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Perissodactyla Workshop

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ABSTRACT BOOK

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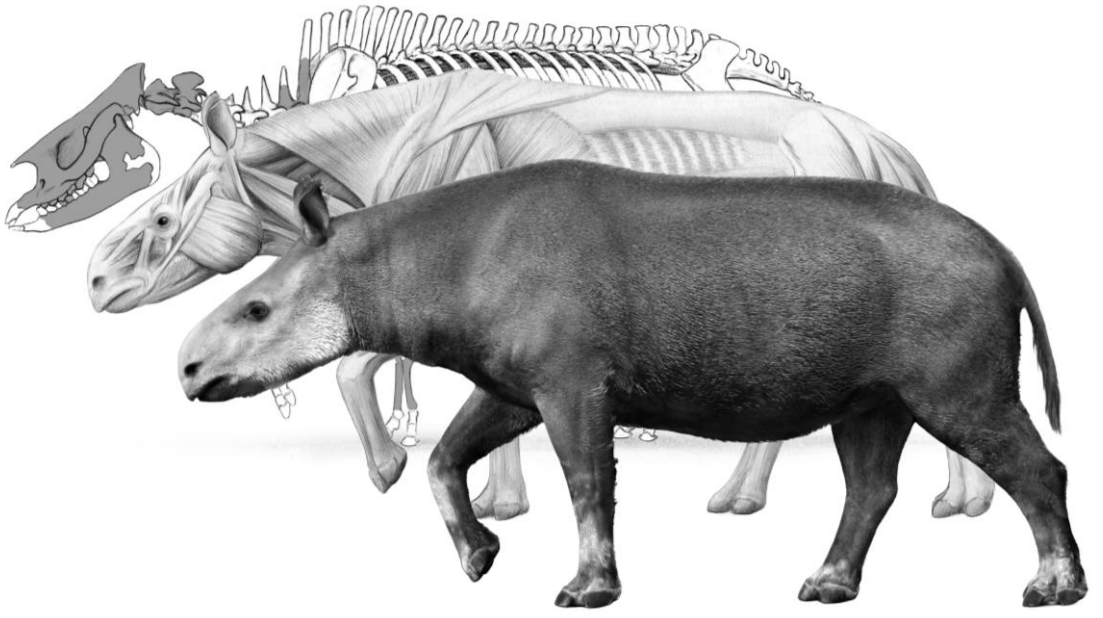
Friday 18th of September		Page
Welcome notes		
14:00-14:15	Damien Becker, Manon Hullot – Official welcome	
Keynote		
14:15-15:00	Juan Cantalapiedra – *What perissodactyls teach us about evolution*	6
Talks		
15:00-15:15	Luke Holbrook – *Early biogeography of Pan-Perissodactyla: current evidence and remaining questions*	16
15:15-15:30	Thierry Smith – *Reassessment of* Olbitherium*, the "perissodactyl-like archaic ungulate" from the early Eocene Wutu Formation, China*	25
15:30-16:00	**Break**	
16:00-16:15	Ryan Paterson – *The potential for resolving the phylogeny of Neogene Perissodactyla via Palaeoproteomics*	23
16:15-16:30	Helder Gomes Rodrigues – *Evolution of dental eruption patterns in Perissodactyla and histological prospects*	13
16:30-16:45	Jérémy Tissier – *Systematics and evolution of early perissodactyls and earliest equoids*	27
16:45-17:00	Léo Henocque – *Paleoecological study of Late Oligocene (MP29) herbivores from Rickenbach (Solothurn, Switzerland)*	15
After talks	**Poster Session**	
1	Damien Becker – *The* Lophiodon *from Réalmont*	31
2	Céline Robinet – *From tooth to food: a multiproxy approach to infer dietary preferences in Lophiodontidae (Mammalia, Perissodactyla) from Southern France*	35
3	Naoto Handa – *The late Cenozoic Rhinocerotidae from the sandpits in Nakhon Ratchasima, Northeastern Thailand and its biostratigraphical implication*	32
4	Eva Simonutti – *A new elasmotheriine species in the European Early Miocene, description and paleobiogeographic implications*	36
5	Olivier Maridet – *First discovery of a skull of* Urtinotherium *Chiu, 1962 from the Late Eocene of Altyn Tagh (Xinjiang, China)*	34
Saturday 19th of September		
Keynote		
9:00-9:45	Ainara Badiola – *Eocene Equoids of the Iberian Peninsula: History of Research, Endemism and Palaeoecology*	5
Talks		
9:45-10:00	Manon Hullot – *Spatio-temporal evolution of the paleoecological preferences of the palaeotheres (Perissodactyla; Mammalia): insights into their extinction around the Grande Coupure*	17
10:00-10:15	Tifanie Duprat – *A new perissodactyl fauna from the Middle Eocene of La Vernière (Vénès, Tarn, France)*	11
10:15-10:30	Jamie MacLaren – *Equids traverse a phenotypic landscape of shoulder anatomy through their evolution*	21
10:30-11:00	**Break**	
11:00-11:15	Hanwen (Steven) Zhang – *Mythbusting the Palaeobiology of 'Giant' Stenonid Horses from the Early Pleistocene*	29
11:15-11:30	Catherine Sharpe – *Ecological Disequilibrium in* Equus ferus*: Multi-Isotope Evidence for Niche Contraction and Physiological Constraints across the Late Glacial–Holocene Transition*	24

