Evolution and Fossil Record of Old World Rhinocerotidae

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Abstract

On the edge of extinction and restricted to scattered areas in Africa and tropical Asia today, rhinoceroses were once conspicuous components of mammalian guilds in most landmasses. The fossil record of the family Rhinocerotidae, ranging the last 40 million years (Ma), includes ~200 extinct species assigned to ~67 genera. They originated in eastern/South Asia and North America, before they dispersed into Central Asia, and Europe after the Eocene–Oligocene transition (33.9 Ma) and into Afro-Arabia by Early Miocene times (~20 Ma). Extinct rhinocerotids widely exceeded their recent kin regarding morphological disparity (horn shape and number; body weight; limb bone proportions) and ecological diversity (feeding habits; habitats). Niche partitioning may explain the presence of multispecific rhinocerotid assemblages in Old World Miocene localities. Their taxonomic diversity dropped drastically by the latest Miocene, with the progressive disappearance of hornless and hippo-like aceratheriines and teleoceratines. Only the rhinocerotines (modern rhinoceroses and kin) and gigantic elasmotheriines survived into the cold-dominated Pliocene–Pleistocene world. Cold steppe dwellers *Elasmotherium* and woolly rhino (*Coelodonta*) became extinct by latest Pleistocene times, leaving five living species as the last Holocene rhinocerotids. A revised list of Old World rhinocerotid genera and species is provided for the Middle Eocene–Recent time interval.

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Introduction

Only five species of rhinoceros are roaming African savannas and riverine areas of tropical Asia today. All of them are highly endangered or on the edge of extinction, due to human activities in the last centuries (overhunting, poaching, and habitat loss; Liu et al., 2021). This miserable condition is fully at odds with the flourishing past history of the Rhinocerotidae family, spanning the last 40 million years over most landmasses (Antoine et al., 2003; Bai et al., 2020).

This chapter aims at outlining the evolutionary history of rhinoceroses in Eurasia and Afro-Arabia, based on their fossil record and palaeobiogeography, and at depicting their past diversity and disparity, from the Eocene epoch onward. Indeed, more than 200 rhinocerotid species have been described in the Rhinocerotidae family since *Rhinoceros* Linnaeus, 1758 (NOW, 2021). At least 67 rhinocerotid genera are valid, further encompassing an unsuspected taxonomic diversity and an astonishing ecomorphological disparity (Cerdeño, 1998). Rhinocerotids originated in eastern Asia or North America, where their early diversification phases are documented in the fossil record, before they dispersed into Europe by the Eocene–Oligocene transition (33.9 Ma), and then into Afro-Arabia and Central America by Early Miocene times (~19.6 Ma; Antoine et al., 2003, 2010; Tissier et al., 2021a). Based on the available fossil record, the Old World's land masses gather about 80% of their taxonomic diversity (54 genera and 168 species; Appendix 1). Among other odd-toed ungulates (perissodac-

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tyls: horses, tapirs, and extinct relatives), Rhinocerotidae are the last living representatives of the Rhinocerotoidea superfamily. Rhinocerotids are now consensually considered as being closely related to giant rhinoceroses of the Eocene–Oligocene Paraceratheriidae family (Deng et al., 2021), whereas the Rhinocerotinae and Elasmotheriinae subfamilies are known to have split as early as ~36 Mya within Rhinocerotidae (Antoine, 2002; Kosintsev et al., 2019; Liu et al., 2021).

As a name, *Rhinoceros* means "horn-on-the-nose" or "nose-horn" in Ancient Greek. If this designation is particularly relevant and distinctive for recent rhino species, all of them having a nasal horn (and three species bearing an additional frontal horn), most extinct representatives of the rhinoceros family, or Rhinocerotidae, had no horn at all, as hypothesised through the absence of vascular prints on the concerned cranial surfaces. Indeed, this hornless condition was the standard in the early evolution of rhinocerotoids. Horns do occur only in rhinocerotids, and some extinct rhinocerotids had paired nasal horns (*Menoceras* and *Pleuroceros*) or lateral blades (*Diceratherium*), whereas other ones, such as derived elasmotheriines (*Sinotherium* and *Elasmotherium*), had a frontal dome/horn but no nasal one (Fig. 2.1). Regarding general body proportions and posture, some extinct rhinocerotids were short-legged and barrel-chested (teleoceratines and chilotheres), whilst other ones were slender-limbed runners (early rhinocerotids and elasmotheriines; Fig. 2.1).

This fascinating 40 million-years-long history over the Old World will be sketched in the next paragraphs.

Material and Methods

As far as possible and as this book is intended for a wide readership, we will avoid technical terms (anatomy, stratigraphy, and systematics) or explain them when necessary.

After a long stand-by throughout the twentieth century (Prothero & Schoch, 1989), the supraspecific classification of Rhinocerotidae and of their extinct relatives among Rhinocerotoidea was much improved in the last years. Here, generic and suprageneric systematics follow consensual arrangements as supported by morphoanatomical and molecular-based phylogenetic analyses published in the last decades (e.g. Antoine, 2002; Antoine et al., 2010, 2022; Geraads et al., 2012; Becker et al., 2013; Pandolfi, 2015; Tissier et al., 2018, 2021a; Bai et al., 2020; Liu et al., 2021; Pandolfi et al., 2021b).

Uppercase and lowercase letters are used for upper and lower teeth, respectively (C/c, canines; I/i, incisors; P/p, premolars; M/m, molars) and the rank of the concerned tooth in the tooth row is denoted by a number (e.g. 1–4 for premolars and 1–3 for molars).

The NOW Community Database (2021) and the rhinocerotid-focused Rhino Resource Center database (Geraads et al., 2021) were used as complementary sources for compiling stratigraphical and biogeographical data on Eocene–Recent rhinocerotid occurrences.

Rhinocerotid-yielding world maps were built with GPlates v2.3 (Müller et al., 2018), with Scotese's (2016) paleomaps as backgrounds.

Evolutionary History of the Old World Rhinocerotids

Rise Above (Eocene)

Genome-based estimated divergence times among Rhinocerotidae suggest that Elasmotheriinae and Rhinocerotinae would have split by 36 Mya, i.e. in the latest Eocene (Liu et al., 2021). Nevertheless, this estimated age does not consider the existence of stem rhinocerotoids and rhinocerotids pre-dating the concerned node (Fig. 2.1). Indeed, *Yimengia magna*, from the Early Eocene of China ca. 54 Mya, is considered as the earliest rhinocerotoid (Bai et al., 2020). Then, eastern Asia and North America would record the appearance of a wide array of non-rhinocerotid taxa in late Early and Middle Eocene times (Fig. 2.1). The small-sized *Teletaceras radinskyi* from the late Middle Eocene of North America is generally considered as the earliest true rhinocerotid, based on two characters (well-developed metastyle on M3, incisors developed as chisels and tusks; Hanson, 1989), but its rhinocerotid affinities have recently been challenged (Bai et al., 2020). Due to land connection between both landmasses, Eurasian rhinocerotids appear almost concurrently, in northeastern Russia (with *Teletaceras borissiaki*; Beliajeva, 1959). Yet, the Eocene rhinocerotid record is particularly elusive in Eurasia. Only a few deciduous dental remains of ? *Teletaceras* sp. and cf. *Teletaceras* sp. have been reported from the latest Middle Eocene of southern China by Antoine et al. (2003) and the Pondaung Fm. in Myanmar (Holroyd et al., 2006), respectively. In the Late Eocene, the record of Rhinocerotidae is still restricted to East Asia, with the northern "*Ronzotherium*" *brevirostre* from Mongolia (of uncertain affinities; Tissier et al., 2021a) and the southern *Guixia simplex* from the Yongle Basin in southern China, ?cf. *Guixia simplex* from Krabi in Thailand (Antoine et al., 2003), and *Epiaceratherium naduongense* from Naduong, northern Vietnam (Fig. 2.2a). The latter species is by far the best documented Eocene rhinocerotid in Eurasia, with complete cranio-mandibular remains, in particular retaining a complete anterior dentition (Böhme et al., 2013).

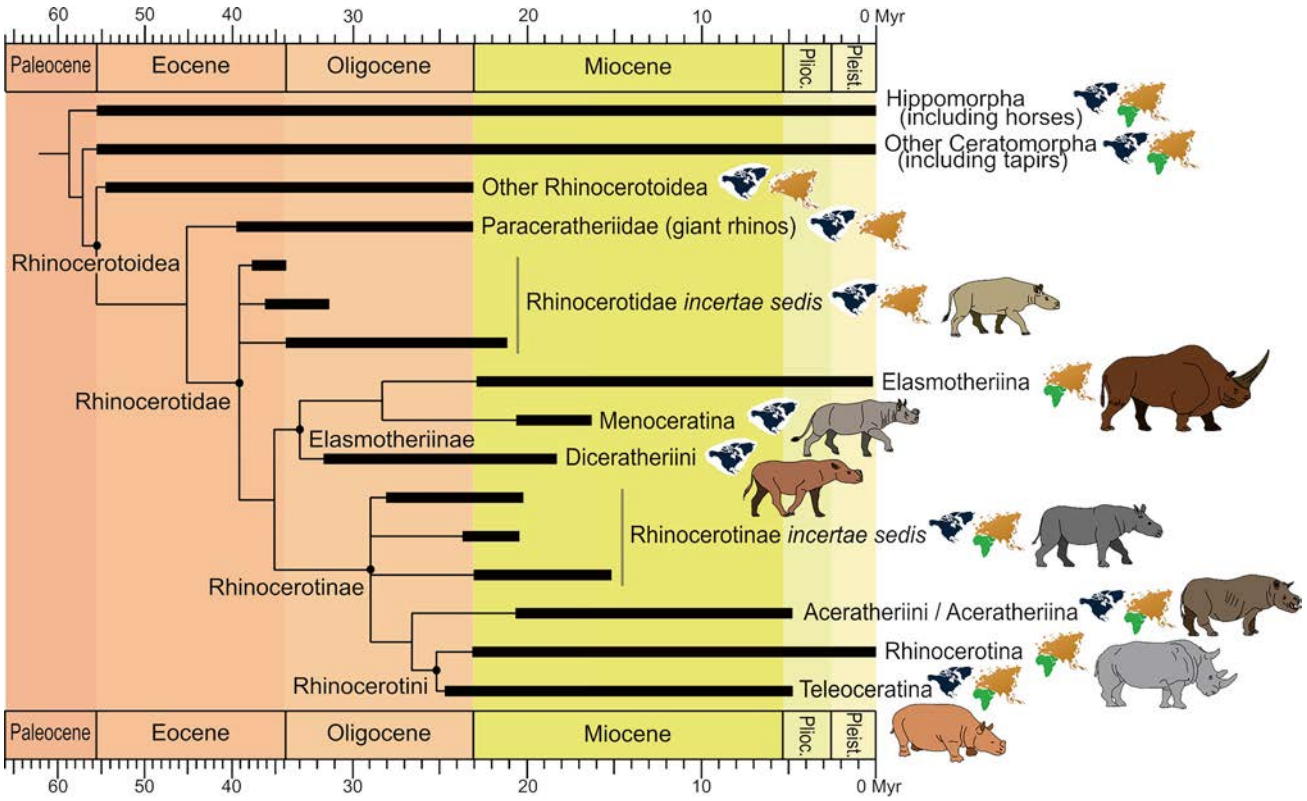

Fig. 2.1 Simplified phylogenetic tree of Rhinocerotidae among Perissodactyla, Ceratomorpha, and Rhinocerotoidea. Based on results from Antoine (2002), Antoine et al. (2010, 2022), Becker et al. (2013), and Pandolfi et al. (2021a). Horizontal bars stand for stratigraphical ranges, retrieved from NOW Community Database (2021) and the Rhino Resource Center database (Geraads et al., 2021). Divergence times are not constrained. Geographic regions considered are North America (black), Eurasia (brown), and Afro-Arabia (green). From top to bottom, rhinocerotid sketches are shown in the same scale and they depict *Trigonias*, *Elasmotherium*, *Menoceras*, *Diceratherium*, *Plesiaceratherium*, *Chilotherium*, *Ceratotherium*, and *Teleoceras*

Spreading Around (Oligocene)

The Oligocene epoch is a real milestone in the history of rhinocerotids, as most tribes are suspected to differentiate in the Oligocene (Fig. 2.1). They would further spread and diversify over most of the Eurasian landmass, including Central Asia, the Indian Subcontinent, Balkanatolia (sensu Licht et al., 2022; see next paragraph), and Europe (Fig. 2.2b). Nevertheless, and up to now, there is no Oligocene record of rhinocerotids in Afro-Arabia, which points to the presence of a long-lasting biogeographical barrier in the neighbouring region (Fig. 2.2b).

