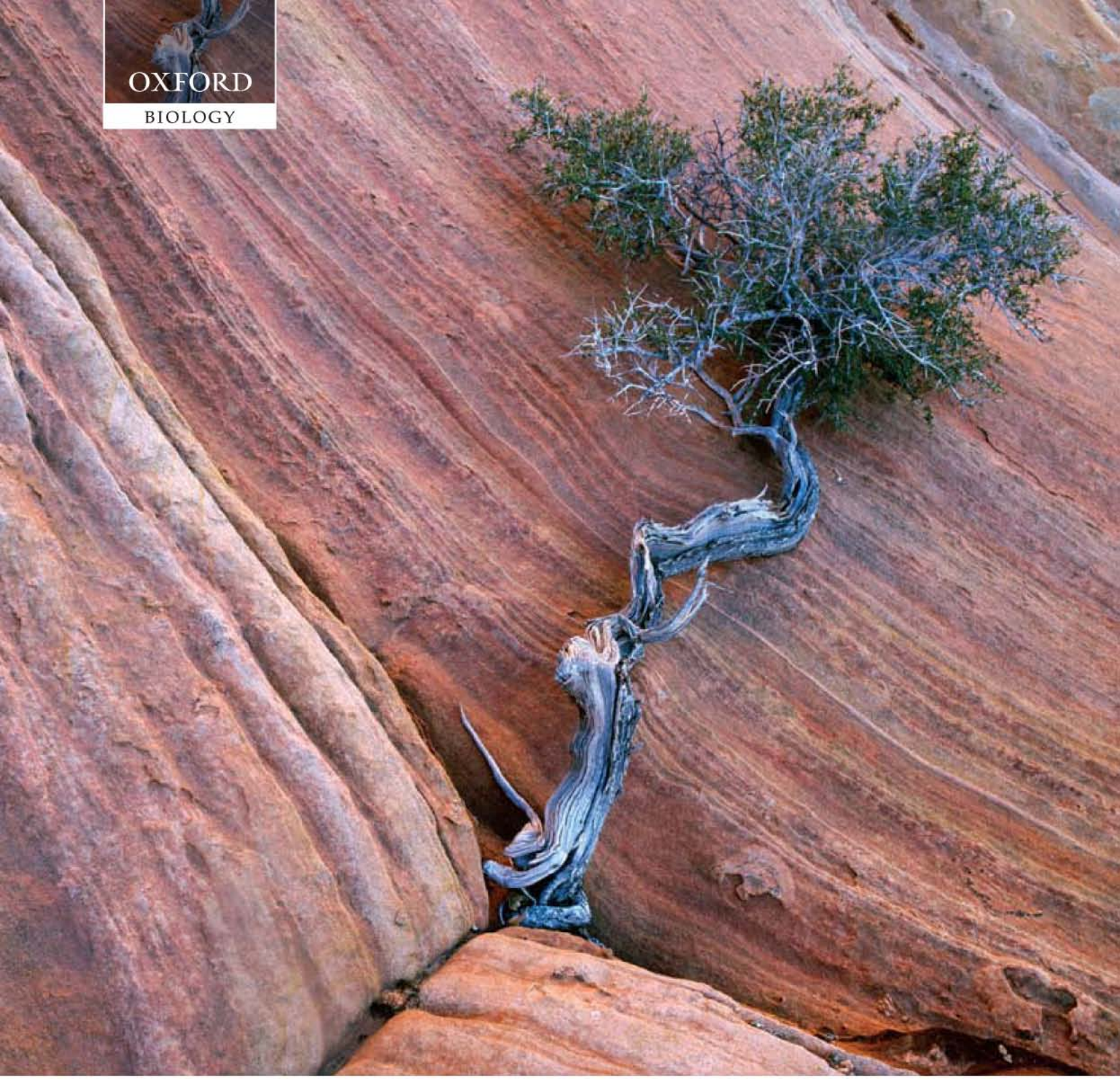

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Rhinoceroses, tapirs, and horses (Perissodactyla)