11:30-11:45	Bin Bai – *Biostratigraphy of brontotheres from the Erlian Basin of Inner Mongolia, China with focus on cranial morphology of* Metatitan	9
11:45-12:00	Pengyang Li – *New materials of Chalicotheriinae (Perissodactyla, Mammalia) from the Early Pliocene in the Linxia Basin of Gansu, China*	19
12:00-12:15	Panagiotis Kampouridis – *Phalangeal morphology in chalicothere systematics*	18
12:15-12:30	Fabrice Lihoreau – *New lophiodontid remains from southern France close to the origination of the genus* Lophiodon	20
12:30-14:00	**Lunch Break**	
Keynote		
14:00-14:45	Danhui Sun – *Revisiting the Miocene Radiation of East Asian Rhinocerotids: New Evidence from Taxonomy, Phylogeny, and Paleoecology*	7
Talks		
14:45-15:00	Georgia Svorligkou – *Observation of the paleodietary habits of the elusive acerathere* Eochilotherium samium *(Perissodactyla, Rhinocerotidae) from the late Miocene of Samos island, Greece, through dental mesowear and microwear analysis*	26
15:00-15:15	Tao Deng – *Introduction to the fascicle on the Rhinocerotoidea of the Perissodactyla in Palaeovertebrata Sinica*	10
15:15-15h30	Antigone Uzunidis – *Body mass, dietary flexibility and extinction vulnerability in the Pleistocene rhinoceros* Stephanorhinus hemitoechus	28
15:30-16:00	**Break**	
16:00-16:15	Luca Pandolfi – *Plio-Pleistocene Palaeartic rhinocerotines: state of the art and future perspectives*	22
16:15-16:30	William Hart – *Differing musculoskeletal development of New World* Tapirus *spp. reflects varied ecological dynamics of browser communities during the Mio-Pliocene transition*	14
16:30-16:45	Joseph Gajewski – *Population structure of a fossil dwarf tapir* (Tapirus polkensis) *assemblage suggests parallel sociality to extant tapirs*	12



Reconstruction of the Early Oligocene rhinoceros "*Molassitherium*" by Patrick Röschli (© JURASSICA)

Keynote speakers

Eocene Equoids of the Iberian Peninsula: History of Research, Endemism and Palaeoecology

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The study of Iberian Eocene perissodactyls has progressed from the first discoveries in the 19th century to the recognition of western Iberia as a distinct palaeobiogeographic region characterized by strong faunal endemism. Early works by Román, Royo y Gómez, Hernández-Pacheco, Crusafont, Villalta, and Antunes, among others, together with later doctoral research by Casanovas, Cuesta, Checa, Badiola and Perales-Gogenola, greatly improved knowledge of Iberian Eocene equoids. The western Iberian region preserves a remarkable diversity of endemic palaeotheres and pachynolophs from the Duero, Almazán, Oviedo, Miranda-Treviño, and northeastern Ebro basins. Seven endemic genera (*Franzenium, Cantabrotherium, Paranchilophus, Metaplagiolophus, Bepitherium, Iberolophus*, and *Idiodontherium*) and 19 species have been described, including endemic Iberian representatives of *Plagiolophus, Palaeotherium, Pachynolophus*, and *Leptolophus*, all unknown elsewhere in Europe, including northeastern Iberia.

The persistence of this endemic fauna during the late Eocene, despite terrestrial connections with Central Europe, may reflect ecological barriers and specialized dietary adaptations. Iberian palaeotheres evolved distinctive dental characters such as early hypsodonty, precocious development of coronal cementum, and reduction of the premolar series associated with enlarged molars, especially in *Leptolophus*. Other genera, including *Idiodontherium* and *Iberolophus*, developed highly specialized dentitions. *Idiodontherium* shows a remarkably shortened jugal tooth row relative to the length of the post-canine diastema, together with an extreme reduction of the premolar series to only two teeth, a condition unknown among other Eocene equoids. In contrast, *Iberolophus* retained a long premolar series, including P1/p1, together with non-lophoid biradicular premolars and a distinctive bumpy enamel texture.

These dental traits may reflect adaptations to specialized feeding strategies and, in some cases, to tougher vegetation or abrasive particles such as soil grit in increasingly open and/or arid environments with stronger seasonality associated with the climatic cooling preceding the Eocene–Oligocene transition. Nevertheless, dietary proxy analyses of *Plagiolophus* do not indicate significant dietary changes through time or between regions, suggesting that this genus remained a highly selective and ecologically stable feeder. Further palaeoecological research on other Eocene equoids is required to achieve a better understanding of these evolutionary and environmental patterns.

***Keywords**: Eocene, Equoids, Iberian Peninsula, Endemism, Palaeoecology.*
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What perissodactyls teach us about evolution

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The fossil record of perissodactyls is widely regarded as one of the best available records of Cenozoic large mammals. Its richness and stratigraphic resolution have made this group a cornerstone in the development of evolutionary theory, informing early ideas about evolutionary trends and fuelling developments in modern quantitative macroevolution.

In the first part of the talk, I will discuss perissodactyl phenotypic evolution in the context of evolutionary trends. I will revisit a selection of classic works that shaped how paleontologists have understood directional morphological change in the fossil record, followed by findings from recent research applying quantitative approaches to evaluate the tempo, mode, and directionality of phenotypic evolution across perissodactyl lineages. I will also preview an ongoing project integrating 3D geometric morphometrics with diversification models to investigate the macroevolutionary dynamics of cranial evolution in horses.

In the second part, I will examine the potential of fossil perissodactyls for the study of diversity dynamics. I will present preliminary estimates of the magnitude of the North American radiation of equids based on neural network approaches that help us to control for temporal and spatial biases in the fossil record.

Together, these two themes illustrate the enduring value of the perissodactyl fossil record as a testing ground for macroevolutionary theory, and the new opportunities that emerging methods and large-scale datasets offer for addressing long-standing evolutionary questions.