Indeed, the large-scale colonisation of Eurasia by rhinocerotids was likely triggered by the drastic climatic deterioration and environmental shift known to have occurred after the Eocene–Oligocene transition (EOT; 34–33.7 Ma) at a global level. This event was named "Grande Coupure" by the Swiss palaeontologist Stehlin (1909), who first observed an extreme shift in ungulate assemblages by that time interval in Western Europe. The colonisation of southeastern Europe by Asian mammals prior the EOT seems to be supported by the existence of an Eocene biogeographic province, notably encompassing Anatolia, the Balkans, and the Adriatic region and designated as Balkanatolia (Licht et al., 2022). After a period of strong endemism between 56 and 40 Ma, a terrestrial corridor connected this region to South Asia by the Late Bartonian onwards, thus facilitating the arrival of Asian land mammals; this configuration paved the way for their dispersal into southeastern Europe in western Europe around the EOT (see "Southern route" in Fig. 2.2b; Licht et al., 2022).

The Early Oligocene interval also documents the earliest multispecific assemblages, with the stem rhinocerotids *Molassitherium* sp. and *Aprotodon* sp. associated in Saint-Jacques, Inner Mongolia (Antoine et al., 2003, revised by Tissier et al., 2020) or *Ronzotherium filholi* and *Epiaceratherium magnum* in Villebramar, southwestern France (Brunet, 1979; Uhlig, 1999).

As for tropical Asia, i.e. the cradle of rhinocerotids in Eurasia (Fig. 2.2a, b), *Guixia youjiangensis* and *Epiaceratherium* cf. *magnum* are recognised in lower Oligocene deposits from the Yongle Basin in southern China and the Bugti Hills in Balochistan, respectively (Antoine

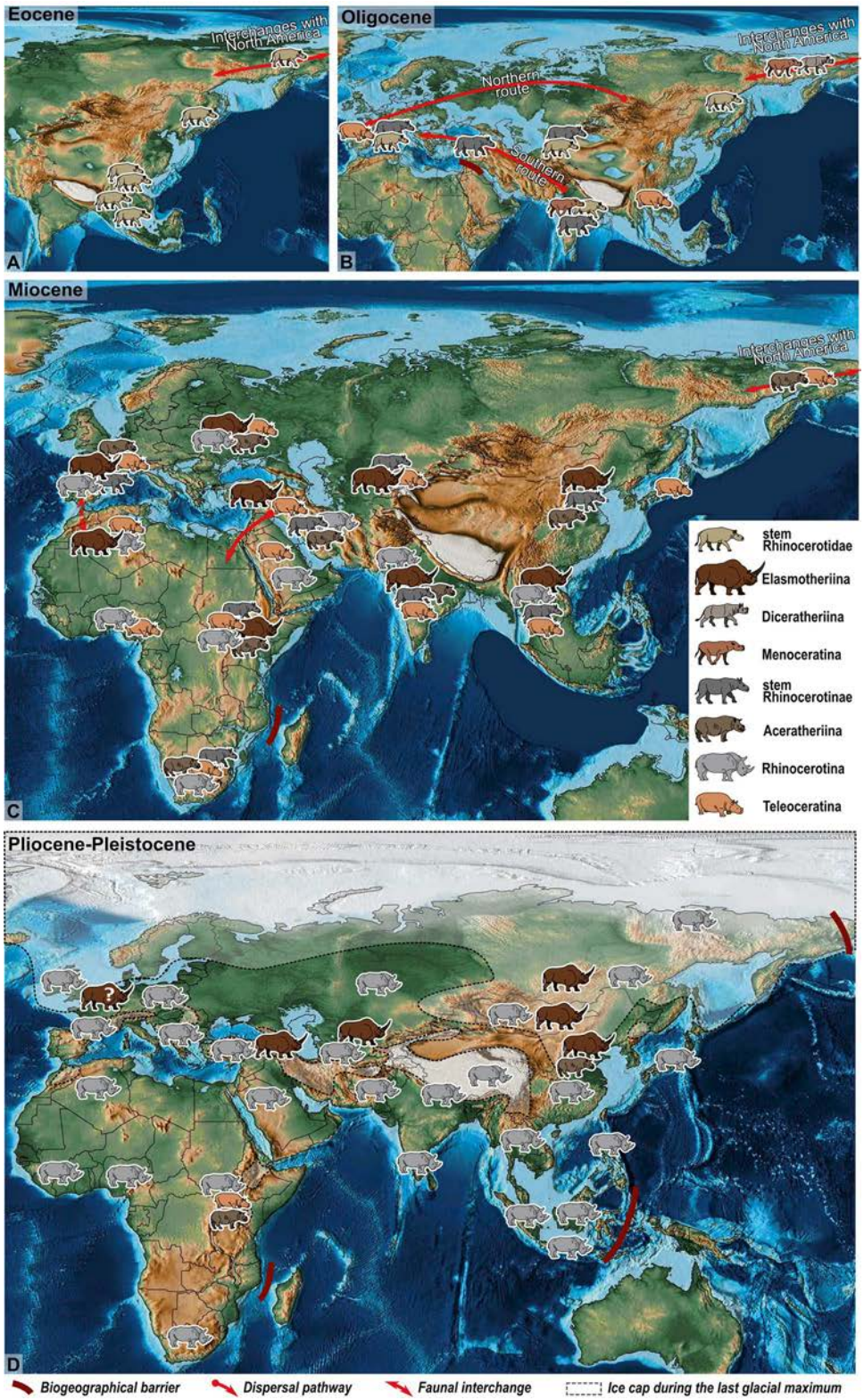

Fig. 2.2 Historical palaeobiogeography of rhinocerotids in the Old World, over Eocene (**a**), Oligocene (**b**), Miocene (**c**), and Pliocene–Pleistocene times (**d**). The presence of *Elasmotherium* in the Pleistocene of Western Europe is disputed (see Antoine, 2002). Paleomaps are from Scotese (2016). See Fig. 2.1 for details on phylogenetic relationships

et al., 2003). The early teleoceratine *Brachydiceratherium* cf. *lamilloquense* is described from upper Oligocene lignites from central Thailand (Marivaux et al., 2004; Sizov et al., 2024). Later on, *Aprotodon smithwoodwardi*, with a hippo-like mandibular symphysis recalling that of Miocene aceratheriine chilotheres, would be recorded in the latest Oligocene of the Bugti Hills (Antoine et al., 2003), found in association with smaller rhinocerotid specimens, probably

documenting the earliest representatives of elasmotheriines and rhinocerotines (POA, pers. obs.). *Aprotodon* is widely distributed in the Late Oligocene of Asia, ranging from Pakistan and Kazakhstan to China. Its last representatives are *Aprotodon lanzhouensis* and *A. aralense*, from the earliest Miocene of northwest China and Kazakhstan, respectively (Antoine et al., 2003; Lu et al., 2021).

In Central Asia and Caucasus, the rhinocerotoid record is widely dominated by gigantic non-rhinocerotid taxa (indricotheres, or paraceratheriids sensu Bai et al., 2020) and amynodontids (Tissier et al., 2018). Very few rhinocerotid remains, of uncertain affinities, have been described in this region. A notable exception is the enigmatic *Meschotherium mescheticum* from Benara, Georgia (Gabunia, 1964), which might be a stem rhinocerotine.

The newly named Balkanatolia yields mid-Cenozoic ungulate assemblages of South and Central Asian affinities (Licht et al., 2022). Aside from the well-documented stem rhinocerotid *Epiaceratherium bolcense*, from the earliest Oligocene Monteviale locality (northeastern Italy; Pandolfi et al., 2017), and *Molassitherium albigense* from the early Late Oligocene of Thrace (Saraç, 2003), rhinocerotids are mostly known by scarce undescribed and/or unrecognisable remains. A probable representative of the slender-limbed stem rhinocerotine *Mesaceratherium* remains to be described in the upper Oligocene Kızılırmak Formation from north-central Anatolia (POA, pers. obs.).

This scattered record strongly contrasts with that of western Europe, where Rhinocerotidae first appeared just after the EOT. There, hornless and mainly cursorial representatives of at least three stem rhinocerotid genera occur during the Early Oligocene, with fairly complete remains: the small-sized *Epiaceratherium* (Fig. 2.3a) and *Molassitherium*, and the large-sized *Ronzotherium* (Fig. 2.3b). The earliest European representative of *Mesaceratherium* is recognised in the latest Early Oligocene of Bumbach in Switzerland. Among these Early Oligocene incomers of Asian affinities, *Epiaceratherium* and *Ronzotherium* have the most plesiomorphic characters (i.e. primitive), notably in retaining an almost complete anterior dentition, thus making them critical for resolving the phylogeny of early-diverging rhinocerotids (Tissier et al., 2021a). Aside from Asian and Balkanatolian representatives (*E. naduongense*, *E.* cf. *magnum*, and *E. bolcense*), *Epiaceratherium* currently includes two European species: *E. magnum* and *E. delemontense* from the Oligocene of western and Central Europe (Uhlig, 1999; Becker, 2009; Tissier et al., 2020).

As recently revised, *Molassitherium* is restricted to the type species, *M. albigense*, from the late Early–early Late Oligocene of Western Europe (and Thrace; see above). Based on symplesiomorphic traits (i.e. ancestral: such as a small size and slender postcranial limb bones), this stem rhinocerotid was formerly assigned to the later-occurring *Protaceratherium* (see discussion in Becker et al., 2013).

The largest-sized and most abundant rhinocerotid remains from the Oligocene of Western Europe can be unambiguously assigned to *Ronzotherium*. Recently, the thorough taxonomic revision by Tissier et al. (2021a) allowed to discriminate five referred species, with the Early Oligocene *R. velaunum* (type species), *R. filholi*, and *R. elongatum*, and the late Early–Late Oligocene *R. romani* and *R. heissigi*. The first description of associated cranio-dental and postcranial elements at Bumbach, Switzerland, revealed that the "short-limbed" "*Diaceratherium*" *massiliae*, described from the late Early–early Late Oligocene of southern France, rather is a junior synonym of *R. romani*, potentially of semi-aquatic habits.

The medium-sized and slender-limbed *Mesaceratherium* genus was erected on *M. gaimersheimense*, from the Late Oligocene of South Germany. During the latest Oligocene, this species is seemingly replaced by *M. paulhiacense*, which survives the Oligocene–Miocene transition (Antoine & Becker, 2013; Blanchon et al., 2018). As seen above, an earlier species, *Mesaceratherium tschani*, was recently described from the latest Early Oligocene (Tissier et al., 2020). Noteworthily, *M. welcommi* has been reported from the species-rich earliest Miocene localities of the Bugti Hills, in Pakistan (Antoine et al., 2010).

By Late Oligocene times, teleoceratines first occur in western Europe, with *Brachydiceratherium lamilloquense* (Late Oligocene of France and Switzerland) and then *B. lemanense* (latest Oligocene—earliest Miocene of France and Germany). Contrary to later representatives of the genus and of teleoceratines, in general (see Miocene subsection), they retain slender limbs. A third species, *B. asphaltense*, may have also occurred in the latest Oligocene of Switzerland (Becker et al., 2018). Unlike *B. lamilloquense*, *B. asphaltense* and *B. lemanense* passed through the Oligocene–Miocene transition and they were relatively abundant until the end of the earliest Miocene (Aquitanian stage). Some cranial specimens of *B. lemanense* and *B. asphaltense* display evidence for the presence of a small nasal horn (Becker et al., 2018; Jame et al., 2019), probably as a sexually dimorphic trait.

A few localities just predating the Oligocene–Miocene transition yield the small-sized cursorial *Protaceratherium minutum*, which will be a conspicuous element of Early Miocene ungulate guilds in western Europe (Antoine & Becker, 2013).

To end with, a handful of latest Oligocene–earliest Miocene French and Swiss localities have yielded the elusive stem rhinocerotine *Pleuroceros pleuroceros*, which was small-sized, quite robustly built, and tandem-horned (Fig. 2.3d; Antoine & Becker, 2013). As for *Mesaceratherium* (see above), its sister species *Pleuroceros blanfordi* is known in lowermost Miocene deposits of South Asia (Bugti Hills and Vietnam; Antoine et al., 2010; Prieto et al., 2018), forerunning the extremely wide geographical range of most Miocene rhinocerotid genera (see next subsection).

