



Earliest perissodactyls reveal large-scale dispersals during the PETM

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Perissodactyls were a diverse order of mammals in the Northern Hemisphere during the Paleogene, but very few species remain today. They first appear during the Paleocene–Eocene Thermal Maximum (PETM; 56 Ma) on the three continents of the Northern Hemisphere. Because they lack modern diversity, the study of their evolutionary history remains difficult, relying almost exclusively on fossils. In addition, their origin and early diversification remain elusive since all main groups appear at the same time with several genera and are already diverse, contrary to other modern mammal orders. Here, we investigate the early evolution of perissodactyls by analyzing a new dataset focusing on early species to obtain a new expansive phylogeny. This new topology, in combination with new observations and comparisons demonstrates that several genera are synonymous, simplifying the evolutionary picture of early perissodactyls. We show that the number of genera was overestimated and should be significantly reevaluated. These results also highlight fast dispersals of two genera, *Pliolophus* and *Cardiolphus*, on the three Northern continents, reflecting that of other modern mammals. The phylogeny also supports a potential Indo-Pakistani origin of perissodactyls. In addition, this large-scale phylogeny shows that many species that were named as “*Hyracotherium*” in the past (or sometimes “*Eohippus*”, the “dawn-horse”) and considered as “horses”, are not actually closely related to horses (Hippomorpha), including *Hyracotherium* itself, but can be considered as basal perissodactyls.

Perissodactyla | *Hyracotherium* | biogeography | phylogeny | Paleocene–Eocene thermal maximum

Perissodactyls, the odd-toed ungulate mammals, including modern horses, tapirs, and rhinoceroses (six genera in total), have experienced an important decline in diversity compared to their large diversity in the fossil record (more than 300 genera). While wild, nonferal species of perissodactyls are currently limited to Asia, Africa, and South America, they once thrived across Europe and North America in addition to Asia, Africa, and South America. This reduced diversity poses a challenge for understanding their evolutionary history, as DNA analysis is not feasible for the vast majority of extinct species. Consequently, morphological data of fossils and modern osteological specimens are the primary source for reconstructing the phylogeny of perissodactyls.

The evolutionary sequence of horses, one of the major groups of perissodactyls, was considered as rather well understood and iconic (1). *Hyracotherium* (also called “*Eohippus*”) has long been considered to be the oldest known horse, and the oldest known perissodactyl (2–5). It was recently shown to comprise many different genera (6), though this opinion has been contested by those who favor the view of a single lineage of *Hyracotherium* in North America, arguing against the use of cladotaxonomy for early perissodactyls (7–9). Thus, the early diversification of horses remains unclear. In addition, the question of the origin and closest relative of perissodactyls is strongly debated. Like other modern placental mammals appearing during the PETM, such as primates and artiodactyls, early perissodactyls have been identified almost simultaneously on the three continents of the Northern Hemisphere, 56 Ma. However, perissodactyls differ from other modern mammals in that their earliest taxa are already highly diversified (Fig. 1) and are thought to belong to more than ten different genera and five distinct groups (Equidae, Isectolophidae, Ceratomorpha, Ancylopoda, and Brontotheriidae). In addition, almost no genus is shared between North America (*Sifrihippus*, *Arenabhippus*, and *Cardiolphus*) (10, 11), Europe (*Cymbalophus*, *Pliolophus*, *Chowliia*) (12–17), and Asia (*Erihippus*, *Orientalophus*, *Protomoropus*, and *Danjiangia*) (18) at the beginning of their radiation, which is unique among modern mammal groups with Eocene ancestors. A single potential occurrence of *Cardiolphus* sp., a typically North American genus, has been mentioned in Mongolia (19).

The closest sister group of perissodactyls also remains enigmatic, which poses a challenge to establish their paleobiogeographic origin. Perissodactyls were thought to originate from

Significance

Although the evolution of horses is regarded as a remarkable evolutionary sequence, early perissodactyls like *Hyracotherium* have been considered as a systematic and paleobiogeographic puzzle for more than 150 y. Here, based on a new large-scale phylogeny focusing on the earliest Eocene fossils, we show that several taxa such as *Hyracotherium* and *Pliolophus* are not horses or even hippomorphs, which reshapes our vision of early perissodactyl evolution. The earliest hippomorphs appear slightly later in the Wasatchian with *Systemodon* or *Xenichippus* in North America. These results also highlight the rapid dispersal of the earliest perissodactyls *Pliolophus* and *Cardiolphus* between North America, Europe, and Asia around the PETM, like other modern mammal orders.