Revisiting the Miocene Radiation of East Asian Rhinocerotids: New Evidence from Taxonomy, Phylogeny, and Paleoecology

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The Miocene epoch represents a pivotal phase in the evolutionary history of Asian rhinocerotids, during which East Asia hosted a remarkably diverse assemblage of rhinocerotids. Here, we synthesize our systematic investigations conducted over the past five years on the Miocene rhinocerotids of China. Recent discoveries from Ningxia, Shaanxi, and Gansu substantially expand the known diversity of East Asian rhinocerotids, including Aceratheriinae, Teleoceratini, and Elasmotheriinae, with primitive members, key transitional forms, and previously undocumented geographic occurrences within their respective lineages. Among the most significant findings are the first confirmed East Asian record of *Prosantorhinus* and the discovery of transitional elasmotheriine taxa, both of which provide critical evidence for evaluating dispersal corridors and evolutionary transformations across Eurasia during the Miocene. Phylogenetic analyses based on expanded morphological character matrices clarify the systematic relationships within major rhinocerotid clades, resolving longstanding ambiguities and refining our understanding of lineage origins and biogeographic affinities. These analyses further support a dynamic model of rhinocerotid diversification driven by multiple dispersal events between Europe and Asia. Paleoecological reconstructions of the Tongxin fauna reveal that sympatrically occurring rhinocerotids exhibited marked differences in craniodental morphology, body size, and inferred dietary and habitat preferences, offering a rare window into community-level processes shaping megafaunal assemblages. These findings demonstrate that East Asian rhinocerotid evolution was shaped by the interplay of lineage diversification, ecological differentiation, and interregional dispersal, and that the northern Chinese records are indispensable for understanding the Miocene radiation of Asian rhinocerotids.

***Keywords**: Rhinocerotidae, Miocene, Morphology, Taxonomy, Phylogeny, Paleoecology*

Regular session

Biostratigraphy of brontotheres from the Erlian Basin of Inner Mongolia, China with focus on cranial morphology of *Metatitan*

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Brontotheres are a diverse group of perissodactyls that mainly inhabited Asia and North America from the early to late Eocene. The Asian brontotheres have been documented primarily from the Erlian Basin of Inner Mongolia, China since the Central Asiatic Expedition by the American Museum of Natural History (AMNH) in the 1920s. Based on recent fieldwork in the Erlian Basin, we have clarified the stratigraphic distribution of brontotheres from the Paleogene deposits of the basin. However, several taxonomic and stratigraphic issues require further investigation in future studies, including (1) it remains controversial about existence of brontotheres from the Arshanto Formation in the Erlian Basin; (2) whether *Metatelmatherium cristatum* from Irdinmanha Asian Land Mammal Age (ALMA) is a junior synonym of *M. ultimum* from the Uintan of North America; (3) whether *Titanodectes minor* probably from the upper part of the Shara Murun Formation and *T. ingens* from the Ulan Gochu Formation are junior synonyms of *Embolotherium grangeri* from Ulangochuian ALMA; and (4) *Metatitan* from the Irdinmanhan ALMA contradicts with its proposed intermediate stage between later *Rhinotitan* and *Embolotherium*. Furthermore, based on a nearly complete subadult skull of *Metatitan khaitchinus* from the Ulan Shireh Formation in the Erlian Basin, we provide some important cranial features that probably give rise to the “battering ram” of *Embolotherium*. The cranial features of *M. khaitchinus* include the frontal rising above the orbit and intruding the lateral side of the nasal which forms a rudimentary nasofrontal horn at their anteriormost joint, a wide emargination posterior to the palatine surrounding the choana, a long vomerine plate which extends to the posterior end of basisphenoid bisecting the nasopharynx, and a pair of large ventral sphenoid fossae. The preliminary phylogenetic analysis shows that the infratribe Embolotheriita is composed of four polytomous lineages: a monophyletic *Metatitan* with three species, an *Aktautian-Gnathotitan-Pollyosbornia* clade, a *Nasamplus-Protembolotherium-Embolotherium* clade, and *Pygmaetitan panxianensis*. Further comparative analysis of the cranial morphology of Embolotheriita will clarify the origin of the “battering ram” in *Embolotherium* and its concomitant respiration system.

***Keywords**: Erlian Basin, Eocene, Brontotheriidae,* Metatitan*,* Embolotherium*, frontonasal horn*

***Fundings**: National Key Research and Development Project of China (2024YFF0807603), and National Natural Science Foundation of China (42272011).*

Introduction to the fascicle on the Rhinocerotoidea of the Perissodactyla in Palaeovertebrata Sinica