Fig. 2.3 Overview of cranial and skeletal disparity in extinct Rhinocerotidae, in lateral views. (**a**) *Epiaceratherium* (stem rhinocerotid; Late Eocene–Early Oligocene, Eurasia), composite 3D rendering of the cranium. (**b**) *Molassitherium albigense* (stem rhinocerotid; late Early–early Late Oligocene, Europe). (**c**) *Victoriaceros kenyensis* (elasmotheriine; Miocene, Africa). (**d**) *Pleuroceros pleuroceros* (stem rhinocerotine; earliest Miocene, western Europe). (**e**) *Turkanatherium acustirostratum* (aceratheriine?; Miocene, Africa). (**f**), *Chilotherium persiae* (aceratheriine; late Miocene, Eurasia). (**g**) *Stephanorhinus etruscus* (rhinocerotine; Late Pliocene–Early Pleistocene, Eurasia). (**h**) *Elasmotherium sibiricum* (elasmotheriine; Middle–Late Pleistocene, Asia). (**i**) *Plesiaceratherium gracile* (stem rhinocerotine; Middle Miocene, China). (**j**) *Prosantorhinus douvillei* (teleoceratine; late Early–early Middle Miocene, Europe). (**k**) *Coelodonta antiquitatis* (rhinocerotine; Middle–Late Pleistocene, Eurasia). Scale bar = 10 cm. Mounted skeletons not to scale. Pictures by authors except for A, E, H–K (courtesy of J. Tissier, M. Goonatilake, S. Hervet, C. Argot, D. Descouëns, and Wikipedia Commons, respectively)

The rhinocerotids, as other mammalian taxa, entered a phase of gradual change by the Oligocene–Miocene transition, with a progressive demise of Oligocene survivors, replaced by earliest Miocene incomers (Scherler et al., 2013).

This unbalanced Oligocene record, with far more occurrences and species described in Western Europe than in any other Eurasian regions, is probably due to a strong bias in the fossil record available, given the massive discrepancies existing in the density of localities per time slice or spatial unit.

Colonising Afro-Arabia (Miocene)

The Miocene epoch, starting 23 Ma ago, witnesses the most spectacular radiation of the rhinocerotids, with both the earliest occurrences and diversification of Elasmotheriina, Aceratheriina, and Rhinocerotina, and the spread of Teleoceratina (Fig. 2.1). The Early Miocene also records the first colonisation of Afro-Arabia by rhinocerotids (Fig. 2.2c; Pandolfi et al., 2021a). Never reported from the earliest Miocene localities of this landmass, they probably immigrated into Africa by ca. 21 Ma, a time that witnessed a major

phase of interchange with Eurasia (Van Couvering & Delson, 2020). Their absence earlier may be linked with ecological barriers or trophic competition. A coeval expansion is also observed in the New World, with North American menoceratines and aceratheriines documented as south as Panama (MacFadden, 2006). Some genera have a geographical range spanning the entire Old World, i.e. from Japan to Portugal and from Palaearctic Europe to South Africa (e.g. *Brachypotherium*; Geraads et al., 2021).

Rhinocerotids are found in most Miocene mammal fossil sites and they certainly made up a major part of the mammalian herbivore biomass over the Old World. This epoch also records the most speciose assemblages in the history of the family (four to five associated species in Asia and Europe as a routine, with up to nine associated species in Himalayan foothills localities throughout Miocene times: Antoine, 2025). Miocene rhinocerotid guilds would typically mix specialist and generalist species, from distinct primary habitats (forested, riparian, and savannah environments), thanks to niche and body-size partitioning (Hullot et al., 2021).

With some notable exceptions, such as representatives of *Protaceratherium* and *Parvorhinus steinheimensis*, Miocene rhinocerotids were usually larger and heavier than their Palaeogene counterparts. Indeed, Elasmotheriinae and Rhinocerotinae followed parallel evolutionary routes throughout the Neogene (Antoine, 2002) but the latter subfamily finally became dominant in the Old World. Many Miocene rhinocerotids still lacked horns or had only small, sometimes paired ones at the tip of the nasals.

Elasmotheriinae

The closest relatives of Elasmotheriina are restricted to North America (diceratheriines and menoceratines; Fig. 2.1), but some of them may have dispersed via the Bering land corridor toward Asia in Late Oligocene times (see above). Initially circumscribed to South Asia in the earliest Miocene, with the Malayan tapir-sized *Bugtirhinus* (Pakistan and Vietnam; Prieto et al., 2018), Elasmotheriina soon became a regular component of Miocene Old World rhinocerotid assemblages. Early in their history, they became adapted to open landscapes, as revealed by their slender limb bones (cursorial animals: adapted to run) and dental adaptations (increased crown heights, complex occlusal patterns, relatively elongated molar row), as found in many other grazing mammal groups (Antoine, 2002).

They appear in western Europe by late Early Miocene times with *Hispanotherium*, a mixed-feeder of larger size, with long nasal bones and slender metapodials adapted to open environments. The genus, recently documented in the Balkans, was particularly widespread in the Iberian Peninsula and in Anatolia during the earliest Middle Miocene (Cerdeño, 1992; Sanisidro et al., 2012; Becker & Tissier, 2020). Elasmotheriina diversified in Asia in the Middle Miocene, with several species of *Caementodon* (Pakistan, China, and north Caucasus) and of *Procoelodonta* (from Anatolia to Mongolia). If most available skulls for these early-diverging elasmotheriines show no horn boss, small nasal horns may have been a sexually dimorphic trait. In contrast, more derived elasmotheriines such as *Huaqingtherium* (China) already show broad nasals carrying a horn and a salient orbital rim (Antoine, 2002, 2003). In Asia, elasmotheriine diversification reached its climax in the Late Miocene, with the opening of terrestrial environments (Antoine, 2003). *Iranotherium* (Iran, China) is a very large form, with complicated cheek-teeth and incisors lost, a large nasal horn, and inflated, rugose zygomatic arches in males (Deng, 2005b). Coeval species of *Ningxiatherium* and *Parelasmotherium*, also from China, are gigantic, with a cranial length exceeding 1 m and an ossified nasal septum (Antoine, 2002; Deng, 2008). The Late Miocene in Asia also records the first occurrence of the most-derived and mammoth-sized elasmotheriines *Sinotherium* and *Elasmotherium* (with *E. primigenium*; Sun et al., 2022).

The elasmotheriine fossil record in Africa is more blurred, showing how much remains to be learnt from Africa. Their earliest occurrence is from the Early Miocene of Uganda, with the hornless *Ougandatherium* (Guérin & Pickford, 2003), closely resembling its South Asian coeval *Bugtirhinus*. *Eoazara* from the Late Miocene of Morocco and perhaps Tunisia has a strong nasal horn, a hint of nasal septum, no upper incisors, but small lower ones (Geraads & Zouhri, 2021; Yans et al., 2021). It was probably closely related to coeval Chinese forms. Together with the early-diverging *Kenyatherium*, known by a few teeth (Aguirre & Guérin, 1974; Handa et al., 2017) of similar age, they were the only unambiguous African elasmotheriines, testifying to long ghost lineages in Africa and/or recurrent dispersals from Asia. Other potential African elasmotheriines are assigned to the medium-sized *Victoriaceros*, from the Early and Middle Miocene of Kenya, represented by short and broad skulls (robust nasal horn, orbits with a salient rim, and moderate-sized incisors; Fig. 2.3c) and numerous postcranials (Geraads et al., 2012, 2016).

Rhinocerotinae

Several Miocene rhinocerotines with uncertain affinities are survivors from the Oligocene, such as the ubiquitous *Pleuroceros* and *Mesaceratherium* from Western Europe and South Asia (see Oligocene subsection; Antoine & Becker, 2013; Prieto et al., 2018; Jame et al., 2019), whilst three other genera have only Miocene representatives: the slender-limbed hornless browser *Plesiaceratherium*, with very long

nasal bones (Fig. 2.3i), ranges from Europe to China in the late Early Miocene, with nine referred species (Appendix 1); the short-legged *Chilotheridium*, well documented in the Middle Miocene of Kenya (Loperot; Hooijer, 1971), has long nasal bones, a small horn, and four functional digits at the manus; *Turkanatherium* is known through a single skull, also from Kenya (Moruorot; Fig. 2.3e; Geraads, 2010).

Aceratheriina include 38 (mostly hornless) species, gathered in seven Old World genera and spanning the Middle Miocene–Early Pliocene interval (Appendix 1). Their earliest representatives are widespread and assigned to *Alicornops* (small-sized), *Hoploaceratherium* (long-limbed and with very long nasals), and *Acerorhinus*, all of them documented in Middle and Upper Miocene deposits over Eurasia (Antoine et al., 2003). The Late Miocene *Aceratherium* (from Europe to southeast Asia) typifies hornless rhinoceroses, with short nasal bones, large incisors, and a tetradactyl manus (Hünermann, 1989; Deng et al., 2013). *Chilotherium* is a Late Miocene genus, ranging from China to the Balkans, counting for almost half of aceratheriine species and clearly needing a taxonomic revision (Appendix 1). Its representatives have a massive skull, with very short nasal bones and limbs. The mandibular symphysis holds huge diverging incisors that were probably used as defence weapons and sexual traits (Chen et al., 2010). The youngest aceratheriines are far less abundant, with *Persiatherium*, only known from Iran, Turkey, and China (Pandolfi, 2015; Antoine & Sen, 2016) and *Shansirhinus* from China, with a very small horn and complex cheek teeth (Deng, 2005a).

Teleoceratine remains are abundant in Miocene fluviolacustrine deposits of the Old World. They have often been compared to hippos, but there is no direct evidence that their mode of life was semi-aquatic (Wang & Secord, 2020). Most of them are hornless, with a broad skull, strongly dimorphic incisors, and stout limb extremities (Fig. 2.3j). Their Early Miocene representatives are assigned to *Diaceratherium*, *Brachydiceratherium,* and *Prosantorhinus* (Sizov et al., 2024), well documented from Portugal to China and from eastern Siberia to Pakistan (Appendix 1). Whilst representatives of the former genera are quite generalist in their body proportions, *Prosantorhinus* has extremely shortened distal limb bones, as its North American sister taxon *Teleoceras*. The largest teleoceratines belong to *Brachypotherium*, with a broad and shortened hornless skull, a robust zygomatic arch, and a body mass almost reaching 4 metric tons (Antoine, 2025). They were widespread, but never very abundant, in the late Early–early Late Miocene of Eurasia (from Japan to Portugal). By Late Miocene times, *Brachypotherium* reached a huge size, with *B. goldfussi* from Europe and *B. perimense* from Indo-Pakistan (Heissig, 1972). *Brachypotherium* also settled in Africa, where it spans the entire Miocene epoch. It is recognised in the earliest African rhino-yielding site at Kajong, Kenya at ca. 20 Ma (Geraads et al., 2021). The small *B. minor* then occurs in Kenya (ca. 17.5 Ma; Geraads & Miller, 2013) and the larger *B. snowi* (= *B. heinzelini*) is a common element in Middle–Late Miocene faunas of northern and eastern Africa, and Namibia (Geraads et al., 2021). The last African brachypothere is the huge *B. lewisi* from Lothagam, at ca. 5.5 Ma (Uno et al., 2011).

Rhinocerotina gather all living rhino species and their kin. All of them have a nasal horn and a tridactyl manus and some also have a frontal horn (Fig. 2.3g, k). They first appear in the earliest Miocene of Pakistan with *Gaindatherium*, the representatives of which span most of the Miocene in tropical Asia and may retain two pairs of upper incisors (Antoine, 2025). Its sister taxon, *Lartetotherium*, occurs in late Early–early Late Miocene localities of western Europe, Balkans, and China, with a Middle Miocene climax (Heissig, 2012; Becker & Tissier, 2020; Appendix 1). Close relatives of both *Lartetotherium* and *Gaindatherium* have been recognised in Saudi Arabia (Middle Miocene) and the Levantine corridor, respectively (Early Miocene; Pandolfi et al., 2021a). *Rusingaceros* and "*Diceros*" *australis* from the Early Miocene of Kenya and Namibia, respectively, are probably closely related to the latter stem rhinocerotines. The skull of *Rusingaceros* is dolichocephalic, with a strong nasal horn, a long face, an elevated occiput, and a robust zygomatic arch (Geraads, 2010). Undoubtedly closer to modern Asian rhinos are several Late Miocene rhinocerotid remains from the Siwaliks of Indo-Pakistan, referred to as *Dicerorhinus* aff. *sumatrensis* and *Rhinoceros sivalensis* (Antoine, 2025), and China (*D. cixianensis*; Appendix 1). Similarly, the two-horned *Paradiceros* from the Middle Miocene of Kenya has tight affinities with modern African rhinos (Geraads, 2010). Later on, the open-country *Hipparion* faunas, widespread from the Balkans to China, would yield two-horned Late Miocene rhinos that foreshadow those of the Pliocene–Pleistocene (Geraads, 1988). Their first offshoots are assigned to *Dihoplus* and to *Pliorhinus*, with *Dih. schleiermacheri* from western Europe and Central Asia (which retains large i2s), *Dih. pikermiensis*, ranging from eastern Mediterranean to China (with small upper and lower incisors), and *Pliorhinus ringstroemi* (same range; Appendix 1). A single Late Miocene species of *Stephanorhinus*, *S. kurmetiensis*, is recorded in Kazakhstan (Geraads et al., 2021), coeval to the earliest *Pliorhinus megarhinus* in Italy (Pandolfi et al., 2021b). Other Late Miocene "dicerotines" are very close to the living "black" (*Diceros bicornis*) and "white" rhinos (*Ceratotherium simum*) of Africa, with extensive peri-Mediterranean ranges and a noticeable species richness (five species are assigned to *Ceratotherium*; Appendix 1). *Diceros* first occurs in the latest Miocene of East and Southern Africa, with both *D. praecox* and perhaps *D. bicornis*). The latest Miocene *Diceros gansuensis* from Inner Mongolia may belong to the same lineage (Deng & Qiu, 2007). Both African rhino lineages would diverge ecologically as well as mor-

phologically, with *Diceros* becoming increasingly a browser (horizontal head posture and brachydont teeth with transverse lophs), whilst representatives of *Ceratotherium* became more and more grazers (inclined head and hypsodont teeth with more complex occlusal pattern): two distinctive strategies that may explain their long range (e.g. Geraads, 2010).