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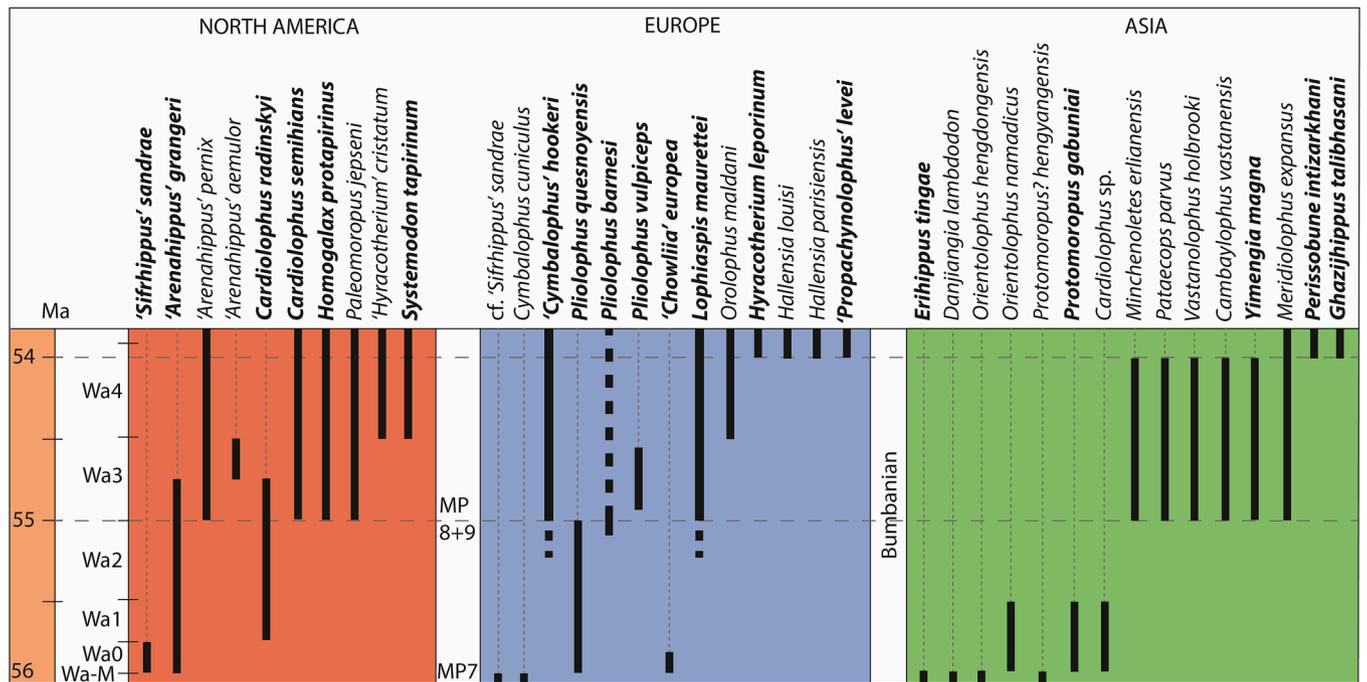


Fig. 1. Biostratigraphic chart of the earliest known perissodactyls near the Paleocene–Eocene boundary (from 56 to 54 Ma). Bold font indicates taxa that are included in the phylogenetic analysis. See [Dataset S2](#) for references, and detailed ages and occurrences of each taxon.

North American phenacodontid condylarths (20) but according to the paleobiogeographic reconstruction of Bai et al. (18), perissodactyls originated in Europe. However, based on a more complete taxonomic sampling, Rose et al. (21) showed that Anthracobunia might be the closest sister-group to perissodactyls. Another hypothesis, suggesting a close relationship between perissodactyls and some South American native ungulates (SANUs) has recently come to light based on paleoproteomic analyses (22, 23). However, according to a recent phylogenetic analysis, the clade Anthracobunia remains more closely related to perissodactyls than any SANU (24).

Here, we propose a phylogeny of perissodactyls based on a new dataset comprising a large-scale sample of perissodactyls, as well as a large selection of early Eocene taxa. Our matrix contains many species that have never before been included into a phylogenetic analysis as well as an original sampling of characters and takes polymorphism (intraspecific variation) into account. The results of the phylogenetic analysis support the synonymy of several genera and offers insights into the early diversification of perissodactyls, in particular that of supposed earliest horses. These results are also further supported by the reexamination and detailed comparisons of the morphology of historical species and specimens. We also clearly redefine *Hyracotherium*, *Pliolophus*, and *Cardiolphus* based on explicit and phylogeny-supported morphological characters. Finally, we discuss the dispersals of the earliest known perissodactyls and their potential origin.

Results and Discussion

Systematic Paleontology. The emended diagnoses provided below are based on the reexamination of the type and referred material of each genus and species, and on the results of the phylogenetic analysis. For more illustrations of *Hyracotherium*, *Pliolophus*, and *Cardiolphus*, please refer to the ([SI Appendix](#), [Table S1](#) and [Figs. S3–S10](#)).

Mammalia Linnaeus, 1758

Perissodactyla Owen, 1848

Hyracotherium Owen, 1841

[Fig. 2](#)

Type species: *Hyracotherium leporinum* Owen, 1841 by original designation.

Included species: no other species.

Distribution: United Kingdom, France.

Emended diagnosis: Anterior border of the orbit above M1–M2 border in lateral view, posterior border of the infraorbital foramen above P3–P4 border, post-P1 diastema present and P1 closer to P2 than to C, protocone of P2 absent, labial cingulum of P3–4 strong, protocone of P3 and P4 positioned below the paracone, paracone of P3–4 distinct, metacone absent on P3 but strong on P4, labial cingulum of M1–3 strong, centrocrista of M1–3 weakly labially flexed, para- and metaconules strong on M1–3 with strong constrictions of the protoloph and metaloph, and labial side of the metacone very convex. Differs from *Pliolophus* by the presence of a diastema between P1 and P2, the absence of protocone on P2, the protocone of P3–4 positioned below the paracone, the presence of a weak postprotocrista on P3, the stronger metacone on P4, the weakly labially flexed centrocrista on M1–3, the stronger metaloph constriction on M1–3 and the very convex labial side of the metacone on M1–3. Differs from *Cardiolphus* by the P1 closer to P2 than to C, the weaker postprotocrista on P4, the weaker parastyle on M1–3 and the stronger metaloph constriction on M1–3. Differs from *Pliolophus* and *Cardiolphus* by the more posterior border of the orbit in lateral view and more posterior infraorbital foramen. Differs from *Hallensia matthesi* by the large parastyle on M1–3, the weakly labially flexed centrocrista on M1–3, the M3 more similar in size to M2 and the ectoloph on M3 more lingual than on M1–2.