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Modern rhinoceroses are a group of perissodactyls with a rather limited species and individuals. All five species are severely poached on the brink of extinction. However, for most of the Cenozoic era, the Rhinocerotoidea was an exceptionally prosperous group, radiating numerous branches in diverse ecological environments and adapting to different lifestyles of herbivorous mammals. China is the country with the richest rhinoceros fossils in the world, with discoveries at almost every mammalian fossil site dating back to the Eocene epoch, and even at many of these sites, rhinoceros fossils are the most dominant taxa. The Rhinocerotoidea fascicle of Palaeovertebrata Sinica is compiled by Tao Deng and Bin Bai. It includes fossils of the Rhinocerotoidea that have been discovered and systematically studied in China up to 2022, totaling 5 families (Hyrachyidae, Hyracodontidae, Amynodontidae, Paraceratheriidae, and Rhinocerotidae), 61 genera, and 147 species. The book introduces the morphology, taxonomy, evolution, and phylogeny of the Rhinocerotoidea, and briefly describes the research history of the Chinese Rhinocerotoidea. The family-level taxa mainly include definition and classification, diagnostic characteristics, distribution and age, as well as remarks on related issues; the genus- and species-level taxa are more detailed, including synonymy, type specimens, diagnostic characteristics, localities and stratigraphy, with discussions on the existing problems. The book includes 151 figures and a scientific name index after the main text. Research on Hyrachyidae fossils from Eurasia, including China, and North America indicates that the Rhinocerotoidea originated during the Eocene. Since the Oligocene, most terrestrial ecosystems in the Northern Hemisphere have had one or multiple rhinoceros species as part of their faunas, and the number of fossil rhinoceros genera far exceeds that of horses, tapirs, chalicotheres, and brontotheres, which are also perissodactyls. In Eurasia, Africa, and North America, the Rhinocerotoidea were abundant during the Cenozoic geological history, and in some localities, their individual numbers even exceeded the total of all other mammals. In terms of body size, rhinoceroses were often one of the largest herbivorous mammals in most Cenozoic faunas. During the Early Oligocene, the families Amynodontidae and Hyracondontidae had declined to only a few genera remaining, while the family Paraceratheriidae continued to thrive, and the family Rhinocerotidae began to undergo adaptive radiation. Since the Neogene period, almost all rhinoceroses on Earth have belonged to the family Rhinocerotidae, with the vast majority of other families becoming extinct. In China, only a small number of Paraceratheriidae still lived in the northwest regions during the Early Miocene. By the end of the Miocene, rhinoceroses, like horses and many other terrestrial mammals, were also strongly affected by the “Messinian salinity crisis” and the wave of extinctions. Rhinoceroses disappeared in North America, and only a few forms survived in the Old World, among which the tribe Rhinocerotini regained development. The woolly rhino, which could tolerate the Quaternary glacial environment, was widely distributed in the northern part of Eurasia during the Pleistocene. However, when the Holocene arrived, the woolly rhino and elasmotheres became extinct together, leaving only a few rhinoceroses wandering on Earth.

A new perissodactyl fauna from the Middle Eocene of La Vernière (Vénès, Tarn, France)

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The Middle Eocene locality of La Vernière, at Vénès, near Réalmont (Tarn, France) is known for its remains of the giant terrestrial crocodile *Dentaneosuchus crassiproratus* (Astre 1931; Martin et al. 2023). It has also yielded a perissodactyl fauna with a high generic diversity. The hippomorph Palaeotheriidae are notably represented by four different genera: *Leptolophus* Remy, 1965, *Anchilophus* Gervais, 1852, *Plagiolophus* Pomel, 1847 and *Palaeotherium* Cuvier, 1804, identified from cranio-dental remains, as well as postcranial material, which remained little described for this group. The comparative study of this fauna supports the synonymy of *Plagiolophus mamertensis* Remy, 2004 with *P. cartailhaci* Stehlin, 1904. Thanks to CT-scanning, we also identify for the first time the p2 and lower decidual teeth of *Anchilophus jeanteti*. Moreover, paleoecological analyses of meso- and micro-wear suggest different browsing and folivorous dietary habits among the identified species. The assemblage is also dominated by a large-sized *Lophiodon*, which exhibits a less abrasive diet than the identified specimens from Robiac locality (Remy, 2015; Hullot et al., 2025). Given the strong similarity between the faunal composition of Robiac and La Vernière, we discuss its correlation with the MP16 reference level (BiochroM'97).

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Population structure of a fossil dwarf tapir (*Tapirus polkensis*) assemblage suggests parallel sociality to extant tapirs

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Inferring sociality in extinct ceratomorph perissodactyls is difficult due to the paucity of studies on their extant relatives, whose population structures are strongly influenced by anthropogenic impacts. In the case of tapirs, such studies are further hindered by nocturnal and solitary lifestyles documented in the four extant species, in addition to their dwindling numbers. By contrast, the Gray Fossil Site (GFS), a late Miocene-early Pliocene paleo-sinkhole complex in eastern Tennessee, USA, offers the largest sample of fossil tapirs (the extinct dwarf *Tapirus polkensis*) from which demographic data can be drawn. Individuals were separated into seven age classes based on dental eruption and attrition, then converted into lifespan percentages using ontogenetic change in m1 crown height. The resulting age-class distribution and mortality curve suggest that young juveniles and adults are overrepresented at the GFS, paired with low subadult representation. Lacking any obvious mortality biases such as predation, a trap, catastrophe, or seasonal die-offs, the GFS *T. polkensis* assemblage is interpreted to be an attritional accumulation of a population sample. Results of the age-class distribution are consistent with observed sociality in extant tapirs, where majority of documented sociality encompasses adult breeding pairs or mother-calf pairs, typically congregating at forested ponds or mineral licks, while subadults are usually absent due to nomadic tendencies. Such modern observations are consistent with paleontological interpretations of the GFS as a pond within a dense hickory-oak forest, suggesting that the GFS played a similar role for *T. polkensis* sociality in the Appalachian region as forested ponds and mineral licks do for modern tapirs. Future demographic work on fossil perissodactyls may continue to imply comparable sociality to their extant relatives.

***Keywords**: Tapiridae, demography, sociality, mortality*

Evolution of dental eruption patterns in Perissodactyla and histological prospects

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Numerous studies on extant mammalian species suggest that a tight relationship might exist between ontogenetic dental traits, ecological traits and life-history traits. Among dental traits, modifications affecting crown height and dental eruption are thought to be associated with changes in growth rates, body masses, or feeding habits. Changes associated with the sequence of dental eruption (i.e., eruption of permanent premolars versus molars) are poorly studied in extinct mammals, despite the interests they might represent for evolutionary insights. The evolution of dental eruption patterns was previously investigated in different groups of hoofed mammals, such as "South American native ungulates" (SANU; e.g., Notoungulata, Astrapotheria, Litopterna) and Artiodactyla, and we here focused on Perissodactyla. Based on large datasets including extant and extinct species, we found that the evolution of these patterns was very dissimilar in hoofed mammals and could be associated with different parameters (e.g. hypsodonty, body mass). For instance, the link between dental eruption and body mass seems major in Perissodactyla, whereas in SANU a putative link was highlighted between dental eruption and hypsodonty. These results also allowed to propose paleobiological (e.g. growth rate) and paleoecological (e.g. diet) hypotheses, which are currently investigated in Equoidea using a standardized protocol of dental histology, to better understand the putative ecological and biological adaptations of herbivorous mammals to environmental variations.