The Ice Age Is Coming (Pliocene–Pleistocene)

Despite the large amount of available data with respect to previous epochs, the Pliocene–Pleistocene time interval (ca. 5.3–0.001 Ma) records a strong decrease of specific and generic diversity. Whilst Rhinocerotidae have gone extinct in North America, only a few representatives of both Rhinocerotinae and Elasmotheriinae are documented over the Old World (Fig. 2.2d).

Rhinocerotina are well represented with *Pliorhinus*, *Stephanorhinus*, *Coelodonta*, *Rhinoceros*, *Nesorhinus*, and *Dicerorhinus* in Eurasia and with *Ceratotherium*, *Diceros*, and perhaps *Stephanorhinus* in Africa. After the last occurrence of *Sinotherium* (Early Pliocene; Titov et al., 2018), *Elasmotherium* is the only elasmotheriine left in Eurasia. The subfamily had disappeared from the African record before Pliocene times (Geraads, 2010).

Pliocene–Pleistocene rhinocerotines were subject of extensive investigation since the eighteenth century, with the pioneering studies of eminent palaeontologists such as Cuvier (1822), de Christol (1834) and Falconer (1868). However, despite a century-long research history on this group, the phylogenetic relationships of various fossil species remain debated (see for instance Pandolfi et al., 2021b; Antoine et al., 2022; Uzunidis et al., 2022). Phylogenomic analyses recently suggested that Rhinocerotina includes three major clades: one composed by the African *C. simum* and *D. bicornis*; one composed by *D. sumatrensis*, *S. kirchbergensis*, and *C. antiquitatis*; and a third one composed by the species of the genus *Rhinoceros* (Liu et al., 2021). The same study also supported the biogeographical hypothesis of rhinoceros evolution (Eurasian species closely related despite the different number of horns) and highlighted contrasting results obtained by means of morpho-anatomical, mitogenomic and palaeoproteomic approaches (Cappellini et al., 2019; Antoine et al., 2022; Liu et al., 2021; Pandolfi et al., 2021b).

Pliocene–Pleistocene rhinocerotid species have either one (nasal in *Rhinoceros*; frontal in *Sinotherium* and *Elasmotherium*) or two horns (nasal and frontal; all other genera) and distinctive cranial and postcranial shapes and proportions. Grazer species are generally characterised by a backwardly and upwardly oriented occipital face with an elongated nuchal crest, complex enamel pattern of the cheek teeth and graviportal limbs (as in the case of *Elasmotherium*, *Ceratotherium*, and *Coelodonta*), whilst browsers usually have an upwardly and forwardly inclined occipital face and a simpler enamel pattern of the cheek teeth (as in the case of *Dicerorhinus* and some *Stephanorhinus* species). However, recent studies suggested that, despite their adaptative traits, some species were able to supplement their diet, and therefore to be ecologically flexible (Kahlke & Kaiser, 2011; Rivals & Lister, 2016).

Rhinocerotinae

In Palearctic Eurasia, the post-Miocene rhinocerotine record is almost restricted to Rhinocerotina, with the notable exception of the last representative of aceratheriines, *Shansirhinus ringstroemi*, from the Early Pliocene of China (Fig. 2.2d; Geraads et al., 2021). Eight genera are documented among Rhinocerotina. *Pliorhinus*, with *P. megarhinus* and *P. miguelcrusafonti*, and *Stephanorhinus*, with *S. jeanvireti* and *S. etruscus*. *Pliorhinus megarhinus* is a large-sized two-horned rhinoceros that both retains small upper and lower incisors and lacks the ossified nasal septum observed in *Stephanorhinus* and *Coelodonta*. It occurs during the latest Miocene in Asia (probably derived from *P. ringstroemi*) and disperses in western Europe around the Miocene–Pliocene boundary, becoming the most documented rhinoceros species during the early Pliocene. Its elusive sister species, *Pliorhinus miguelcrusafonti*, roams western Eurasia during the Mid- and Late Pliocene (Pandolfi et al., 2021b). *Stephanorhinus* first occurs in Europe with *S. jeanvireti*, frequently documented from the latest Pliocene localities of France and Italy (Guérin, 1980). It has a partly ossified nasal septum, low-crowned teeth, and dimensions comparable to those of *P. megarhinus*. Throughout the latest Pliocene–Early Pleistocene interval, *S. etruscus* occurs in more than 200 Eurasian localities (Pandolfi et al., 2017; Geraads et al., 2021). Comparable in size to the extant *D. sumatrensis*—which explains its former generic assignment—this species has a partly ossified nasal septum, no incisors and low-crowned teeth, typical of a browser, a diet preference confirmed by both mesowear and microwear analyses (Fig. 2.3g; Rivals & Lister, 2016). Its extinction is likely to be related to the climatic deterioration recorded in the latest Early Pleistocene. During the Pleistocene, *Stephanorhinus* is particularly widespread in Eurasia (Guérin, 1980) with at least six species. In eastern Asia, this genus is documented by *S. yunchuchenensis*, *S. lantianensis*, and *S. kirchbergensis*. The first two only occur in China during the Early Pleistocene whilst the latter is present in eastern Asia from the late Early to the latest Pleistocene. *Stephanorhinus kirchbergensis*, commonly called the Merck's rhino or the forest rhinoceros, reaches western Europe during the early Middle Pleistocene and spreads in Siberia during the Middle and Late Pleistocene.

In Europe, by the end of the Early Pleistocene, the browser *S. etruscus* is replaced by the mixed-feeder *S. hundsheimensis*, the most ecologically tolerant rhinoceros of the Palearctic Pleistocene (Kahlke & Kaiser, 2011). *Stephanorhinus hemitoechus* (the steppe or narrow-nosed rhino), a grass-dominated mixed-feeder with high-crowned teeth, occurs in Europe by the late Middle Pleistocene and survives in southern Europe until the latest Pleistocene (Guérin, 1980). *Coelodonta thibetana*, from the Pliocene of Tibet, is the first representative of its genus. It displays intermediate characters between *Stephanorhinus* and the more derived *C. antiquitatis*, suggesting a strong relationship between both genera, as recently supported by molecular analyses (Cappellini et al., 2019; Liu et al., 2021). Later representatives are *C. nihowanensis*, from the Early Pleistocene of China, *C. tologoijensis* from Russia (and perhaps Central Europe) and *C. antiquitatis*, the real woolly rhinoceros (Uzunidis et al., 2022), which occurs throughout Palearctic Eurasia during the cold stages of the Late Pleistocene (more than 1200 occurrences; Geraads et al., 2021) and gets extinct at ca. 14 ka BP (Stuart & Lister, 2012). The discovery of carcasses of the latter species within the Siberian permafrost allows to list, among its morphological traits, a laterally flattened nasal horn, thick coat and thick skin, short tail, and small ears (Fig. 2.3k). Cave paintings, mostly in Europe, also concur to a better picture of the woolly rhino general outline and behaviour. At least four species belonging to the one-horned genus *Rhinoceros* are documented in the Indo-Malayan region during the concerned period: *Rhinoceros platyrhinus*, *R. sivalensis*, *R. unicornis* (Indian rhino), and *R. sondaicus* (Javan rhino). *Rhinoceros platyrhinus*, one of the largest Pleistocene rhinocerotines of Eurasia, is probably adapted to feed on abrasive food (Pandolfi & Maiorino, 2016). *Rhinoceros sivalensis*, likely misidentified in South-East Asia as *R. sondaicus* (see also Antoine, 2012), is a latest Miocene-sourced, relatively small and browser species. *Rhinoceros sondaicus*, widespread in South-East Asia and India until historical times, also occurs in several Pleistocene localities on the Indo-Malaysian archipelago and southern China. *Rhinoceros unicornis* (Indian rhino), widely distributed within the Indo-Malayan region since the Early Pleistocene, is recognised in Java, southern China, southern India, Pakistan, and other nearby areas under various names (Antoine, 2012). Other *Rhinoceros* species described during the past century, such as *R. sinensis* and *R. kendengindicus*, have a scarce and poorly documented record and their taxonomic validity is still debated (Antoine et al., 2022). *Nesorhinus* includes a Pleistocene rhinoceros from Luzon, Philippines, *N. philippinensis*, and a coeval species from Taiwan (Fig. 2.2d), *N. hayasakai*. *Nesorhinus* is the sister-group to the *Dicerorhinus* plus *Rhinoceros* clade. *Nesorhinus* would be the first perissodactyl supporting the island-rule hypothesis, with decreased body weight and limb-bone robustness (Antoine et al., 2022). *Dicerorhinus gwebinensis* occurs in the Pliocene–Early Pleistocene of Myanmar whilst *D. sumatrensis* (Sumatran rhino), first recorded during the late Early Pleistocene in South China, then spreads into South-East Asia (Antoine, 2012). Another *Dicerorhinus* species, *D. fusuiensis*, is documented in South China during the Early Pleistocene (Antoine et al., 2022). All these species are brachydont browsers (with low-crowned teeth) that probably inhabited dense tropical forests.

In Africa, the rhinocerotine record is restricted to four dominant species: *Ceratotherium mauritanicum*, *C. simum* (white rhino), *Diceros praecox*, and *D. bicornis* (black rhino). In North Africa, *C. mauritanicum* spans the Late Pliocene–Late Pleistocene interval whilst the extant *C. simum* firstly occurs in East Africa during the Early Pleistocene. The latter species then spreads in the whole continent, replacing *C. mauritanicum* (Geraads, 2005). *Diceros praecox* occurs throughout the Pliocene in East Africa, foreshadowing *D. bicornis* morphologically and ecologically. The oldest Pleistocene record of the black rhinoceros is from East Africa, around ca. 2.5 Ma. Although widespread in sub-Saharan Africa, it was never recorded North to the concerned area, contrary to *C. simum* (Geraads, 2010). A species of Eurasian affinities, recorded in the Pliocene of North Africa, has been dubitatively assigned to *Stephanorhinus*, *S.? africanus* (Geraads, 2010); its phylogenetic and taxonomic affinities, however, need to be confirmed. During Late Pleistocene times, the narrow-nosed rhinoceros, *Stephanorhinus hemitoechus*, widespread in Europe, is recorded in various sites of North Africa (Michel et al., 2010).

Elasmotheriinae

Two gigantic elasmotheriine genera first occurring in latest Miocene times are recorded in the Pliocene–Pleistocene of Palaearctic Asia (Fig. 2.2d). Both are characterised by the presence of a huge and hemispheric frontal prominence (either for a very long horn [Antoine, 2002] or a massive dome [Titov & Uchytel, 2021]), ever-growing teeth with prominent enamel foldings, and quite slender limbs (Fig. 2.3h). *Sinotherium* went extinct in the Early Pliocene

(Southwestern Russia; Titov et al., 2018) but at least three Pliocene–Pleistocene *Elasmotherium* species are considered as valid: *E. peii* (Early Pleistocene, central Asia and Black Sea region), *E. caucasicum* (late Early–Middle Pleistocene, Azov Sea area), and *E. sibiricum* which spreads from the Black Sea region to Transbaikalia from the late Middle Pleistocene to the latest Pleistocene (Antoine, 2002; Sun et al., 2022). Other described species, such as *E. inexpectatum* and *E. chaprovicum*, are considered junior synonyms of either *E. caucasicum* or *E. peii*. The presence of *Elasmotherium* is disputed in western Europe (Antoine, 2002). Although this species is generally considered as having been extirpated well before the last glacial period, recent

radiocarbon ages showed that *E. sibiricum* had survived at least until 39 ka (Kosintsev et al., 2019). This species, with good running abilities, is a highly specialised grazer adapted to dry steppes of Central Asia recently nicknamed "the Siberian unicorn" (Kosintsev et al., 2019).

