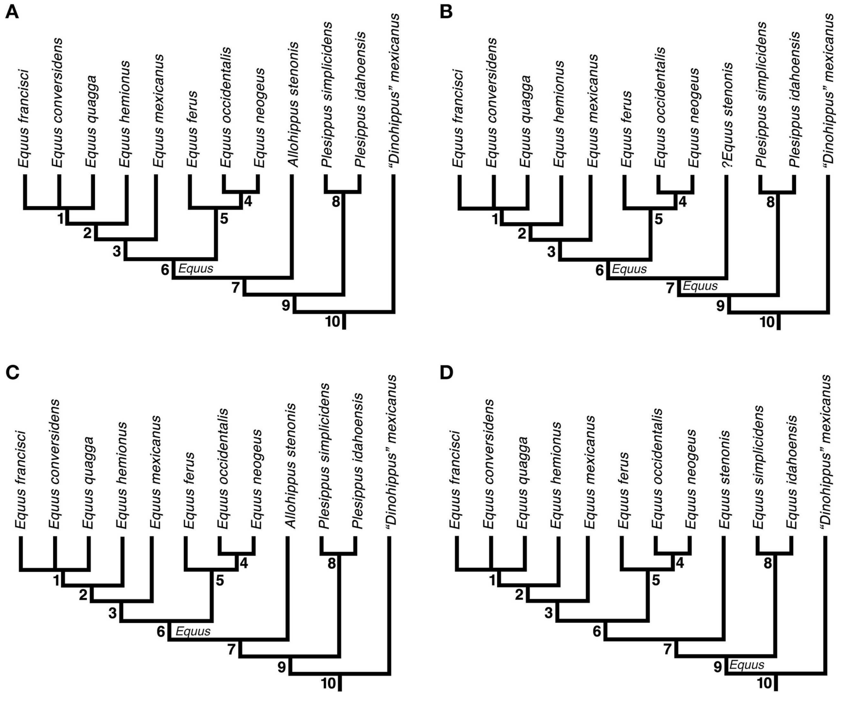

**FIGURE 2 |** Taxonomic position of *Equus* in the strict consensus tree (**Figure 1**) based on four explicit criteria (in addition to monophyly) previously used to delimit mammalian genera: phylogenetic gaps **(A)**, uniqueness of adaptive zone **(B)**, crown group definition **(C)**, and divergence 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,

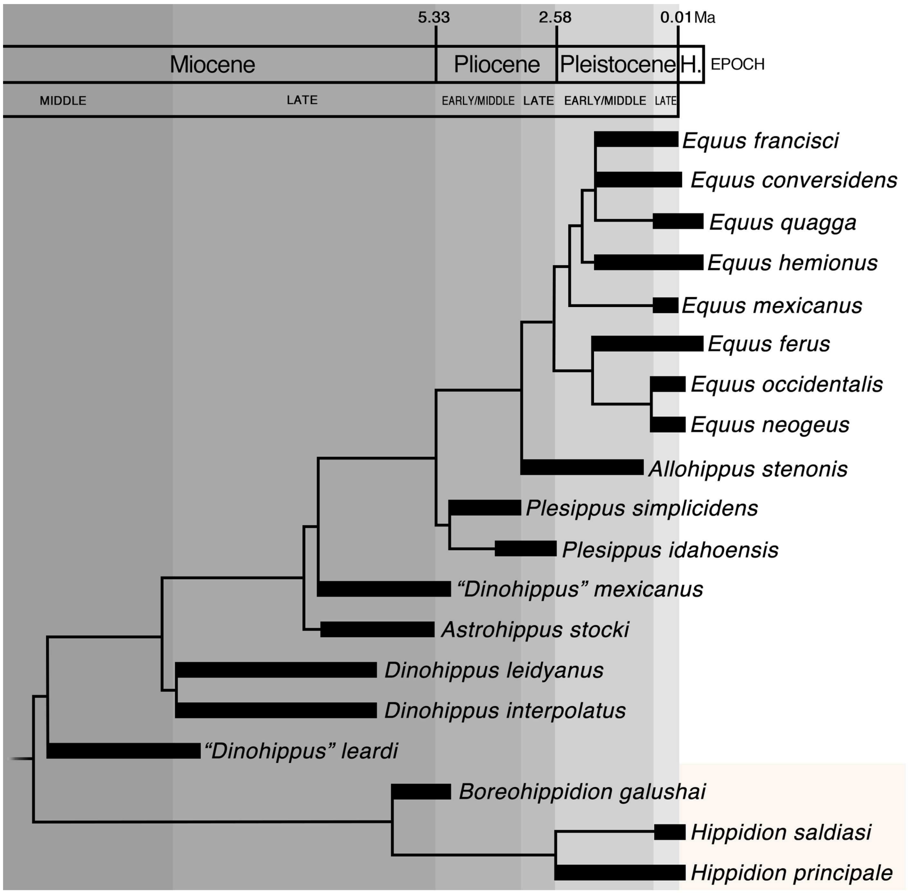

**FIGURE 3 |** Time-calibrated phylogeny of Equini based on fossil occurrences and the most parsimonious cladogram of 85 steps, consistency index (CI) of 0.57 and retention index (RI) of 0.80 using a matrix of 32 morphological characters and 21 Equini taxa (**Table 1**). Outgroups (*Acritohippus stylodontus* 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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