***Keywords**: Dental ontogeny, body mass, dental histology, Equoidea, growth rate*
***Funding**: Emergence project, Sorbonne Université (France), ANR-IDEX-0004_02 SUPER*

Differing musculoskeletal development of New World *Tapirus* spp. reflects varied ecological dynamics of browser communities during the Mio-Pliocene transition

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Historically, *Tapirus* spp. were thought to have a conservative bauplan, with adaptive postcranial morphology recently identified. Utilizing anatomical descriptions and dimensional measurements (e.g., length, proximal width, distal width, and diaphyseal thickness) of seven different elements (humeri, radii, ulnae, femora, tibiae, astragali, and third metatarsi) grounded in an ontogenetic framework informed by crania (e.g., dental eruption and wear), three *Tapirus* species were assessed: the extinct *T. polkensis* and *T. lundeliusi,* with *T. bairdii* as an extant control. Extinct species were selected based on observed life history of and phylogenetic proximity to *Tapirus bairdii*, and because Gray Fossil Site *T. polkensis* and *T. lundeliusi* of Haile 7C/7G are the most sampled attritional assemblages of tapirs in the fossil record. Of the *Tapirus* spp. examined here, postcrania in subadulthood have epiphyseal fusion despite open sutures co-occurring with muscle attachment development, consistent with known extant life history. Though morphological similarities exist between *T. polkensis* and *T. bairdii* postcrania, *T. lundeliusi* deviates not only due to being more phylogenetically derived but also in ontogenetic trajectory, representing differing functional morphology. Both *T. lundeliusi* and *T. bairdii* have accelerated growth compared to *T. polkensis*. Combined with adaptations for graviporality, *T. lundeliusi* and *T. bairdii* may be peramorphic, whereas delayed growth and acquisition of adult morphology in *T. polkensis* support the hypothesis of paedomorphic development. The latest Miocene to earliest Pliocene Gray Fossil Site, interpreted as a closed forest pond, presumably would have carrying capacity for a rich browser community. However, apomorphic small body size and paedomorphic development of *T. polkensis* may imply ecological displacement as a result of overcrowding. *T. lundeliusi,* whilst co-occurring with other tapir species in the Blancan of Florida and retaining large body size, coincides with the disappearance of browser community members and comparatively open habitat space, which may have enabled peramorphic development. The retained large body size in the extant *T. bairdii* represents not only the importance of conservation in the modern-day, but also the storied ecology and evolution of persistent browsing of the North American *Tapirus* lineage, chronicled in morphological variation on the intraspecific and interspecific resolution.

Keywords: Tapirus*, ontogeny, functional morphology, bone growth, community ecology*
Funding: *Don Sundquist Center for Excellence in Paleontology, the Department of Geosciences and Graduate School of East Tennessee State University, and the Collins Chew Research Award.*

Paleoecological study of Late Oligocene (MP29) herbivores from Rickenbach (Solothurn, Switzerland)

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The site at Rickenbach (Canton of Solothurn, Switzerland), formerly mined for its Eocene sands, is now a protected biogeotope of national importance. Since the early 20th century, several paleontological studies have been conducted there, leading to its recognition as the type locality of the 29th Paleogene mammalian biochronological unit (MP29). In addition, thousands of remains of herbivorous mammals and plants have been discovered there. As a result, Rickenbach is an ideal case study for a paleoecological investigation. Thus, the objective of this internship is to conduct an integrative paleoecological study, the first of its kind for the Rickenbach site, using various proxies (mesowear and dental hypoplasia) applied to the dental remains of artiodactyls (Anthracotheriidae, Cainotheriidae, Suidae, Ruminantia) and perissodactyls (Rhinocerotidae, Tapiridae), as well as to plant macroremains using the coexistence approach (CA). Mesowear results indicate dietary patterns ranging from grazers to omnivores, though with differences in dietary preferences and habitat between species. Dental hypoplasia suggests that the animals were relatively stressed (18.4%), particularly species classified as aquaphilic, implying drought conditions at the site. Finally, the taxa present and the various proxies made it possible to reconstruct the climate and environment of Rickenbach. The climate was Mediterranean/warm-temperate with distinct seasonal variations, and the environment consisted of a mosaic of forest habitats ranging from riparian woodlands to mesothermophilic forests of the wooded savanna type.

Keywords: *Perissodactyla; ecology; mesowear; hypoplasia; Oligocene*
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Early biogeography of Pan-Perissodactyla: current evidence and remaining questions

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The evolutionary history of the extant order Perissodactyla links two problems in placental mammal biogeography. Perissodactyls are one of three extant orders (the others being artiodactyls and primates) that appear abruptly at the beginning of the Eocene. This abrupt appearance is attributed to migration during the Paleocene-Eocene thermal maximum (PETM). Perissodactyls appear at this time in North America, Europe, and Asia, but the actual place of origin of perissodactyls is still uncertain. For many years, perissodactyl origins were placed in North America, in part due to supposed relationships with North American phenacodontids. The recognition of cambaytheriids and other anthracobunians from India and Pakistan as close relatives of perissodactyls narrows the most likely place of origin to mainland Asia or the Indian Plate.