Cardiolphus Gingerich, 1991

[Fig. 2](#)

Junior synonym: *Chowliia* Tong and Wang, 2006

Type species: *Cardiolphus radinskyi* Gingerich, 1991 by original designation.

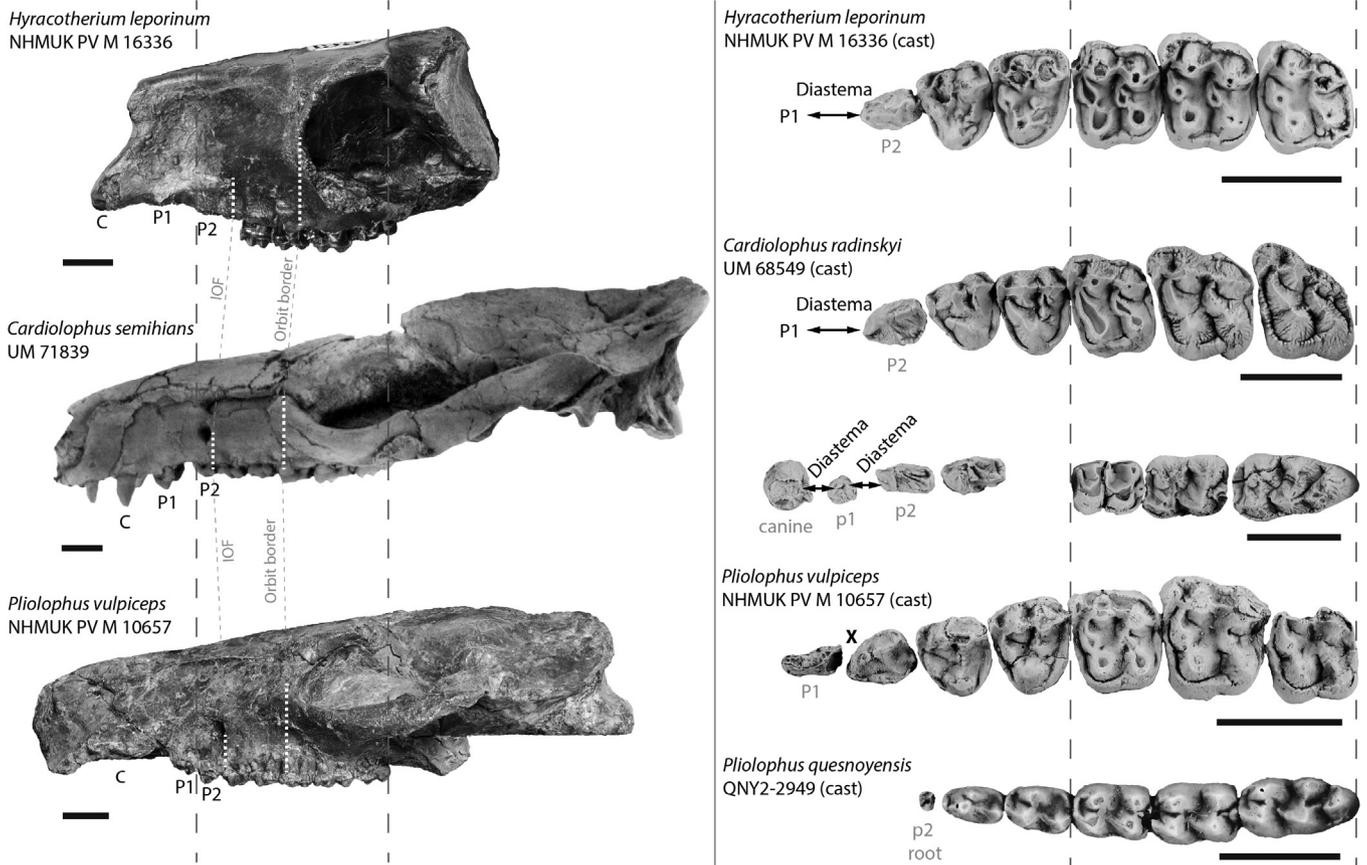


Fig. 2. Comparisons of the craniodental morphology of *Hyracotherium* (Top), *Cardiolophus* (Middle), and *Pliolophus* (Bottom), three early perissodactyls from the Early Eocene. The three genera can be differentiated by a combination of characters (position of the IOF and the orbit, presence or absence of diastema between P/p1 and P/p2, morphology of the upper and lower dentition). "X" indicates the absence of diastema. Abbreviation: IOF = infraorbital foramen. See [SI Appendix, Figs. S3–S10](#) for detailed illustrations and comparisons of these three genera and additional morphology. Illustration of the skull of *Cardiolophus semihians* taken from Gingerich (25) with permission from the author. The photos of the skull and dentition of *Pliolophus vulpiceps* have been inverted for comparison. (Scale bar, 1 cm.)

Included species: *Cardiolophus semihians* Gingerich 1991; *Cardiolophus* sp. Hooker and Dashzeveg 2004; *Cardiolophus laoshanensis* (Tong and Wang, 2006); *Cardiolophus europaeus* (Bronnert, Gheerbrant, Godinot, & Métais, 2018).

Distribution: United States, France, Mongolia, China.