Conclusion: The Holocene as a Turning Point

After the demise of ice-age megafauna in most landmasses by the Pleistocene–Holocene transition and the extinction of *Coelodonta antiquitatis* ca. 14 ka BP, only the living rhino species are left in Asia and Africa (Moodley and Robovský, Chap. 1 this book). The Indian rhino (*Rhinoceros unicornis*) is recorded all over the Himalayan piedmont, whilst the Javan rhino (*Rhinoceros sondaicus*) and the Sumatran rhinos (*Dicerorhinus sumatrensis*) are spanning all Southeast Asia, from Bangladesh to Borneo, and eastern China (Antoine, 2012). During most Holocene times, *Diceros bicornis* would be widespread in sub-Saharan Africa and *Ceratotherium simum* all over Africa except forested areas (Rookmaaker & Antoine, 2013). African rhinoceroses have been drawn in Holocene rock paintings and engravings, especially in North Africa, where they have gone extinct since then (Muzzolini, 1995). The decline of all five species and their subspecies (e.g. northern Javan rhino, western black rhino, and northern white rhino) is unambiguously related to human pressure in the last centuries (overhunting, poaching, and habitat fractionation; Chaps. 9, 10, 15 this book). The question is: how long would the last representatives of this 40-million-year-old successful family survive, at least in the wild?

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Appendix 1 Rhinocerotid Genera and Species Recognised in the Old World, from Eocene Times Onwards, with their Stratigraphical and Geographical Ranges and Last References

Genus	Species	Stratigraphical range	Geographical range	References
Rhinocerotidae				
Aprotodon	*aralensis*	Late Oligocene–earliest Miocene	Kazakhstan	Antoine et al., 2003
Aprotodon	*lanzhouensis*	Late Oligocene–Early Miocene	China	Geraads et al., 2021; Liu et al., 2021
Aprotodon	*smithwoodwardi*	Late Oligocene	Pakistan	Antoine et al., 2013
"*Dicerorhinus*"	*abeli*	Late Oligocene–earliest Miocene	Pakistan	Antoine et al., 2013; Geraads et al., 2021
Epiaceratherium	*bolcense*	Early Oligocene	Italy	Geraads et al., 2021
Epiaceratherium	*delemontense*	Early Oligocene	Switzerland	Geraads et al., 2021; Tissier et al., 2021a
Epiaceratherium	*magnum*	Early Oligocene	Western Europe (Pakistan: cf.)	Geraads et al., 2021
Epiaceratherium	*naduongense*	Late Eocene	Vietnam	Böhme et al., 2013
Guixia	*youjiangensis*	Earliest Oligocene	China	Antoine et al., 2003
Guixia	*simplex*	Late Eocene	China, Thailand	Antoine et al., 2003
Molassitherium	*albigense*	Late Early–early Late Oligocene	Western Europe, Thrace	Saraç, 2003; Antoine et al., 2013; Becker et al., 2013
Protaceratherium	*betpakdalense*	Earliest Miocene	Kazakhstan	Kordikova, 2001; Antoine et al., 2003
Protaceratherium	*minutum*	Latest Oligocene-Early Miocene	Western Europe, Czech Republic, Kazakhstan	Geraads et al., 2021
Ronzotherium	*elongatum*	Early Oligocene	France, Switzerland	Tissier et al., 2021
Ronzotherium	*filholi*	Early Oligocene	France, Germany, Romania	Tissier et al., 2021
Ronzotherium	*heissigi*	Late early–early Late Oligocene	France, Switzerland	Tissier et al., 2021
Ronzotherium	*romani*	Late early–Late Oligocene	France, Germany, Switzerland	Tissier et al., 2021
Ronzotherium	*velaunum*	Early Oligocene	France, Germany	Tissier et al., 2021

Genus	Species	Stratigraphical range	Geographical range	References
Teletaceras	*borissiaki*	Late Middle Eocene	Russia	Antoine et al., 2003
Elasmotheriinae Elasmotheriina				
Bugtirhinus	*praecursor*	Early Miocene	Pakistan (Vietnam: sp.)	Geraads et al., 2021
Caementodon	*caucasicus*	Early Middle Miocene	North Caucasus	Geraads et al., 2021
Caementodon	*fangxianensis*	Early Middle Miocene	China	Geraads et al., 2021
Caementodon	*oettingenae*	Middle–early Late Miocene	Pakistan	Geraads et al., 2021
Elasmotherium	*caucasicum*	Early Pleistocene	Russia, Moldova, China, Mongolia, Tajikistan	Geraads et al., 2021
Elasmotherium	*sibiricum*	Middle–Late Pleistocene	Russia, Kazakhstan, Moldova, Ukraine	Geraads et al., 2021
Elasmotherium	*primigenium*	Latest Miocene	China	Sun et al., 2022
Eoazara	*xerrii*	Late Miocene	Morocco (?Tunisia)	Geraads & Zouhri, 2021; Yans et al., 2021
Hispanotherium	*beonense*	Late early Miocene	France	Geraads et al., 2021
Hispanotherium	*corcolense*	Late early Miocene	Spain	Geraads et al., 2021
Hispanotherium	*grimmi*	Middle Miocene	Turkey (Anatolia)	Geraads et al., 2021
Hispanotherium	*matritense*	Late early–early Middle Miocene	Iberia, France (Bosnia-Herzegovina: cf.)	Geraads et al., 2021
Huaqingtherium	*lintungense*	Late Middle Miocene	China, Mongolia	Antoine, 2003; Geraads et al., 2021
Iranotherium	*morgani*	Late Miocene	Iran, China	Geraads et al., 2021
Kenyatherium	*bishopi*	Early late Miocene	Kenya (Namibia: sp.)	Geraads et al., 2021
Ougandatherium	*napakense*	Early Miocene	Uganda	Geraads et al., 2021
Ningxiatherium	*euryrhinus*	Early late Miocene	China	Deng, 2008
Ningxiatherium	*longirhinus*	Late Miocene	China	Geraads et al., 2021
Parelasmotherium	*linxiaense*	Early late Miocene	China	Geraads et al., 2021
Parelasmotherium	*schansiense*	Late Miocene	China	Antoine, 2002, 2003
Procoelodonta	*borissiaki*	Middle–early Late Miocene	Mongolia, China, Kazakhstan	Antoine, 2002; Geraads et al., 2021
Procoelodonta	*tekkayai*	Early Middle Miocene	Turkey (Anatolia)	Antoine, 2002; Geraads et al., 2021
Samburuceros	*ishidai*	Late Miocene	Kenya	Handa et al., 2017
Sinotherium	*lagrelii*	Late Miocene	China Kazakhstan (Mongolia: sp.)	Antoine, 2002; Geraads et al., 2021
Victoriaceros	*hooijeri*	Early Miocene	Kenya	Geraads et al., 2021
Victoriaceros	*kenyensis*	Early Middle Miocene	Kenya	Geraads et al., 2021
Rhinocerotinae				
Chilotheridium	*pattersoni*	Early–Middle Miocene	Kenya, Namibia, Uganda	Geraads et al., 2021
Mesaceratherium	*gaimersheimense*	Late Oligocene	Germany, France, Switzerland	Antoine et al., 2010; Blanchon et al., 2018; Tissier et al., 2021b
Mesaceratherium	*paulhiacense*	Latest Oligocene–earliest Miocene	France	Geraads et al., 2021
Mesaceratherium	*tschani*	Late Early Oligocene	Switzerland	Geraads et al., 2021; Tissier et al., 2020
Mesaceratherium	*welcommi*	Early Miocene	Pakistan	Antoine et al., 2010
Plesiaceratherium	*aquitanicum*	Early Miocene	France	Antoine & Becker, 2013; Becker & Tissier, 2020
Plesiaceratherium	*balkanicum*	Early Middle Miocene	Bosnia-Herzegovina	Becker & Tissier, 2020
Plesiaceratherium	*fahlbuschi*	Early Middle Miocene	Germany	Peter, 2002; Geraads et al., 2021
Plesiaceratherium	*gracile*	Late Early–early Middle Miocene	China	Becker & Tissier, 2020; Geraads et al., 2021
Plesiaceratherium	*lumiarense*	Late Early–early Middle Miocene	Western Europe	Antoine et al., 2000; Geraads et al., 2021
Plesiaceratherium	*mirallesi*	Late Early Miocene	Spain, France	Geraads et al., 2021
Plesiaceratherium	*naricum*	Early Miocene	Pakistan, Myanmar	Antoine et al., 2013; Geraads et al., 2021
Plesiaceratherium	*platyodon*	Early Miocene	France, Bosnia-Herzegovina, Portugal, Spain	Antoine et al., 2000; Geraads et al., 2021

Genus	Species	Stratigraphical range	Geographical range	References
Pleuroceros	*blanfordi*	Early Miocene	Pakistan, Vietnam	Prieto et al., 2018; Geraads et al., 2021
Pleuroceros	*pleuroceros*	(?Latest Oligocene)–earliest Miocene	France, Germany, Switzerland	Geraads et al., 2021
Turkanatherium	*acutirostratum*	Miocene	Congo, Kenya, Uganda	Geraads et al., 2021
Aceratheriini Aceratheriina				
Aceratherium	*incisivum*	Late Miocene–(Pliocene?)	Europe, Eastern Mediterranean, Central Asia	Geraads et al., 2021
Aceratherium	*porpani*	Late Miocene	Thailand	Geraads et al., 2021
Aceratherium	*simplex*	Late Miocene	Moldova	Geraads et al., 2021
Aceratherium	*transcaucasicum*	Late Miocene	Georgia	Geraads et al., 2021
Acerorhinus	*fuguensis*	Late Miocene	China	Geraads et al., 2021
Acerorhinus	*hezhengensis*	Late Miocene	China	Geraads et al., 2021
Acerorhinus	*neleus*	Late Miocene	Greece	Geraads et al., 2021
Acerorhinus	*palaeosinensis*	Late Miocene	China, Thailand	Geraads et al., 2021
Acerorhinus	*tianzhuensis*	Late Miocene	China	Geraads et al., 2021
Acerorhinus	*tsaidamensis*	Middle–Late Miocene	China	Geraads et al., 2021
Acerorhinus	*zernowi*	Late Middle–Late Miocene	Ukraine, Greece, Georgia, Turkey, Moldova, China	Geraads et al., 2021
Alicornops	*alfambrense*	Late Miocene	Spain, Germany, France	Geraads et al., 2021
Alicornops	*complanatum*	Late Miocene	South Asia	Antoine, 2025
Alicornops	*laogouense*	Middle Miocene	China	Geraads et al., 2021
Alicornops	*simorrense*	Middle–early Late Miocene	Europe, Eastern Mediterranean (Pakistan: cf.)	Geraads et al., 2021; Antoine, 2025
Chilotherium	*anderssoni*	Late Miocene	China, Kazakhstan, Kyrgyzstan	Geraads et al., 2021
Chilotherium	*gracile*	Late Miocene	China	Geraads et al., 2021
Chilotherium	*eldaricum*	Late Miocene	Georgia	Geraads et al., 2021
Chilotherium	*habereri*	Late Miocene	China, Kyrgyzstan, Mongolia, Turkey	Geraads et al., 2021
Chilotherium	*kiliasi*	Late Miocene	Greece, Bulgaria, Turkey	Geraads et al., 2021
Chilotherium	*kowalevskii*	Late Miocene	Moldova, Bulgaria, Turkey, Ukraine	Geraads et al., 2021
Chilotherium	*licenti*	Late Miocene	China	Geraads et al., 2021
Chilotherium	*orlovi*	Late Miocene	Kazakhstan	Sharipova & Ospanova, 2014
Chilotherium	*persiae*	Late Miocene	Iran	Pandolfi, 2015; Geraads et al., 2021
Chilotherium	*primigenium*	Late Miocene	China	Geraads et al., 2021
Chilotherium	*samium*	Late Miocene	Greece, Turkey	Geraads et al., 2021
Chilotherium	*sarmaticum*	Late Miocene	Bulgaria, Romania, Ukraine	Geraads et al., 2021
Chilotherium	*schlosseri*	Late Miocene	Greece, Turkey, and Central Asia	Geraads et al., 2021
Chilotherium	*wimani*	Late Miocene	China, Mongolia	Geraads et al., 2021
Chilotherium	*xizangense*	Late Miocene	China	Geraads et al., 2021
Chilotherium	*tanggulaense*	Late Miocene	China	Geraads et al., 2021
Hoploaceratherium	*belvederense*	Middle–Late Miocene	Germany, France, Austria, Hungary	Geraads et al., 2021
Hoploaceratherium	*depereti*	Middle Miocene	Kazakhstan	Geraads et al., 2021
Hoploaceratherium	*gobiense*	Early–Middle Miocene	Mongolia, Kazakhstan	Geraads et al., 2021
Hoploaceratherium	*tetradactylum*	Middle–early Late Miocene	Western Europe, Poland, Turkey	Geraads et al., 2021
Persiatherium	*huadeense*	Late Miocene	China	Pandolfi, 2015; Geraads et al., 2021
Persiatherium	*rodleri*	Late Miocene	Iran, Turkey (Thrace: sp.)	Antoine & Sen, 2016; Pandolfi, 2015
Shansirhinus	*ringstroemi*	Late Miocene–Pliocene	China	Geraads et al., 2021
Rhinocerotini Teleoceratina				
Brachydiceratherium	*aginense*	Earliest Miocene	France, Germany, Switzerland	Geraads et al., 2021; Sizov et al., 2024