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Abstract

Rhinoceroses, tapirs, and horses, comprising 16 species, constitute the three surviving families of the mammalian Order Perissodactyla. Based on recent DNA sequence data, the perissodactyl timetree supports previous views of diversification into two suborders: Hippomorpha (containing living horses, asses, and zebras) and Ceratomorpha (containing living rhinos and tapirs). Although once considered perissodactyls, recent DNA sequencing studies have provided new evidence that hyraxes are neither perissodactyls nor closely related to them. The earliest divergence among these three families occurred ~56 million years ago (Ma), and the extant species of Equidae diversified most recently.

Perissodactyls comprise the odd-toed ungulates, an order of mammals that was once more species-rich and that occupied a wide variety of terrestrial habitats. The surviving species of this order include the horses, asses, zebras of the Family Equidae (Fig. 1), four extant species of tapirs that are included in a monogeneric family, Tapiridae, and the surviving species of rhinoceros that constitute the four genera of the Rhinocerotidae (*1*). The Equidae contains seven extant species (*2*). Four species of tapir survive, and five extant species of rhinoceros survive in Africa and Asia (*1*).

Early perissodactyls are thought to have diverged from condylarths. Combined mitochondrial DNA and nuclear DNA sequence data sets, as well as analysis of rare insertions and deletions, support carnivoriform and phioldotiform affinities for extant perissodactyls, these ordinal groups being part of the Laurasiatheria (*3, 4*). *Hyracotherium*, or a *Hyracotherium*-like hippomorph, is generally regarded as the ancestral hippomorph from which all living equids descend, while *Hyrachyus* is hypothesized to be the ancestral ceratomorph, the ancestor of tapirs and rhinos. Although a remarkable radiation of hippomorphs took place and, eventually, all continents (except Australia and Antarctica) were occupied by hippomorph perissodactyls, the only extant genus of hippomorphs is *Equus*, regarded as monophyletic.

Within the Ceratomorpha, cladogenesis of tapiriform and rhinocerosiform perissodactyls resulted in a remarkable radiation. Subsequently, extinctions have reduced the tapirs to a single genus and the rhinoceroses to four genera. Of the four species of tapirs, three occur in Central and South America and one inhabits Asia. The three extant families of Perissodactyls, Equidae, Tapiridae, and Rhinocerotidae, are regarded as monophyletic.

Multiple studies of mammalian phylogeny and systematics have produced data estimating the divergence of Perissodactyla from other orders (*3–9*) and the divergence of the Ceratomorpha and Hippomorpha (*3, 4*). Nearly all of these estimates incorporate a fossil calibration for the horse–rhino divergence of 58–54 Ma and, accordingly, the consistency among the Perissodactyla divergence time estimates is influenced by this common

Fig. 1 Grévy's Zebra (*Equus grevyi*) survive in Northern Kenya and Somalia. Credit: Zoological Society of San Diego.

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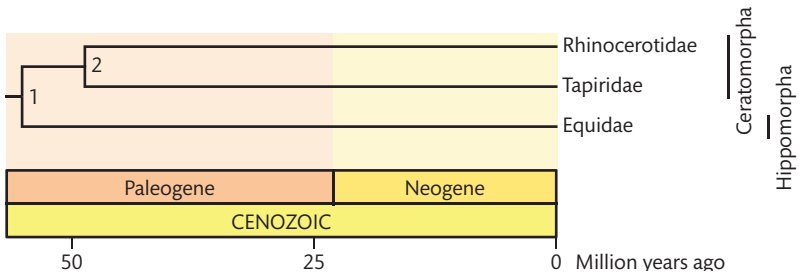

Fig. 2 A timetree of rhinoceroses, tapirs, and horses (Perissodactyla). Divergence times are from Table 1.