Emended diagnosis: Diastema at the front and back of P/p1, with P1 closer to the canine than to P2, but p1 either contacting the canine or closer to it than to p2; Anterior border of the orbit above P4–M1 border in lateral view, posterior border of the infraorbital foramen above P2–3 border, protocone of P2 mostly absent or very small, protocone of P4 positioned below the paracone, postprotocrista of P4 usually present and strong forming a metaloph and endoprotocrista also sometimes present, lingual cingulum of M1–3 discontinuous or absent, parastyle of M1–3 very large, paraconule strong on M1–3, with constriction of the protoloph, and the metaconule can be strong or totally merged in the metaloph, with weak metaloph constriction. Posterior border of the symphysis between p1 and p2 or below p2, metaconid of p3 weak, poorly separated from the protoconid, paraconid of p4 large and paralophid angular, entoconid of p4 totally absent, labial cingulid of m1–3 strong, protolophid of m1–3 high, hypoconulid of m1–2 strong, cristid obliqua of m1–3 oriented toward the protoconid, postcristid of m3 high. Differs from *Pliolophus* by the diastema between P1 and P2, with P1 closer to C than to P2, the presence of a postprotocrista on P3, the protocone of P4 positioned below the paracone, the usually strong postprotocrista on P4, the stronger parastyle on M1–3, the stronger metaconule on

M1–3, sometimes merged in the metaloph, the p1 closer to the canine than to p2, or contacting it, the absence of entoconid on p4 and the higher protolophid on m1–3. Differs from *Hyracotherium* by the P1 closer to C than to P2, the stronger postprotocrista on P4, the stronger parastyle on M1–3 and the weaker metaloph constriction on M1–3. Differs from *Hallensia matthesi* by the usually strong postprotocrista on P4, the very large parastyle on M1–3, the ectoloph of M3 that is more lingually directed than on M1–2, the presence of a weak hypoconid on p2, the large paraconid on p4, the angular curve of the paralophid on p4, the absence of entoconid on p4, the strong labial cingulid on m1–3, the higher protolophid on m1–3, and the higher and more developed postcristid on m3. Differs from *Hyracotherium* and *Hallensia matthesi* by the more anterior border of the orbit in lateral view and more anterior infraorbital foramen.

Pliolophus Owen, 1858

Fig. 2

Junior synonyms: *Sifhippus* Froehlich, 2002;

Minippus Froehlich, 2002;

Arenahippus Froehlich, 2002

Type species: *Pliolophus vulpiceps* Owen, 1858 by original designation.

Included species: *Pliolophus grangeri* (Kitts, 1956); *P. pernix* (Marsh, 1876); *P. sandrae* (Gingerich, 1989); *P. aemulor* (Gingerich, 1991); *P. barnesi* Hooker, 2010; *P. quesnoyensis* Bronnert, Gheerbrant, Godinot & Métais, 2017.

Distribution: United States, United Kingdom, France, Belgium.

Emended diagnosis: As in *Cardiolphus*, the anterior border of the orbit is close to P4/M1 and the posterior border of the infraorbital foramen is above the border between P2 and P3. Post-P1 diastema absent or reduced, protocone of P2 small and poorly distinguished from the cingulum, endoprotocrista, and postprotocrista usually absent or weak on P3 and P4, protocone positioned centrally on P3-4, lingual cingulum of M1-3 usually strong, metaconule weak but distinct on M1-3, centrocrista straight, labial side of the metacone slightly flattened compared to the paracone on M1-3, posterior border of the symphysis below p1 or between p1 and p2, post-p1 diastema absent or reduced (p1 closer to p2 than to the canine), paraconid of p3-4 large, weak entoconid on p4 poorly distinguished from the cingulid, metaconid of the lower molars very weakly twinned, protolophid and hypolophid of m1-3 notched, cristid obliqua oriented closer to the protoconid than to the metaconid, hypoconulid connected by a crest to the hypoconid or entoconid. Differs from *Cardiolphus* by the much more reduced or absent diastema between P1 and P2, the postprotocrista of P3 usually absent, the protocone of P4 positioned centrally, the weak or absent postprotocrista on P4, the weaker parastyle of M1-3, the usually weaker metaconule on M1-3, the p1 closer to p2 than to the canine, the presence of a weak entoconid on p4 and the notched protolophid on m1-3. Differs from *Hyracotherium* by the weak protocone on P2, the protocone of P3-4 positioned centrally, the straight centrocrista on M1-3, the weaker metaloph constriction on M1-3, and the slightly flattened labial side of the metacone on M1-3. Differs from *Hallensia matthesi* by the presence of a small protocone on P2, the protocone of P3-4 positioned centrally, the larger parastyle on M1-3, the usually weaker metaconule on M1-3, the flattened labial side of the metacone compared to the paracone, the more anterior posterior border of the symphysis of the mandible, the more anterior position of the posterior foramen mentale, the p1 closer to p2 than the canine, the presence of a weak hypoconid on p2, the presence of a large paraconid on p3-4, the angular curve of the paralophid on p4, a weak and low hypolophid usually present on p4 and the hypoconulid connected by a crest to the hypolophid or hypoconid on m1-2. Differs from *Hyracotherium* and *Hallensia matthesi* by the more anterior border of the orbit in lateral view and more anterior infraorbital foramen, the reduced or absent diastema between P1 and P2, the absence of postprotocrista on P3 and the weaker metaconule on P4.

Earliest Known Perissodactyls Are Not Closely Related to Horses.

The phylogenetic analysis provided 1254 most parsimonious trees of 760 steps. The majority-rule (50%) consensus tree is almost entirely resolved (Fig. 3), with a Retention index (RI) of 0.61, a Consistency index (CI) of 0.39 and a Homoplasy index (HI) of 0.85. The strict consensus tree is presented in *SI Appendix*. Seventeen additional nodes are resolved on the majority-rule consensus tree compared to the strict consensus. These uncertainties appear inside the clade *Pliolophus*, Tapiromorpha and Hippomorpha. In addition, the dichotomy between Tapiromorpha and Hippomorpha is only supported in the majority-rule consensus tree (with a frequency value of 73). The Bremer support values are low, with most nodes having only a support of 1. This may be due to the limited number of characters and thus of potential synapomorphies.