South American native ungulates (SANUs), specifically litopterns and notoungulates, have also been allied with perissodactyls in Pan-Perissodactyla. This is mainly based on molecular data from Pleistocene SANUs, but recent studies using fossils and morphology also link these groups. SANUs are one group of therians that appear at the beginning of the Paleocene of South America. Therians reach other Gondwanan landmasses early in the Cenozoic, including SANUs and marsupials in Antarctica and marsupials in Australia. However, South America's known Mesozoic mammals are entirely non-therian, with the exception of some possible therian remains in the latest Cretaceous. Thus, SANUs and other therians are thought to have North American ancestors who migrated into South America near the K-Pg boundary.

The combination of the recent work on these different phylogenetic and biogeographic problems raises some interesting questions. Where is the place of origin of Pan-Perissodactyla? Interestingly, the answer to this question likely involves North American archaic ungulates, including phenacodontids. How and when did ancestral pan-perissodactyls migrate a) to South America to give rise to SANUs; and b) to Asia, or to the Indian Plate, or to wherever Perissodactyla originated? Phylogenetic work on known taxa might provide the necessary answers, but new information from the Paleocene of North and South America, Europe, mainland Asia, and the Indian Plate would provide the most helpful data.

Spatio-temporal evolution of the paleoecological preferences of the palaeotheres (Perissodactyla; Mammalia): insights into their extinction around the Grande Coupure

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Palaeotheres are an extinct family of equoids (Perissodactyla; Mammalia) from Eurasia that lived from the Middle Eocene to the Early Oligocene. Although very abundant and prosperous during the Eocene, most palaeotheres became extinct during the "Grande Coupure" (33.9 to 33.4 Mya), a major biological crisis marking the transition from the Eocene to the Oligocene. Two main causes have been suggested to explain this faunal turnover: the deterioration of climatic conditions, due to a drop in p_{CO2} responsible for the Terminal Eocene Event (~ 33.9 Mya) – an abrupt cooling of about 4 to 6°C – and a glaciation during the Oi-1 event (~ 33.5 Mya), resulting in drier and more open habitats during the Early Oligocene; the immigration of Asiatic taxa via new continental bridges following a drop in global eustatic sea level caused by the cooling event. These immigrations marked the end of the insular context of Europe (middle and late Eocene) and of the associated endemism.

Competition with newcomers is often cited as the cause of the extinction of endemic European taxa, such as palaeotheres. However, recent studies on artiodactyls in Quercy (southwestern France) have challenged this view, and suggested a passive replacement of endemic European taxa by newcomers from Asian, better adapted to the new environmental conditions. Here, we studied the palaeotheres species from various fossil sites in Germany, France, and Switzerland ranging from MP16 to MP23. We used a multi-proxy approach based on dental material to evaluate body mass, stress levels (enamel hypoplasia), dietary and habitat preferences (dental micro- and meso- wear, $\delta^{13}C$ and $\delta^{18}O$) of these palaeotheres species. The results suggest a large range of body masses (5 to 800 kg) and various browsing diets (little overlap in the dental wear signals), although all in the C3 range. Indeed, the prevalence of hypoplasia was low (<10 %) for most taxa at all localities, indicating a context of low physiological stresses. This was probably due to favorable environmental conditions (warm and humid) during the Eocene as reconstructed by stable isotopes, and low competition for resources, as suggested by dental wear and carbon isotopes. At several localities however, water stress was identified (more positive $\delta^{13}C$ values), but it did not impact hypoplasia prevalence.

***Keywords**: Palaeotheriidae, dietary preferences, Eocene, Grande Coupure*
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Phalangeal morphology in chalicothere systematics

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Chalicotheres are fascinating extinct perissodactyl mammals that survived up to the Pleistocene in Africa and Asia. They are best known for their peculiar large and deeply cloven claws and limb proportions that deviate from the typical perissodactyl morphology. While the claws are most characteristic and the most studied phalanges, the other finger bones can also be informative for the systematics of the group, despite often being overlooked. For instance, within the subfamily of Schizotheriinae the clade including the genera *Moropus*, *Phyllotillon*, *Tylocephalonyx*, *Metaschizotherium*, and *Ancylotherium* fuses the proximal and medial phalanges of the second digit of the hand. In some taxa of this group also the phalanges of the second digit of the pes fuse. This character is otherwise not seen in any other chalicothere. Additionally, proximal phalanges of chalicotheriids exhibit proximal articular facets tilted towards the dorsal side of the bone, while the distal articulation is shifted ventrally. The angle of the facets and the overall shape of the proximal phalanges differ between the two subfamilies. In the genus *Ancylotherium*, the shape of the proximal phalanges is highly diagnostic and differs from all other schizotheriines and in the manus even differs from digit to digit. While the medial phalanges are not as informative, they can be diagnostic to some extent, with their shape differing between the two subfamilies. Lastly, the emblematic chalicothere claws are known to vary between the two subfamilies, but they exhibit also differences within the two groups that allow the distinction of certain taxa. The observed morphological differences reflect distinct ecological adaptations related to feeding behaviour and locomotion among different chalicothere species. A detailed study of these traits may provide new insights into the palaeobiology of these enigmatic animals.