Genus	Species	Stratigraphical range	Geographical range	References
Brachydiceratherium	*asphaltense*	Latest-Oligocene–Earliest Miocene	France, Switzerland	Geraads et al., 2021; Sizov et al., 2024
Brachydiceratherium	*aurelianense*	Early Miocene	Western Europe, Czech Republic, Kazakhstan	Geraads et al., 2021; Sizov et al., 2024
Brachydiceratherium	*fatehjangense*	Early–early Late Miocene	Pakistan, Myanmar	Geraads et al., 2021; Antoine, 2025
Brachydiceratherium	*intermedium*	Late early–early Late Miocene	Pakistan, India, Thailand, Turkey	Geraads et al., 2021; Sizov et al., 2024; Antoine, 2025
Brachydiceratherium	*lamilloquense*	Late Oligocene	France (Thailand: cf.), Switzerland	Ménouret & Guérin, 2009; Tissier et al., 2021b; Sizov et al., 2024
Brachydiceratherium	*lemanense*	Earliest Miocene	France, Germany, Switzerland, Czech Republic	Geraads et al., 2021; Sizov et al., 2024
Brachydiceratherium	*shanwangense*	Early Miocene	China, eastern Siberia	Lu et al., 2021; Sizov et al., 2024
Brachypotherium	*brachypus*	Late early–early Late Miocene	Europe, Eastern Mediterranean	Geraads et al., 2021
Brachypotherium	*gajense*	Early Miocene	Pakistan	Antoine et al., 2013; Antoine, 2025
Brachypotherium	*goldfussi*	Middle–early Late Miocene	Germany, France, Austria	Geraads et al., 2021
Brachypotherium	*lewisi*	Late Miocene	East Africa (Saudi Arabia: cf.)	Geraads et al., 2021
Brachypotherium	*minor*	Early Miocene	Kenya	Geraads et al., 2021
Brachypotherium	*perimense*	Late early–Late Miocene	South and Southeast Asia; Iraq	Geraads et al., 2021; Antoine, [2025]
Brachypotherium	*pugnator*	Late early–Late Miocene	Japan	Geraads et al., 2021
Brachypotherium	*snowi*	Early–Late Miocene	North Africa, East Africa, Namibia	Geraads et al., 2021
Diaceratherium	*tomerdingense*	Earliest Miocene	Germany	Jame et al., 2019; Sizov et al., [2024]
Prosantorhinus	*douvillei*	Late early–earliest Middle Miocene	France, Spain	Geraads et al., 2021; Sizov et al., [2024]
Prosantorhinus	*germanicus*	Late early–earliest Middle Miocene	Germany, France (Portugal?)	Geraads et al., 2021; Sizov et al., [2024]
Prosantorhinus	*laubei*	Early Miocene	Czech Republic	Geraads et al., 2021; Sizov et al., [2024]
Prosantorhinus	*shahbazi*	Early Miocene	Pakistan	Geraads et al., 2021; Antoine, [2025]
Rhinocerotini Rhinocerotina				
Ceratotherium	*advenientis*	Latest Miocene	Italy	Geraads et al., 2021
Ceratotherium	*douariense*	Late Miocene (+Pliocene?)	North Africa	Geraads et al., 2021; Yans et al., 2021
Ceratotherium	*mauritanicum*	Late Miocene–Pleistocene	North and East Africa Namibia	Geraads et al., 2021
Ceratotherium	*neumayri*	Late Miocene	Eastern Mediterranean, Pakistan	Geraads et al., 2021; Antoine, [2025]
Ceratotherium	*primaevum*	Middle–Late Miocene	Algeria, Saudi Arabia	Geraads et al., 2021
Ceratotherium	*simum*	Pliocene–Recent	Africa (mostly North East and Southern Africa)	Geraads et al., 2021
Coelodonta	*antiquitatis*	Middle–Late Pleistocene	Northern Eurasia	Geraads et al., 2021; Uzunidis et al., 2022
Coelodonta	*nihowanensis*	Early Pleistocene	China	Geraads et al., 2021; Uzunidis et al., 2022
Coelodonta	*thibetana*	Late Pliocene	Tibet (China)	Geraads et al., 2021; Uzunidis et al., 2022
Coelodonta	*tologoijensis*	Middle Pleistocene	Russia, Mongolia, Romania	Geraads et al., 2021; Uzunidis et al., 2022
Dicerorhinus	*cixianensis*	Late Miocene	China	Geraads et al., 2021
Dicerorhinus	*fusuiensis*	Pleistocene	China	Antoine et al., 2022
Dicerorhinus	*gwebinensis*	Pleistocene	Myanmar	Geraads et al., 2021

Genus	Species	Stratigraphical range	Geographical range	References
Dicerorhinus	*sumatrensis*	(Late Miocene) Pleistocene–Recent	South and Southeast Asia (Pakistan: aff.)	Geraads et al., 2021; Liu et al., 2021; Antoine, 2025
"*Diceros*"	*australis*	Late early Miocene	Namibia	Geraads et al., 2021
Diceros	*bicornis*	Latest Miocene–Recent	East and Southern Africa	Geraads et al., 2021
Diceros	*gansuensis*	Latest Miocene	China	Geraads et al., 2021
Diceros	*praecox*	Latest Miocene–Pleistocene	East and Southern Africa	Geraads et al., 2021
Dihoplus	*bethlehemsis*	Late Pliocene	Levant	Pandolfi et al., 2021
Dihoplus	*pikermiensis*	Late Miocene	Eastern Mediterranean, Russia, China	Geraads et al., 2021
Dihoplus	*schleiermacheri*	Late Miocene–Pliocene	Western Europe, Balkans, Moldova, Ukraine	Geraads et al., 2021
Gaindatherium	*browni*	Early–early Late Miocene	Pakistan, India, Thailand	Geraads et al., 2021; Antoine, 2025
Gaindatherium	*vidali*	Middle–Late early Miocene	Pakistan, India	Geraads et al., 2021; Antoine, 2025
?Itanzatherium	*angustirostre*	Pleistocene	Siberian Russia	Vangengejm et al., 1966
Lartetotherium	*sansaniense*	Late early–early Late Miocene	Europe, Balkans (?Saudi Arabia)	Geraads et al., 2021
Nesorhinus	*hayasakai*	Early–Middle Pleistocene	Taiwan	Antoine et al., 2022
Nesorhinus	*philippinensis*	Middle Pleistocene	Luzon, Philippines Archipelago	Antoine et al., 2022
Paradiceros	*mukirii*	Middle Miocene	Kenya, Morocco, Uganda	Geraads et al., 2021
Parvorhinus	*steinheimensis*	Late middle–early Late Miocene	Europe, China	Geraads et al., 2021
Pliorhinus	*megarhinus*	Latest Miocene–Pliocene	Europe, Russia, Turkey, Ukraine	Geraads et al., 2021; Pandolfi et al., 2021
Pliorhinus	*miguelcrusafonti*	Pliocene	Spain, France Georgia	Geraads et al., 2021; Pandolfi et al., 2021
Pliorhinus	*ringstroemi*	Late Miocene–Pliocene	China, Afghanistan, Ukraine, Turkey	Geraads et al., 2021
Rhinoceros	*kendengindicus*	Pleistocene	Indonesia	Antoine et al., 2022
Rhinoceros	*platyrhinus*	Pleistocene	Indian Subcontinent	Geraads et al., 2021
Rhinoceros	*sivalensis*	Late Miocene–Pliocene	Indian Subcontinent	Geraads et al., 2021
Rhinoceros	*sinensis*	Middle–Late Pleistocene	China, India	Geraads et al., 2021
Rhinoceros	*sondaicus*	(Late Miocene) Pleistocene–Recent	South and Southeast Asia	Geraads et al., 2021; Antoine et al., 2022; Antoine, 2025
Rhinoceros	*unicornis*	Pleistocene–Recent	South and Southeast Asia	Antoine et al., 2022; Lu et al., 2021
Rusingaceros	*leakeyi*	Early–Middle Miocene	Kenya	Geraads et al., 2021
Stephanorhinus	*africanus*	Pliocene(–Pleistocene)	Tunisia, Morocco, Chad	Geraads et al., 2021
Stephanorhinus	*etruscus*	Late Pliocene–Early Pleistocene	Europe, Eastern Mediterranean, Central Asia	Geraads et al., 2021; Pandolfi et al., 2021
Stephanorhinus	*hemitoechus*	Pleistocene	Europe, North Africa, Eastern Mediterranean	Geraads et al., 2021; Pandolfi et al., 2021
Stephanorhinus	*hundsheimensis*	Pleistocene	Europe, Balkans, Eastern Mediterranean	Geraads et al., 2021; Pandolfi et al., 2021
Stephanorhinus	*jeanvireti*	Late Pliocene-Pleistocene	Europe	Geraads et al., 2021; Pandolfi et al., 2021
Stephanorhinus	*kirchbergensis*	Pleistocene	Europe, China, Iran, Israel, Libya, Russia	Geraads et al., 2021; Pandolfi et al., 2021
Stephanorhinus	*kurmetiensis*	Late Miocene	Kazakhstan	Geraads et al., 2021
Stephanorhinus	*lantianensis*	Pleistocene	China	Geraads et al., 2021; Pandolfi et al., 2021
Stephanorhinus	*yunchuchenensis*	Pleistocene	China	Geraads et al., 2021; Pandolfi et al., 2021

References

Aguirre, E., & Guérin, C. (1974). Première découverte d'un Iranotheriinae (Mammalia, Perissodactyla, Rhinocerotidae) en Afrique: *Kenyatherium bishopi* nov. gen. sp. de la formation vallésienne (Miocène supérieur) de Nakali (Kenya). *Estudios Geológicos, 30*, 229–233.

Antoine, P.-O., Bulot, C., & Ginsburg, L. (2000). Les rhinocérotidés (Mammalia, Perissodactyla) de l'Orléanien (Miocène inférieur) des bassins de la Garonne et de la Loire : intérêt biostratigraphique. *Comptes Rendus de l'Académie des Sciences, Sciences de la Terre et des Planètes, Paris, 330*, 571–576.

Antoine, P.-O. (2002). Phylogénie et évolution des Elasmotheriina (Mammalia, Rhinocerotidae). *Mémoires du Muséum National d'Histoire Naturelle, 188*, 1–359.

Antoine, P.-O. (2003). Middle Miocene elasmotheriine Rhinocerotidae from China and Mongolia: Taxonomic revision and phylogenetic relationships. *Zoologica Scripta, 32*, 95–118.

Antoine, P.-O. (2012). Pleistocene and Holocene rhinocerotids (Mammalia, Perissodactyla) from the Indochinese Peninsula. *Comptes Rendus Palevol, 11*, 159–168.

Antoine, P.-O., & Becker, D. (2013). A brief revision of Agenian Rhinocerotidae in Western Europe.S *wiss. Journal of Geosciences*, 106, 135–146.

Antoine, P.-O., Métais, G., Orliac, M. J., Crochet, J.-Y., Flynn, L. J., Marivaux, L., Rajpar, A. R., Roohi, G., & Welcomme, J.-L. (2013). Mammalian Neogene biostratigraphy of the Sulaiman Province, Pakistan. In X.-M. Wang, L. J. Flynn, & M. Fortelius (Eds.), *Fossil mammals of Asia: Neogene biostratigraphy and chronology* (pp. 400–422). Columbia University Press.

Antoine, P.-O. (2025). Chapter 18. Rhinocerotids from the Siwalik faunal sequence. In C. Badgley, D. Pilbeam, & M. Morgan (Eds.), *At the foot of the Himalayas: Paleontology and ecosystem dynamics of the Siwalik record of Pakistan*. Johns Hopkins University Press.

Antoine, P.-O., Downing, K. F., Crochet, J.-Y., Duranthon, F., Flynn, L. J., Marivaux, L., Métais, G., Rajpar, A. R., & Roohi, G. (2010). A revision of *Aceratherium blanfordi* Lydekker, 1884 (Mammalia: Rhinocerotidae) from the early Miocene of Pakistan: postcranials as a key. *Zoological Journal of the Linnean Society, 160*, 139–194.

Antoine, P.-O., Ducrocq, S., Marivaux, L., Chaimanee, Y., Crochet, J.-Y., Jaeger, J.-J., & Welcomme, J.-L. (2003). Early rhinocerotids (Mammalia, Perissodactyla) from South Asia and a review of the Holarctic Paleogene rhinocerotid record. *Canadian Journal of Earth Sciences, 40*, 365–374.

Antoine, P.-O., Duranthon, F., & Welcomme, J.-L. (2003). *Alicornops* (Mammalia, Rhinocerotidae) dans le Miocène supérieur des Collines Bugti (Balouchistan, Pakistan): Implications phylogénétiques. *Geodiversitas, 25*, 575–603.