Our phylogeny redefines our vision of early perissodactyl evolution and particularly that of North American equoids. Previously, they were all generally considered to belong to a single *Hyracotherium* lineage (25–27), even though *Hyracotherium* was also considered as a wastebasket taxon (6, 28). Our analysis shows that *Hyracotherium* and many taxa previously referred to as *Hyracotherium* must be excluded from Equoidea, and even from Hippomorpha (even in the strict consensus tree). Among those,

Pliolophus, senior synonym of *Sifhippus* and *Arenahippus*, is now considered as a stem-perissodactyl instead. Previously, *Hallensia* and sometimes *Hyracotherium* were occasionally recovered as nonequoids in several other phylogenies (16, 18, 29). *Arenahippus* was also recently recovered as a nonequoid perissodactyl by Rose et al. (21), but not *Sifhippus*. A table summarizing all the characters differentiating *Hyracotherium* from *Sifhippus*, *Arenahippus*, *Systemodon*, and *Xenicohippus* is provided in *SI Appendix*, Table S1.

Systemodon tapirinum and “*Xenicohippus*” *osborni* from the early Eocene (Wasatchian) of North America are considered as the earliest-branching hippomorphs in our majority-rule consensus tree. The first Equoidea only appeared after diverging from stem-hippomorphs during the early Eocene, but not during the earliest Eocene. Based on our phylogeny (strict and majority-rule), “*Propalaeotherium*” *helveticum* from the middle Eocene (MP14) of Egerkingen (Switzerland) is considered as the earliest-branching equoid (Bremer support = 3). The genus *Propalaeotherium* is here paraphyletic, as also found by Remy (30) and Remy et al. (31) and should thus be entirely revised. Brontotherioidea are deeply nested within Hippomorpha, as recovered by Froehlich (32), and sister-group of the European *Pachynolophus* (in the majority-rule consensus tree), rather than belonging to Tapiromorpha (21). In our phylogeny, Palaeotheriidae may be paraphyletic, or limited to *Metanchilophus* and *Palaeotherium*. Derived palaeotheres were out of the scope of our study and should be reevaluated with a larger taxonomic sample. Finally, we find that Chalicotheriidae are deeply nested in Tapiromorpha, and sister-group of Lophiodontidae (in both the majority-rule and strict consensus trees), thus supporting the Ancylopoda hypothesis (18, 33) rather than a close relationship with Palaeotheriidae (29).

The clade Hippomorpha, that includes *Systemodon* and all other taxa more closely related to it than to *Erihippus*, is supported by five unambiguous synapomorphies: The anterior border of the choanae is at the level of M2, or anterior, the metaconule of P3 is present but weak, the height of the corpus mandibulae is constant and the cristid obliqua of p4 and of m1-3 is oriented toward the metaconid or closer to the metaconid than to the protoconid (this state is preserved on m1-3 in all hippomorph taxa). The orientation of the cristid obliqua on m1-3 is an important character to distinguish hippomorphs from tapiromorphs. Indeed, among all other perissodactyls, only Lophiodontidae and Chalicotheriidae (which form the clade Ancylopoda) share this trait with hippomorphs, indicating a case of convergence between Ancylopoda and Hippomorpha. Other ambiguous synapomorphies of Hippomorpha are the small size of the paraconid of p3 and of p4.

Tapiromorpha are only characterized by two unambiguous synapomorphies: The paraconule of upper molars is indistinctly merged in the protoloph, without strong constriction, and the length/width ratio of m1/2 is above 1.45. Eight additional synapomorphies may support this clade but are ambiguous due to unknown states in *Erihippus tingae*, although they are all unambiguously present in the next more derived taxon, *Karagalax*. These synapomorphies are the P1 contacting P2, the protocone located below the paracone of P3, the paraconule merged in the protoloph of P3, the absence of diastema between lower incisors and canines, the presence of a paraconid on p1, the strong labial cingulum on p3-4, and the high protolophid on p3 and on p4.

Synonymy of *Sifhippus* and *Arenahippus* with *Pliolophus*.

Sifhippus and *Arenahippus* were two genera created based on a phylogenetic analysis (6). They are both restricted to the early and early-middle Wasatchian of Wyoming and Colorado. Prior to revision, the species referred to these two genera (“*S.*” *sandrae*,