A new skull of *Nestoritherium linxiaense* (Mammalia, Chalicotheriidae) from the Early Pliocene Linxia Basin of the Gansu Province (China)

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A chalicothere skull (IVPP V34658) was unearthed from the Shilidun locality, Guanghe County, Gansu Province, China. The fossil can be identified as *Nestoritherium linxiaense* based on its low crown, large size, highly reduced premolars (the premolar row length less than 40% of the molar row length), rhombic upper molars, strong isolated protocone, weak but developed protoconule and protoloph, reduced ectoloph posterior lobe and retromolar space. This discovery represents the first documented occurrence of *Nestoritherium* from the Pliocene, filling an important gap in the fossil record of Chalicotheriinae in Eurasia. Through morphological comparison and phylogenetic analysis, two key findings emerge. First, *N. fuguense* is considered a junior synonym of N*. linxiaense*, as the new fossil can reconcile the morphological differences between the two previously recognized forms, and the phylogenetic analysis puts *N*. *linxiaense*, *N*. *fuguense* and the new specimen (IVPP V34658) together. The geochronological distribution also supports the argument. Second, the taxonomy of *N*. *linxiaense* and N*. wuduense* may require re-evaluation.

N. sivalense, the type species, shares more similarities with species in *Hesperotherium* (a genus from the Early Pleistocene in China, which was recognized as the descendant of *Nestoritherium*) than with other species in *Nestoritherium*, though *N*. *sivalense* presents typical *Nestoritherium* features (a lower canine and a less retracted mandibular symphysis). Moreover, the phylogenetic analysis puts *N*. *sivalense* and *Hesperotherium* in a clade, which indicates that *N*. *sivalense* is closer to *Hesperotherium*. Therefore, more fossil material is needed to determine whether a new genus should be built for *N*. *linxiaense* and N*. wuduense*.

Beyond taxonomy, the research discusses the palaeoecology of *N*. *linxiaense*. Paleoecological evidence, including dietary analysis, associated fauna, cenogram, and stable isotopes, suggests that the Early Pliocene Linxia Basin was a subarid steppe with interspersed forest patches. This environment likely persisted from the Late Miocene to the Early Pliocene in northwestern China, with *N. linxiaense* possibly surviving in small forest habitats within vast grassland environments.

***Keywords**: Linxia Basin, Early Pliocene,* Nestoritherium*,* Hesperotherium
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When did *Lophiodon* appear? A taxonomic revision of the earliest European lophiodontids

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Lophiodontidae is an endemic European family of perissodactyls closely related to Chalicotherioidea that originated in southern Europe during the early Eocene, shortly after the PETM, during the Neustrian ELMA. Among lophiodontids, *Lophiodon* rapidly became the dominant large browsing mammal of Western Europe and experienced a marked increase in body size throughout the Eocene (from the Grauvian to the Robiacian). Its first appearance has recently been proposed as one of the defining events for the base of the Grauvian-2 biozone during the Early Eocene Climatic Optimum (EECO), making the timing of its origin critical for both mammalian biochronology and the evolution of early Cenozoic herbivore communities. However, the earliest history of *Lophiodon* remains controversial. The taxonomy of early representatives is obscured by nineteenth-century taxonomic oversplitting, high levels of intraspecific variation, and the absence of a comprehensive comparison between northern and southern European populations. As a result, the diversity, geographic distribution, and age of the earliest species remain poorly constrained.

Here we present new lophiodontid material from the late Neustrian locality of Sainte-Eulalie and the early Grauvian locality of Naples 2, together with recently published specimens from Mas de Gimel and Le Lien (southern France). These exceptionally abundant and well-constrained assemblages represent one of the largest available sample documenting the earliest evolutionary stages of Lophiodontids. Their study enables us to quantify intraspecific morphological variation and to reassess most small-bodied Ypresian lophiodontids from western Europe, including material from the Paris Basin, northern Spain, and southern France.

Our revision substantially reduces the taxonomic diversity previously recognized for the earliest *Lophiodon* and supports the hypothesis that several nominal species erected during the nineteenth/early twenty centuries represent morphological variants of a more limited number of taxa. This revised framework clarifies the sequence of appearance of the earliest *Lophiodon* populations, strengthens correlations between the Neustrian and Grauvian mammalian faunas, and refines the biochronological significance of the genus. More broadly, it provides new insights into the emergence of large-bodied browsing perissodactyls during the EECO and their role in the restructuring of European terrestrial ecosystems.

***Keywords**: Systematic, Comparative anatomy, Ypresian,* Eolophiodon, Lophiodon.
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Equids traverse a phenotypic landscape of shoulder anatomy through their evolution

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Throughout their evolution, equids have undergone several ecological shifts, including a transition from living predominantly in dense tropical forests to inhabiting more open woodlands, with various lineages specialising in different habitats. Lineage-specific habitat shifts are often associated with morphological changes; in equids, these include increased cheek-tooth crown height (hypsodonty), a reduction in medial and lateral digit size (and functionality), and modifications to lock the shoulder and knee joints, facilitating stationary grazing with minimal energetic expenditure. Among these features, the shoulder bones and rotator cuff muscles have not been closely examined through the transition from four-toed to one-toed taxa. In this study we investigated the scapula and humerus morphologies of available equids through time, and compared them to other perissodactyls and artiodactyls with known ecologies to explore morphofunctional changes in the musculoskeletal anatomy of the shoulder across an ecological spectrum. Two-dimensional images of ~370 scapulae and humeri from 90+ species (including 38 equids and basal equoids) were collated and the areas of the scapula fossae (sites of muscle origin) were measured, yielding a mean scapula fossa ratio (SFR) for each species. SFRs were then compared to a series of other ecologically informative measures, including hypsodonty index, estimated body mass, and proximal humerus shape. Phylogenetic signal was strong across most variables, with no strong or significant relationships between hypsodonty or body mass and SFR after accounting for relatedness. Species with hypertrophied intermediate tubercles of the humerus (equines, okapi), indicative of a stay apparatus, had notably different SFRs to those with closed bicipital grooves (e.g. “hyracotheres”, tapirs) or open bicipital grooves (e.g. anchitheres, cervines), suggesting the evolution of the shoulder stay apparatus likely resulted in a shift of shoulder muscle origination sites. When exploring equid SFRs across a phenotypic landscape (incorporating hypsodonty as an ecological proxy), we observe a notable shift in SFR between tetra- and tridactyl forms, and a unique SFR-hypsodonty combination in anchithere equids. This study highlights the importance of integrating detailed knowledge of soft tissues to understand broad-scale trends in the osteological record and offers new avenues for exploring locomotor evolution and ecology in Euungulates.