Antoine, P.-O., Reyes, M. C., Amano, N., Bautista, A. P., Chun-Hsiang Chang, C.-H., Claude, J., De Vos, J., & Ingicco, T. (2022). A new rhinoceros clade from the Pleistocene of Asia sheds light on mammal dispersals to The Philippines. *Zoological Journal of the Linnean Society, 20*, 1–15.

Antoine, P.-O., & Sen, S. (2016). Upper Miocene mammal locality of Küçükçekmece, European Turkey: Rhinocerotidae and Chalicotheriidae (Perissodactyla, Tapiromorpha). *Geodiversitas, 38*, 245–259.

Bai, B., Meng, J., Zhang, C., Gong, Y. X., & Wang, Y. Q. (2020). The origin of Rhinocerotoidea and phylogeny of Ceratomorpha (Mammalia, Perissodactyla). *Communications Biology, 3*(1), 1–16.

Becker, D. (2009). Earliest record of rhinocerotoids (Mammalia: Perissodactyla) from Switzerland: systematics and biostratigraphy. *Swiss Journal of Geosciences, 102*(3), 489–504.

Becker, D., Antoine, P.-O., & Maridet, O. (2013). A new genus of Rhinocerotidae (Mammalia, Perissodactyla) from the Oligocene of Europe. *Journal of Systematic Palaeontology, 11*, 947–972.

Becker, D., Antoine, P.-O., Mennecart, B., & Tissier, J. (2018). New rhinocerotid remains in the latest Oligocene–Early Miocene of the Swiss Molasse Basin. *Revue de Paléobiologie, 37*(2), 395–408.

Becker, D., & Tissier, J. (2020). Rhinocerotidae from the early Middle Miocene locality Gračanica (Bugojno Basin, Bosnia-Herzegovina). *Palaeobiodiversity and Palaeoenvironments, 100*(2), 395–412.

Beliajeva, E. I. (1959). Sur la découverte de rhinocéros tertiaires anciens dans la Province Maritime de l'U.R.S.S. *Vertebrata PalAsiatica, 3*, 81–91.

Blanchon, M., Antoine, P.-O., Blondel, C., & de Bonis, L. (2018). Rhinocerotidae (Mammalia, Perissodactyla) from the latest Oligocene Thézels locality, SW France, with a special emphasis on *Mesaceratherium gaimersheimense* Heissig 1969. *Annales de Paléontologie, 104*, 217–229.

Böhme, M., Aigstorfer, M., Antoine, P.-O., Appel, E., Havlik, P., Hung, N. V., Métais, G., Schneider, S., Setzer, F., Tappert, R., Tran, D. N., Uhl, D., & Prieto, J. (2013). Na Duong (Northern Vietnam)—an exceptional window into Eocene ecosystems from South-East Asia. *Zitteliana A, 53*, 120–167.

Brunet, M. (1979). *Les grands mammifères chefs de file de l'immigration Oligocène et le problème de la limite Eocène-Oligocène en Europe*. Fondation Singer-Polignac.

Cappellini, E., Welker, F., Pandolfi, L., Ramos-Madrigal, J., Samodova, D., Rüther, P. L., Fotakis, A. K., Lyon, D., Moreno-Mayar, J. V., Bukhsianidze, M., Jersie-Christensen, R. R., Mackie, M., Ginolhac, A., Ferring, R., Tappen, M., Palkopoulou, E., Dickinson, M. R., Stafford, T. W., Jr., Chan, Y. L., Götherström, A., Nathan Senthilvel, K. S. S., Heintzman, P. D., Kapp, J. D., Kirillova, I., Moodley, Y., Agustí, J., Kahlke, R.-D., Kiladze, G., Martínez-Navarro, B., Liu, S., Velasco, M. S., Sinding, M.-H. S., Kelstrup, C. D., Allentoft, M. E., Orlando, L., Penkman, K., Shapiro, B., Rook, L., Dalén, L., Gilbert, M. T. P., Olsen, J. V., Lordkipanidze, D., & Willerslev, E. (2019). Early Pleistocene enamel proteome from Dmanisi resolves *Stephanorhinus* phylogeny. *Nature, 574*, 103–107.

Cerdeño, E. (1992). Spanish neogene rhinoceroses. *Palaeontology, 35*, 297–308.

Cerdeño, E. (1998). Diversity and evolutionary trends of the family Rhinocerotidae (Perissodactyla). *Palaeogeography, Palaeoclimatology, Palaeoecology, 141*, 13–34.

Chen, S., Deng, T., Hou, S., Shi, Q., & Pang, L. (2010). Sexual dimorphism in perissodactyl rhinocerotid *Chilotherium wimani* from the late Miocene of the Linxia Basin (Gansu, China). *Acta Palaeontologica Polonica, 55*, 587–597.

Cuvier, G. (1822). *Recherches sur les ossemens fossiles de quadrupèdes, nouvelle édition* (Vol. 2, p. 684). G. Dufour et E. D'Ocagne.

de Christol, J. (1834). Recherches sur les caractères des grandes espèces de Rhinocéros fossiles. *Annales des Sciences Naturelles, Paris, series, 2*(4), 44–112.

Deng, T. (2005a). New cranial material of *Shansirhinus* (Rhinocerotidae, Perissodactyla) from the lower Pliocene of the Linxia basin in Gansu, China. *Geobios, 38*, 301–313.

Deng, T. (2005b). New discovery of *Iranotherium morgani* (Perissodactyla, Rhinocerotidae) from the Late Miocene of the Linxia Basin in Gansu, China, and its sexual dimorphism. *Journal of Vertebrate Paleontology, 25*, 442–450.

Deng, T. (2008). A new elasmothere (Perissodactyla, Rhinocerotidae) from the Late Miocene of the Linxia Basin in Gansu, China. *Geobios, 41*, 719–728.

Deng, T., Hanta, R., & Jintasakul, P. (2013). A new species of *Aceratherium* (Rhinocerotidae, Perissodactyla) from the Late Miocene of Nakhon Ratchasima, northeastern Thailand. *Journal of Vertebrate Paleontology, 33*, 977–985.

Deng, T., Lu, X., Wang, S., Flynn, L. J., Sun, D., He, W., & Chen, S. (2021). An Oligocene giant rhino provides insights into *Paraceratherium* evolution. *Communications Biology, 4*(1), 1–10.

Deng, T., & Qiu, Z.-X. (2007). First discovery of *Diceros* (Perissodactyla, Rhinocerotidae) in China. *Vertebrata PalAsiatica, 45*, 287–306.

Falconer, H. (1868). On the European Pliocene and post-Pliocene species of the genus *Rhinoceros*. In C. Murchison (Ed.), *Palaeontological memoirs and notes of the late Hugh Falconer, (2) mastodon, elephant, rhinoceros, ossiferous caves, primeval man and his contemporaries* (pp. 309–403). Robert Hardwicke.

Gabunia, L. K. (1964). *Benara fauna of Oligocene vertebrates [in Georgian]* (pp. 1–267). Metsniereba Press.

Geraads, D. (1988). Révision des Rhinocerotidae (Mammalia) du Turolien de Pikermi. Comparaison avec les formes voisines. *Annales de Paléontologie, 74*, 13–41.

Geraads, D. (2005). Pliocene Rhinocerotidae (Mammalia) from Hadar and Dikika (lower Awash, Ethiopia), and a revision of the origin of modern African rhinos. *Journal of Vertebrate Paleontology, 25*, 451–461.

Geraads, D. (2010). Chapter 34—Rhinocerotidae. In L. Werdelin & W. J. Sanders (Eds.), *Cenozoic mammals of Africa* (pp. 675–689). University of California Press.

Geraads, D., Cerdeño, E., García Fernandez, D., Pandolfi, L., Billia, E., Athanassiou, A., Albayrak, E., Codrea, V., Obada, T., Deng, T., Tong, H., Lu, X., Pícha, S., Marciszak, A., Jovanovic, G., Becker, D., Zervanova, J., Chaïd Saoudi, Y., Bacon, A.-M., Sévêque, N., Patnaik, R., Brezina, J., Spassov, N., & Uzunidis, A. (2021). A database of old world neogene and quaternary rhino-bearing localities. www.rhinoresourcecenter.com/about/fossil-rhino-database.php

Geraads, D., Lehmann, T., Peppe, D. J., & McNulty, K. P. (2016). New Rhinocerotidae from the Kisingiri localities (lower Miocene of Western Kenya). *Journal of Vertebrate Paleontology, 36*(3), e1103247. https://doi.org/10.1080/02724634.2016.1103247

Geraads, D., McCrossin, M., & Benefit, B. (2012). A new rhinoceros, *Victoriaceros kenyensis* gen. et sp. nov., and other Perissodactyla from the Middle Miocene of Maboko, Kenya. *Journal of Mammalian Evolution, 19*, 57–75.

Geraads, D., & Miller, E. (2013). *Brachypotherium minor*, a new rhinoceros from the Early Miocene of Buluk, Northern Kenya. *Geodiversitas, 35*, 359–375.

Geraads, D., & Zouhri, S. (2021). *Eoazara xerrii* n.gen. n.sp. (Mammalia, Rhinocerotidae, Elasmotheriinae) from the upper Miocene of Skoura, Ouarzazate, Morocco. *Acta Palaeontologica Polonica, 66*(4), 753–765. https://doi.org/10.4202/app.00904.2021

Guérin, C. (1980). Les Rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon, 79*, 1–1185.

Guérin, C., & Pickford, M. (2003). *Ougandatherium napakense* nov. gen. nov. sp., le plus ancien Rhinocerotidae Iranotheriinae d'Afrique. *Annales de Paléontologie, 89*, 1–35.

Handa, N., Nakatsukasa, M., Kunimatsu, Y., Tsubamoto, T., & Nakaya, H. (2017). A new Elasmotheriini (Perissodactyla, Rhinocerotidae) from the upper Miocene of Samburu Hills and Nakali, northern Kenya. *Geobios, 50*, 197–209.

Hanson, C. B. (1989). *Teletaceras radinskyi*, a new primitive rhinocerotid from the Late Eocene Clarno formation of Oregon. In D. R. Prothero & R. M. Schoch (Eds.), *The evolution of perissodactyls* (pp. 379–398). Oxford University Press.

Heissig, K. (1972). Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. *Abhandlungen der Bayerische Akademie der Wissenschaften. Mathematisch Naturwissenschaftliche Klasse, 152*, 1–112.

Heissig, K. (2012). Les Rhinocerotidae (Perissodactyla) de Sansan. *Mémoires du Muséum National d'Histoire Naturelle, 203*, 317–485.

Holroyd, P. A., Tsubamoto, T., Egi, N., Ciochon, R. L., Takai, M., Tun, S. T., Sein, C., & Gunnell, G. F. (2006). A rhinocerotid perissodactyl from the late Middle Eocene Pondaung Formation, Myanmar. *Journal of Vertebrate Paleontology, 26*(2), 491–494.

Hooijer, D. A. (1971). A new rhinoceros from the Late Miocene of Loperot, Turkana district, Kenya. *Bulletin of the Museum of Comparative Zoology, 142*, 339–392.

Hullot, M., Antoine, P.-O., Laurent, Y., & Merceron, G. (2021). Paleoecology of the Rhinocerotidae (Mammalia, Perissodactyla) from Béon 1, Montréal-du-Gers (late Early Miocene, SW France): insights from dental microwear texture analysis, mesowear, and enamel hypoplasia. *Palaeontologia Electronica, 24*(2), 24.2.a27.

Hünermann, K. A. (1989). Die Nashornskelette (*Aceratherium incisivum* Kaup 1832) aus dem Jungtertiär vom Höwenegg im Hegau (Südwestdeutschland). *Andrias, 6*, 1–116.

Jame, C., Tissier, J., Maridet, O., & Becker, D. (2019). Early Agenian rhinocerotids from Wischberg (Canton Bern, Switzerland) and clarification of the systematics of the genus *Diaceratherium*. *PeerJ, 7*, e7517.

Kahlke, R.-D., & Kaiser, T. M. (2011). Generalism as a subsistence strategy: advantages and limitations of the highly flexible feeding traits of Pleistocene *Stephanorhinus hundsheimensis* (Rhinocerotidae, Mammalia). *Quaternary Science Reviews, 30*, 2250–2261.

Kordikova, E. G. (2001). Remarks on the Oligocene-Miocene mammal paleontology and sequence stratigraphy of South-Western Betpakdala Steppe, South Kazakhstan. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 221*, 35–79.