calibration. Poux *et al.* (*9*) obtained similar results if the horse–rhino calibration point was omitted, incorporating five additional well-established fossil calibration points. By sequentially removing each calibration to exclude the possibility that individual calibration constraints produce bias in the dating analyses, the molecular clock dates remained highly congruent, lending credence to the estimates noted in Table 1. Time estimates for clade divergences based on molecular data have been developed for events within each perissodactyl family (Fig. 2). Tougard (*10*) evaluated the divergence of the four rhinoceros genera utilizing *12S* and control region sequences. Additional control region sequence data have been provided by Fernando *et al.* (*11*). Mitochondrial *12S* and control region sequences were developed for extant equids by Oakenfull *et al.* (*12*), and additional control region sequences have been generated by Weinstock *et al.* (*13*). For tapirs, mitochondrial *cytochrome oxidase II* and *12S* sequences have been generated by Norman and Ashley (*14*).

The evolution of monodactyly in horses became, for a time, a classic tale of orthogenesis, told as if morphological evolution was a straightforward pattern of cladogenesis that occurred with replacement of one species by another via a rather linear process (*16*). More recent considerations have emphasized patterns of species proliferation, migrations, extinctions, and survival of relatively few lineages to lead to new taxa that undergo a similar process (*16*). In this way, the evolution of *Equus* remains an instructive example of the scientific interpretation of fossil evidence and the changing patterns of scientific endeavor and interpretation itself (*17*). Another feature of note in equids is their rapid rate of chromosomal evolution, varying from a diploid number of 66 chromosomes in Przewalski's Horses to 32 chromosomes in Mountain Zebras (*18*). Dramatic chromosomal differences occur between the Old World and New World tapirs, while rhinoceros karyotypes appear to have changed little over the period of divergence of the four extant genera (*15*).

Once dominant ungulates, perissodactyl species diversity declined as artiodactyls radiated (*19*). However, this trend has accelerated in the last centuries, largely as a result of human activities. Hunting and habitat loss have affected equids, tapirs and rhinos alike. Domestication of horses and asses has seemingly assured their continued survival, albeit under the selective influence of humans. The only extant perissodactyl not currently under some level of conservation concern is the Plains Zebra, which in some African regions, survives in numbers from hundreds of thousands to millions of individuals. That its extinct component subspecies, the Quagga, was once the most numerous zebroid in all of southern Africa, is not a fact that should lead to complacency. The Grévy's Zebra has declined recently due to drought and human–wildlife conflicts in a region of the world undergoing human suffering and strife (*20*). But, perhaps the most threatened perissodactyls are the rhinoceroses. The Javan Rhinoceros numbers ~60 individuals in Indonesia and perhaps fewer than six in Vietnam (*21*). The Sumatran Rhinoceros has continued to decline as forest habitat is replaced by agricultural and agroforestry operations in concert with continued poaching impacts (*22*). The value of Rhinoceros horn and other body parts continues to place rhino species at great risk (*23*). The Northern White Rhinoceros may be extirpated from the Congo basin where, in its last stronghold in Garamba National Park, in spite of heroic efforts, numbers continue to decline with just five animals remaining (*24*). The Southern White Rhinoceros, once on the brink of extinction, has recovered dramatically (*23*)—with appropriate intervention, rhinos need not go extinct.

Table 1. Divergence times (Ma) and their credibility/confidence intervals (CI) among rhinoceroses, tapirs, and horses (Perissodactyla).

Timetree		Estimates													
Node	Time	Ref. (*3*)		Ref. (*4*)		Ref. (*5*)		Ref. (*6*)		Ref. (*7*)		Ref. (*8*)		Ref. (*9*)	
		Time	CI	Time	CI	Time	CI	Time	CI	Time	CI	Time	CI	Time	CI
1	55.1	56.5	58–54	56.3	58–54	55.2	59–52	56.3	59–54	53.4	56–51	53	58–50	54.8	59–50
2	48.6	48.8	52–45	48.4	52–44	–	–	–	–	–	–	–	–	–	–

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