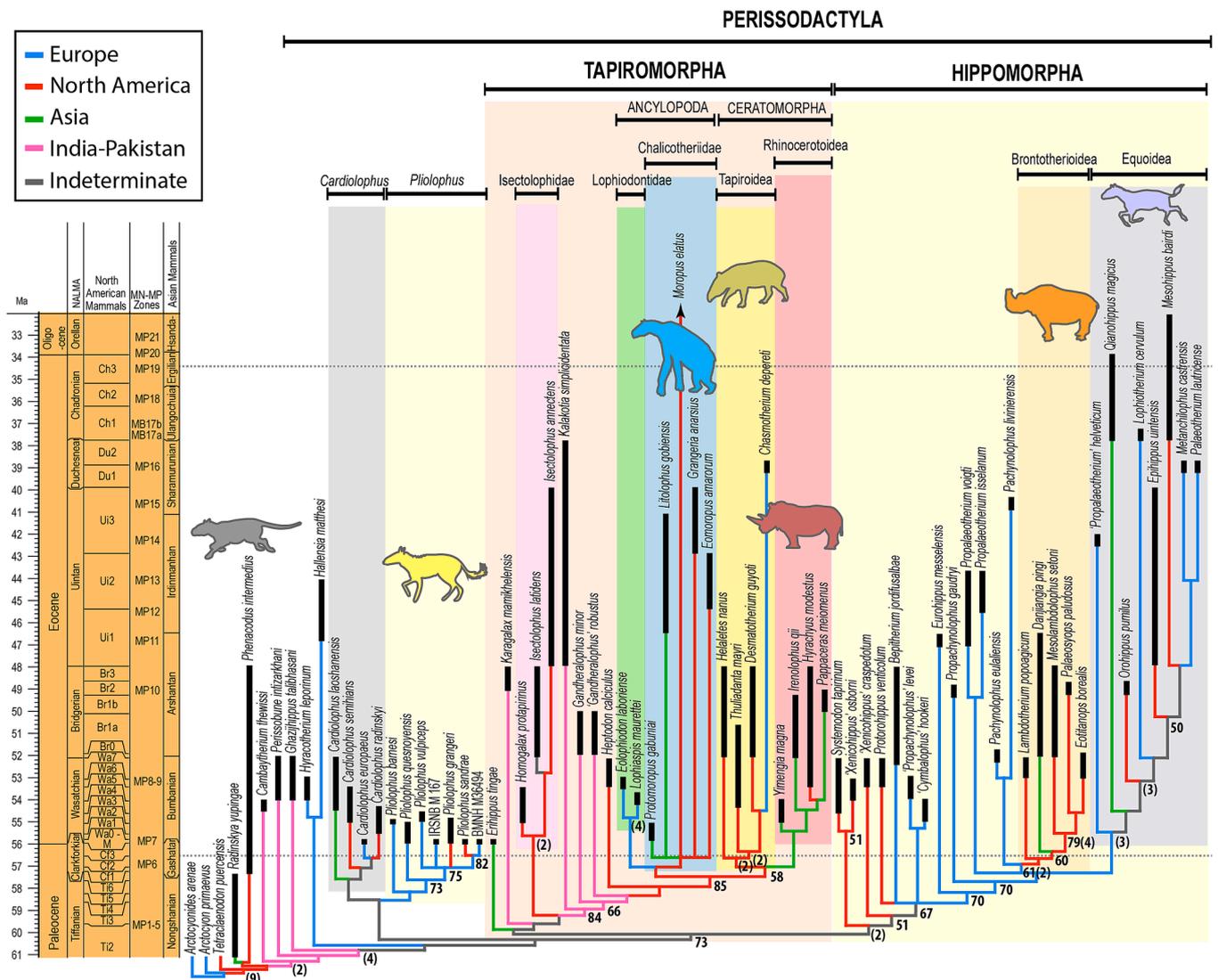


Fig. 3. Majority-rule (50%) consensus of 1254 trees (760 steps) of early perissodactyls, calibrated in time. The matrix consists of 71 terminals and 102 characters. Numbers below nodes indicate the majority rule consensus frequencies below 100%, whereas numbers between parentheses indicate Bremer support values that are above 1. Branch colors represent the most parsimonious paleobiogeographic reconstruction obtained in Mesquite. Black lines represent the temporal distributions of the taxa. Silhouettes modified from Phylopic (www.phylopic.org) public domain images. See [Datasets S2](#) and [S3](#) for references, and detailed ages and occurrences of each taxon.

A. grangeri, *A. aemulor*, and *A. pernix*) were all referred to as *Hyracotherium* (25). Our results show that at least the two species *S. sandrae* and *A. grangeri* (type species of their genus) should not be referred to the genus *Hyracotherium*.

In our analysis, the clade comprising *Sifrihippus sandrae*, *Arenahippus grangeri*, and all species of *Pliolophus* is supported by four unambiguous synapomorphies: the central position of the protocone on P3, the strong and continuous lingual cingulum on M1-3, the slightly flattened labial side of the metacone on M1-3, and the metaconid of p3 as strong as the protoconid. Four additional ambiguous synapomorphies may also support this clade. *Sifrihippus sandrae* and *Arenahippus grangeri* are only characterized by one and two unambiguous synapomorphies, respectively. Secord et al. (34) already mentioned that characters used to separate *Sifrihippus sandrae* from *Arenahippus grangeri* are highly variable and not useful for generic identification, and referred both species to *Sifrihippus* pending formal revision. Many similarities have also been observed on the postcranial skeleton of *Pliolophus quesnoyensis*, *P. barnesi* and *Arenahippus grangeri* (14). Therefore, we consider that the two genera *Sifrihippus* and *Arenahippus* should

be considered as junior synonyms of *Pliolophus*, following the rule of priority in taxonomy.

Synonymy of *Chowliia* and *Cardiophus*. Unlike *Hyracotherium* and *Pliolophus*, which were named as early as in the mid-19th century (35, 36), *Cardiophus* and *Chowliia* have been named relatively recently. *Cardiophus* was created by Gingerich (25) based on specimens from the Bighorn Basin (Wyoming) and included a newly named species, *C. radinskyi*, type species of the genus, and *C. semihians*. *Chowliia* was named by Tong & Wang (37) with a new species from the early Eocene of Wutu (China), *Chowliia laoshanensis*, and another new species from the earliest Eocene of Le Quesnoy (France), *Chowliia europea*, was later referred to this genus. Both genera were considered as Isectolophidae. However, most phylogenies were unable to retrieve a monophyletic clade for Isectolophidae comprising *Isectolophus*, *Homogalax*, *Cardiophus*, and *Chowliia* (6, 19, 21, 29, 38–44). The family Isectolophidae should thus be reevaluated.