Kosintsev, P., Mitchell, K. J., Devièse, T., van der Plicht, J., Kuitems, M., Petrova, E., Tikhonov, A., Higham, T., Comeskey, D., Turney, C., Cooper, A., van Kolfschoten, T., Stuart, A. J., & Lister, A. M. (2019). Evolution and extinction of the giant rhinoceros *Elasmotherium sibiricum* sheds light on Late Quaternary megafaunal extinctions. *Nature Ecology and Evolution, 3*, 31–38. https://doi.org/10.1038/s41559-018-0722-0

Licht, A., Métais, G., Coster, P., Ibilioğlu, D., Ocakoğlu, F., Westerweel, J., Mueller, M., Campbell, C., Mattingly, S., Wood, M. C., & Beard, K. C. (2022). Balkanatolia: The insular mammalian biogeographic province that partly paved the way to the Grande Coupure. *Earth-Science Reviews, 226*, 103929.

Liu, S., Westbury, M. V., Dussex, N., Mitchell, K. J., Sinding, M.-H. S., Heintzman, P. D., Duchêne, D. A., Kapp, J. D., von Seth, J., Heiniger, H., Sánchez-Barreiro, F., Margaryan, A., André-Olsen, R., DeCahsan, B., Meng, G., Yang, C., Chen, L., van der Valk, T., Moodley, Y., Rookmaaker, K., Bruford, M. W., Ryder, O., Steiner, C., Bruins-van Sonsbeek, L. G. R., Vartanyan, S., Guo, C., Cooper, A., Kosintsev, P., Kirillova, I., Lister, A. M., Marques-Bonet, T., Gopalakrishnan, S., Dunn, R. R., Lorenzen, E. D., Shapiro, B., Zhang, G., Antoine, P.-O., Dalén, L., & Gilbert, M. T. P. (2021). Ancient and modern genomes unravel the evolutionary history of the rhinoceros family. *Cell, 184*, 1–12.

Lu, X., Cerdeño, E., Zheng, X., Wang, S., & Deng, T. (2021). The first Asian skeleton of *Diaceratherium* from the early Miocene Shanwang Basin (Shandong, China), and implications for its migration route. *Journal of Asian Earth Sciences: X, 6*, 100074.

MacFadden, B. J. (2006). North American Miocene land mammals from Panama. *Journal of Vertebrate Paleontology, 26*(3), 720–734.

Marivaux, L., Chaimanee, Y., Yamee, C., Srisuk, P., & Jaeger, J.-J. (2004). Discovery of *Fallomus ladakhensis* Nanda and Sahni, 1998 (Mammalia, Rodentia, Diatomyidae) in the lignites of Nong Ya Plong (Phetchaburi Province, Thailand): systematic, biochronological and paleoenvironmental implications. *Geodiversitas, 26*, 493–507.

Ménouret, B., & Guérin, C. (2009). *Diaceratherium massiliae* nov. sp. des argiles oligocènes de Saint-André et Saint-Henri à Marseille et de Les Milles près d'Aix-en-Provence (SE de la France), premier grand Rhinocerotidae brachypode européen. *Geobios, 42*, 293–327.

Michel, P., Campmas, E., Stoetzel, E., Nespoulet, R., Abdeljalil El Hajraoui, M., & Amani, F. (2010). Upper Palaeolithic (layer 2) and Middle Palaeolithic (layer 3) large faunas from El Harhoura 2 Cave (Témara, Morocco): paleontological, paleoecological and paleoclimatic data. *Historical Biology, 22*, 327–340.

Müller, R. D., Cannon, J., Qin, X., Watson, R. J., Gurnis, M., Williams, S., Pfaffelmoser, T., Seton, M., Russell, S. H. J., & Zahirovic, S. (2018). GPlates: building a virtual Earth through deep time. *Geochemistry, Geophysics, Geosystems, 19*(7), 2243–2261.

Muzzolini, A. (1995). Les images rupestres du Sahara. Published by the author, p. 447.

NOW Community. (2021). New and old worlds database of fossil mammals (NOW). Licensed under CC BY 4.0. Retrieved December 12, 2021 from https://nowdatabase.org/now/database/. https://doi.org/10.5281/zenodo.4268068

Pandolfi, L. (2015). *Persiatherium rodleri*, gen. et sp. nov. (Mammalia, Rhinocerotidae) from the upper Miocene of Maragheh (northwestern Iran). *Journal of Vertebrate Paleontology, 36*, e1040118. https://doi.org/10.1080/02724634.2015.1040118

Pandolfi, L., Antoine, P.-O., Bukhsianidze, M., Lordkipanidze, D., & Rook, L. (2021b). Northern Eurasian rhinocerotines (Mammalia, Perissodactyla) by the Pliocene–Pleistocene transition: Phylogeny and historical biogeography. *Journal of Systematic Palaeontology, 19*(15), 1031–1057. https://doi.org/10.1080/14772019.2021.1995907

Pandolfi, L., Calvo, R., Grossman, A., & Rabinovich, R. (2021a). Rhinocerotidae from the early Miocene of the Negev (Israel) and implications for the dispersal of early Neogene rhinoceroses. *Journal of Paleontology, 95*(6), 1340–1351.

Pandolfi, L., Cerdeño, E., Codrea, V., & Kotsakis, T. (2017). Biogeography and chronology of the Eurasian extinct rhinoceros *Stephanorhinus etruscus*, Mammalia, Rhinocerotidae. *Comptes Rendus Palevol, 16*(7), 762–773.

Pandolfi, L., & Maiorino, L. (2016). Reassessment of the largest Pleistocene rhinocerotine *Rhinoceros platyrhinus* (Mammalia, Rhinocerotidae) from the Upper Siwaliks (Siwalik Hills, India). *Journal of Vertebrate Paleontology, 36*(2), 1–12.

Peter, K. (2002). Odontologie der Nashornverwandten (Rhinocerotidae) aus dem Miozän (MN5) von Sandelzhausen (Bayern). *Zitteliana, 22*, 3–168.

Prieto, J., Antoine, P.-O., Böhme, M., van der Made, J., Métais, G., Phuc, L. T., Quan, Q. T., Schneider, S., Tran, D. N., Vasilyan, D., & Viet, L. T. (2018). Biochronological and paleobiogeographical significance of the earliest Miocene mammal fauna from Northern Vietnam. *Palaeobiodiversity and Palaeoenvironments, 98*, 287–313.

Prothero, D. R., & Schoch, R. M. (1989). Classification of the Perissodactyls. In D. R. Prothero & R. M. Schoch (Eds.), *The evolution of Perissodactyls* (pp. 530–539). Oxford University Press.

Rivals, F., & Lister, A. M. (2016). Dietary flexibility and niche partitioning of large herbivores through the Pleistocene of Britain. *Quaternary Science Reviews, 146*, 116–133.

Rookmaaker, L. C., & Antoine, P.-O. (2013). New maps representing the historical distribution of the African species of rhinoceros: *Diceros bicornis*, *Ceratotherium simum* and *Ceratotherium cottoni*. *Pachyderm, 52*, 91–96.

Sanisidro, O., Alberdi, M. T., & Morales, J. (2012). The first complete skull of *Hispanotherium matritense* (Prado, 1864) (Perissodactyla, Rhinocerotidae) from the Middle Miocene of the Iberian Peninsula. *Journal of Vertebrate Paleontology, 32*, 446–455.

Saraç, G. (2003). Discovery of *Protaceratherium albigense* (Rhinocerotidae, Mammalia) in Oligocene coastal deposits of Turkish Thrace. In J. W. F. Reumer & W. Wessels (Eds.), *Distribution and migration of Tertiary mammals in Eurasia* (pp. 509–518). DEINSEA Special Issue.

Scherler, L., Mennecart, B., Hiard, F., & Becker, D. (2013). Evolutionary history of hoofed mammals during the Oligocene–Miocene transition in Western Europe. *Swiss Journal of Geosciences, 106*(2), 349–369.

Scotese, C. R. (2016). Tutorial: PALEOMAP paleoAtlas for GPlates and the paleoData plotter program.

Sharipova, A. K., & Ospanova, A. K. (2014). To the question of studying species composition of location of hipparion fauna "Gusiny perelet" in Kazakhstan. *Fundamental'nyye i prikladnyye issledovaniya: problemy i rezul'taty, 16*, 15–19.

Sizov, A., Klementiev, A., & Antoine, P.-O. (2024). *An early Miocene skeleton of Brachydiceratherium Lavocat, 1951 (Mammalia, Perissodactyla) from the Baikal area, Russia, and a revised phylogeny of Eurasian teleoceratines*. PCI Paleontology. DOI: 10.1101/2022.07.06.498987

Stehlin, H. G. (1909). Remarques sur les faunules de Mammifères des couches éocènes et oligocènes du Bassin de Paris. *Bulletin de la Société géologique de France, 4*(9), 488–520.

Stuart, A. J., & Lister, A. M. (2012). Extinction chronology of the woolly rhinoceros *Coelodonta antiquitatis* in the context of Late Quaternary megafaunal extinctions in northern Eurasia. *Quaternary Science Reviews, 51*, 1–17.

Sun, D., Deng, T., & Jiangzuo, Q. (2022). The most primitive *Elasmotherium* (Perissodactyla, Rhinocerotidae) from the Late Miocene of northern China. *Historical Biology, 34*(2), 201–211.

Tissier, J., Antoine, P.-O., & Becker, D. (2020). New material of *Epiaceratherium* and a new species of *Mesaceratherium* clear up the phylogeny of early Rhinocerotidae (Perissodactyla). *Royal Society Open Science, 7*, 200633.

Tissier, J., Antoine, P.-O., & Becker, D. (2021a). New species, revision, and phylogeny of *Ronzotherium* Aymard 1854 (Perissodactyla, Rhinocerotidae). *European Journal of Taxonomy, 753*, 1–80.

Tissier, J., Geiger-Schütz, P., Peter F. Flückiger, P. F. & Becker, D. (2021b). Neue Erkenntnisse über die Nashörner von Rickenbach (Oberes Oligozän, Kanton Solothurn, Schweiz) des Naturmuseums Olten. *Mitteilungen der Naturforschenden Gesellschaft des Kantons Solothurn*, 44, 25–50.

Tissier, J., Becker, D., Codrea, V., Costeur, L., Fărcaş, C., Solomon, A., Venczel, M., & Maridet, O. (2018). New data on Amynodontidae (Mammalia, Perissodactyla) from Eastern Europe: Phylogenetic and palaeobiogeographic implications around the Eocene-Oligocene transition. *PLoS One, 13*(4), e0193774.

Titov, V. V., Baigusheva, V. S., & Uchytel, R. S. (2021). The experience in reconstructing of the head of *Elasmotherium* (Rhinocerotidae). *Russian Journal of Theriology, 20*, 173–182. https://doi.org/10.15298/rusjtheriol.20.2.06

Titov, V., Tesakov, A., & Syromyatnikova, E. (2018). Early pliocene vertebrate fauna from the Manych River Valley (Orlovskiy District, Rostov Region). *Trudy SSC Russian Academy of Sciences, 7*, 243–246. [In Russian]. https://doi.org/10.23885/1993-6621-2018-7-243-246

Uhlig, U. (1999). Die Rhinocerotoidea (Mammalia) aus der unteroligozänen Spaltenfüllung Möhren 13 bei Treuchtlingen in Bayern. *Abhandlungen der Bayerischen Akademie der Wissenschafen, Mathematisch-Naturwissenschaftliche Klasse, N. F., 170*, 1–254.

Uno, K. T., Cerling, T. E., Harris, J. M., Kunimatsu, Y., Leakey, M. G., Nakatsukasa, M., & Nakaya, H. (2011). Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. *Proceedings of the National Academy of Sciences of the USA, 108*(16), 6509–6514.

Uzunidis, A., Antoine, P.-O., & Brugal, J.-P. (2022). A Middle Pleistocene *Coelodonta antiquitatis praecursor* Guérin, 1980 (Mammalia, Perissodactyla) from Les Rameaux, SW France, and a revised phylogeny of *Coelodonta* Bronn, 1831. *Quaternary Science Reviews, 288*, 107594.

Van Couvering, J. A., & Delson, E. (2020). African land mammal ages. *Journal of Vertebrate Paleontology, 40*(5), e1803340.

Vangengejm, E. A., Belyaeva, E. I., Garutt, V. E., Dmitrieva, E. I., & Zazhigin, V. S. (1966). *Mlekopitayushchie eopleistocena zapadnogo Zabaikal'ya*. Nauka.

Wang, B., & Secord, R. (2020). Paleoecology of *Aphelops* and *Teleoceras* (Rhinocerotidae) through an interval of changing climate and vegetation in the Neogene of the Great Plains, central United States. *Palaeogeography, Palaeoclimatology, Palaeoecology, 542*, 109411.

Yans, J., Verhaert, M., Gautheron, C., Antoine, P.-O., Moussi, B., Dekoninck, A., Decrée, S., Chaftar, H.-R., Hatira, N., Dupuis, C., Pinna-Jamme, R., & Jamoussi, F. (2021). (U-Th)/He dating of supergene iron (oxyhydr-)oxides of the Nefza-Sejnane district (Tunisia): new insights on mineralization and mammalian biostratigraphy. *Minerals, 11*, 260.