According to our phylogeny, only *Homogalax protapirinus*, *Isectolophus latidens*, and *Isectolophus annectens* form a clade that

can be named Isectolophidae (in the strict and majority-rule consensus trees), as previously considered by Radinsky (45). *Cardiolophus radinskyi*, *Cardiolophus semihians*, “*Chowliia*” *laoshanensis*, and “*Chowliia*” *europa* are found together in another clade, more basal than *Isectolophus* and sister group of *Pliolophus*. This result is consistent with the first description of “*Chowliia*” *laoshanensis* by Tong and Wang (37), who noted that “*C.*” *laoshanensis* was “very similar to contemporaneous *Homogalax* and *Cardiolophus* in dental morphology” but “closer to *Cardiolophus* than to *Homogalax*”. In our phylogeny, the clade including *Cardiolophus radinskyi*, *Cardiolophus semihians*, “*Chowliia*” *laoshanensis*, and “*Chowliia*” *europa* differs from the clade *Pliolophus* and is supported by five unambiguous synapomorphies: the presence of a strong endoprotocrista or postprotocrista forming a metaloph on P4, the parastyle of M1-3 is very large, the p1 is closer to the lower canine than to p2, or contacting the canine, the entoconid of p4 is totally absent, and the postcristid of m3 is high. Five additional synapomorphies may also further support this clade, but their position is ambiguous. The genus *Chowliia* also shares with *Pliolophus* two unambiguous synapomorphies: The anterior border of the orbit is close to P4/M1 (it is close to M1/2 in *Isectolophus* and *Homogalax*), and the labial cingulum of P3-4 is absent, weak, or discontinuous.

“*Chowliia*” *laoshanensis* (type species of the genus) is found at the base of the genus in the strict consensus tree, but only has four autapomorphies: the presence of a weak metaconule on P3, the surface of M3 smaller than M2, the p1 contacting the canine, and the twin metaconids clearly distinct. However, three of those autapomorphies are also found in “*Chowliia*” *europa*, which is sister-group of *Cardiolophus radinskyi* (type species of *Cardiolophus*) and not “*Chowliia*” *laoshanensis*, whereas the last character is unknown for this species (position of the p1). This shows that these characters are subject to variability within this clade and do not justify separating *Chowliia* from *Cardiolophus* as a distinct genus, and so we consider *Chowliia* as a junior synonym of *Cardiolophus*, according to the rule of priority in taxonomy.

Early Evolution of Perissodactyls and Paleobiogeography.

The question of the origin of perissodactyls remains far from resolved, but our phylogeny primarily supports an Asian origin of perissodactyls. Indeed, the most basal perissodactyl in our phylogeny (strict and majority-rule consensus tree), *Gazijhippus*, comes from Pakistan but dates from the early Eocene, between 54 and 52 Ma (46). Given its relatively young age, this would imply the existence of a ghost lineage, since derived perissodactyls are known from around 56 Ma. In addition, the two closest-sister groups to perissodactyls, *Perissobune intizarkhani* and *Cambaytherium thewissi*, also come from India–Pakistan. These two taxa belong to Anthracobunia according to Rose et al. (21) and are endemic to the Indian subcontinent (21), but *Perissobune* was originally considered as a perissodactyl. Our topology (strict and majority-rule consensus tree) indicates that it might be more closely related to perissodactyls than other Anthracobunia, but our sample of anthracobunids is too limited to completely refute the hypothesis that it belongs to this group; thus, we do not consider *Perissobune* as a perissodactyl. *Perissobune* is known from the same layer and locality as *Gazijhippus*, whereas *Cambaytherium* is only known from the Cambay Shale Formation of India, dated from around 54 Ma (21), which also indicates the presence of ghost lineages leading to those taxa. These ghost lineages could potentially indicate a poor fossil record for perissodactyls near the Paleocene–Eocene boundary in this region or globally.

Within Perissodactyla, the next more derived clade (*Hyacotherium*–*Hallensia*) is endemic to Europe, whereas the next one (*Cardiolophus*–*Pliolophus*) is found in North America, Asia, and Europe, indicating fast dispersals on the three continents of the Northern Hemisphere, at the beginning of the radiation of perissodactyls. As mentioned previously, earliest Eocene perissodactyls were an exception among other mammals, because of their very large number of genera. In addition, many of these genera were monospecific, and their distribution was often restricted to one continent, or even one locality (13, 18, 33, 38). This greatly differs from other earliest Eocene mammals, which comprise genera that are often found in at least two continents, such as Hyaeodontidae (e.g., *Prototomus* and *Galecyon* in North America and Europe, and *Arfia* in North America, Europe, and Asia) (47–49), Carnivora (e.g., *Gracilocyon* in North America and Europe) (49–51), primates (e.g., *Teilhardina* in North America, Europe, and Asia) (49), Hyopsodontidae (e.g., *Hyopsodus* in North America, Europe, and Asia, and *Lessnessina* in Europe and Asia) (52), Artiodactyla (e.g., *Diacodexis* in North America, Europe, and Asia) (53, 54), Phenacodontidae (e.g., *Lophocion* in Asia and North America, and *Phenacodus* in North America and Europe) (55, 56), or Rodentia (e.g., *Microparamys* and *Paramys* in North America and Europe) (57). Here, we show that perissodactyls do not differ from other modern mammals.

According to our paleobiogeographic optimization (Fig. 3), many uncertainties remain on the diversification of early perissodactyls. However, trends related to the major dichotomy between Hippomorpha and Tapiomorpha can be observed. Early tapiromorphs are indeed predominantly Asian and North American according to our analysis. Indeed, during the early Eocene, the only European tapiromorphs are represented by Lophiodontidae. On the contrary, early hippomorphs are mostly European and North American. Indeed, Palaeotheriidae are endemic to Europe (except some very rare exceptions) (58), whereas Equidae remain endemic to North America during the Eocene. Furthermore, this topology strongly supports a European origin of the two major hippomorph clades: Brontotherioidea and Equoidea. This is quite unexpected, as brontotheres are almost exclusively found in Asia and North America and very rarely in Europe (59). Interestingly, *Lambdotherium*, one of the earliest brontotheres, was thought to be closely related to Palaeotheriidae (44), which are endemic to Europe, and thus does suggest strong connections between North American and European early hippomorphs. Consequently, paleobiogeography may have played an important role in shaping the diversification of perissodactyls, with some groups remaining endemic or partially endemic in Europe, such as Lophiodontidae and Palaeotheriidae. On the contrary, the earliest known perissodactyls such as *Pliolophus* and *Cardiolophus* had a widespread distribution in the Northern hemisphere, indicating fast dispersals between North America, Europe, and Asia during the PETM.

Materials and Methods

Abbreviations. MP: Reference level of the European Paleogene land mammal scale; Wa: Wasatchian North American land mammal age.

C/c: upper/lower canine; M/m: upper/lower molar; P/p: upper/lower premolar. CI: consistency index; RI: retention index.

Photos. The dental specimens and casts were photographed using a digital camera and coated with ammonium chloride to bring out the morphological structures and obtain a uniform colour scale.

Morphological Character Matrix. A morphological character matrix (Dataset S1) was created for this study with an emphasis on characters resolving the phylogeny of the earliest Eocene perissodactyls. It comprises 101 characters, including seven

cranial, 42 from the upper cheekteeth, five mandibular, and 47 from the lower dentition. No postcranial characters were included in this matrix, because they are unknown or very incompletely preserved for many early Eocene perissodactyls and because of the potential risk of attributing them to the wrong taxon, when craniodental remains are not clearly associated with a postcranial skeleton. This is a recognized problem that has been previously discussed (42).

More than 50% of the characters are multistate. We used the "B coding" approach (or "composite coding strategy") formulated by Pleijel (60), to favor the independency and nonredundancy of characters (61). In addition, all of them can be considered as forming morphological sequences and are thus considered as additive, such as for example character 15 (P2 hypocone: 0 = absent, 1 = very weak, 2 = present, strong), except characters 25, 27, 31, 34, 41, 42, and 94, which do not form morphoclines. The large number of multistate characters also explains the relatively low number of characters in our matrix.

Character states were scored based on original specimens, casts, and literature. Polymorphism was taken into account during the scoring of the characters matrix, and all observed states were thus scored when they were present on several specimens from a single locality. Character names and state names are given in *SI Appendix, Table S2*.

Taxonomic Sample. The matrix comprises a total of 71 terminals. The list of all sources and specimens used for the scoring of the matrix, as well as the distribution of each taxon, is provided in *SI Appendix, Table S3*. The main goal of our phylogenetic analysis was to study early Eocene perissodactyls, based on recent advances on European perissodactyls, and in particular, the discoveries of several new taxa (namely *Pliolophus barnesi* in 2010, *Pachynolophus eulaliensis* in 2013, *Eolophiodon laboriense* in 2015, *Pliolophus quesnoyensis* in 2017 and "*Chowliia*" *europaea* in 2018) and replace them in the tree of perissodactyls. We thus included several early representatives of all major groups of perissodactyls: Brontotherioidea, Equoidea, "Palaeotheriidae", Isectolophidae, Lophiodontidae, Chalicotheriidae, Rhinocerotidae, and Tapiroidea to test the position of these early perissodactyls.

We also included two specimens from the earliest Eocene of Europe that are fairly complete, but whose identification has been debated: the well-preserved lower jaw IRSNB M 167 from Erquelines (Belgium) and another fragmentary lower jaw BMNH M36494 from Ferry Cliff (UK).

Cymbalophus cuniculus had to be excluded from the analysis, as it is only represented by a few isolated teeth from Kyson (UK), and included mostly unscored character states, and thus acted as a wildcard taxon. The strict consensus tree resulting from this analysis is included in *SI Appendix*. We did not include *Minippus* in our sample, as it was recently shown that it is a junior synonym of *Sifrhippus* and that *M. index* and *M. jicarillai* were both junior synonyms of *Sifrhippus sandrae* (62).

We included a variety of outgroup taxa, comprising condylarths, phenacodontids, *Radinskya* and anthracobunids, and *Arctocyonides arenae* was set as outgroup during the analysis in TNT.

Phylogenetic Analysis. The matrix was analyzed with a parsimony algorithm in TNT Version 1.6 (63) and is available in *Dataset S1*. All multistate characters except characters 25, 27, 31, 34, 41, 42, and 94 were considered as additive/ordered. *Arctocyonides arenae* was set as outgroup. We ran the analysis using the Traditional Search in TNT using the Tree Bisection and Reconnection (TBR) heuristic search algorithm. We ran 10'000 replicates saving up to 10 trees per replication. Several random seeds were tested and was set to 1 in the TNT file. Bremer support values were calculated by running the Bremer.run script in TNT. Throughout the text, we define "unambiguous synapomorphies" as synapomorphies whose position at the node is not ambiguous and which do not depend on the choice of character optimization.

Data, Materials, and Software Availability. All study data are included in the article and/or [supporting information](#).

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