Plio-Pleistocene Palaearctic rhinocerotines: state of the art and future perspectives

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Pliocene and Pleistocene rhinocerotines were among the most characteristic large herbivores of the Palaearctic realm, yet their fossil record remains heterogeneously documented and taxonomically challenging. This is especially true for the Pliocene-Pleistocene transition and the Early Pleistocene, when lineages traditionally referred to *Pliorhinus*, *Stephanorhinus*, *Coelodonta*, *Dicerorhinus* and *Rhinoceros* dispersed, diversified or disappeared across Eurasia. Despite more than two centuries of research, the systematics, phylogenetic relationships and palaeobiogeographic history of several taxa remain debated, partly because of fragmentary key specimens, conservative dental and postcranial morphologies, ontogenetic and sexual variability, and repeated convergent evolution of similar morphological traits. This contribution provides an overview of Plio-Pleistocene Palaearctic rhinocerotines, integrating recent systematic revisions, phylogenetic hypotheses, biochronological evidence and palaeoecological data. Particular attention is given to the emergence and diversification of northern Eurasian lineages, the debated status of Pliocene taxa from Western and Eastern Eurasia, the turnover of *Stephanorhinus* species during the Early and Middle Pleistocene, and the expansion of *Coelodonta* from Asia to Europe. Revised records from the Caucasus, the Balkans, the Mediterranean area, and eastern Asia are considered as key evidence for reconstructing dispersal routes, turnover and ecological partitioning. Cranial morphology, dental wear, isotopes, body-mass estimates and palaeobotanical evidence reveal a broad spectrum of feeding adaptations, from browsing and mixed feeding to grazing, and suggest that ecological flexibility varied markedly among taxa. These patterns are crucial for interpreting persistence, replacement and extinction under unstable climatic and environmental conditions. Future research requires critical revision of historical collections, broader comparative datasets, explicit consideration of intraspecific variability, and integration of morphometrics, phylogenetics, geochronology and multi-proxy palaeoecology. This approach will refine the taxonomy of problematic taxa, clarify the timing and paleogeography of dispersal events, and improve our understanding of how rhinocerotines responded to long-term environmental change.

***Keywords**:* Stephanorhinus*; Coelodonta; biochronology; paleobiogeography; intraspecific variability*

The potential for resolving the phylogeny of Neogene Perissodactyla via Palaeoproteomics

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Historically, the broader phylogenetic relationships of Perissodactyla were difficult to disentangle. In the 1980's, a major breakthrough in understanding the macro-evolution of the clade occurred upon the decoupling of Hyracoidea and Perissodactyla, based on amino acid sequence data from extant perissodactyls. In 2015, the acknowledgement of a wider Panperissodactyla was suggested by ancient amino acid sequence data, with at least some meridiungulate taxa recategorized within a sister clade to crown Perissodactyla. Additional ancient biomolecular studies have further reshuffled the inter-relationships of fossil perissodactyls from the Pleistocene.

Generally, Perissodactyla represents an ideal target for palaeoproteomic investigations, owing to the widespread availability of reference genomes, the relatively-high abundance of fossils, and the extensive research history of the clade. Last year, we published on the oldest ancient proteome used successfully to test a phylogenetic hypothesis, up to 24 million years from Canada's High Arctic. Now, our predictive models and pilot data suggest it should be possible to extract proteins from Miocene perissodactyls in non polar conditions. Recent advances in database-free protein 'sequencing' technologies offer increased resolution and accuracy. Here, I present only modest preliminary data demonstrating that extensive ancient peptides can preserve in Early Pliocene and Late Miocene perissodactyl enamel from non-polar contexts in Eurasia, and discuss the implications of this finding for resolving aspects of Perissodactyla phylogeny.

***Keywords**: Proteins, phylogenetics, Palaeoproteomics, Miocene, Deep-learning*
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Ecological Disequilibrium in *Equus ferus*: Multi-Isotope Evidence for Niche Contraction and Physiological Constraints across the Late Glacial–Holocene Transition

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The decline of *Equus ferus* in Europe during the Late Glacial period and Holocene is commonly explained through climatic change, habitat restructuring and anthropogenic pressure. However, the biological mechanisms that may have constrained equid resilience are less frequently considered. This study reconstructs the dietary and ecological niche of *E. ferus* across Western and Northern Europe between approximately 19,000 and 8,000 BP, integrating palaeoecological evidence with species-specific physiological perspectives.
Published $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values from *E. ferus* and associated herbivore communities were compiled into a harmonised regional dataset. Temporal trends were assessed against the NGRIP $\delta^{18}O$ climate record, while Bayesian isotopic-niche modelling in R and spatial interpolation were used to examine changes in niche breadth, environmental conditions and geographic patterning from the Late Glacial through the Holocene.

The results indicate substantial spatial heterogeneity and pronounced shifts in $\delta^{15}N$ and $\delta^{34}S$ during periods of climatic instability, whereas $\delta^{13}C$ values remained comparatively stable. This pattern suggests that *E. ferus* retained a specialised grazing strategy despite the contraction and fragmentation of its wider ecological niche as open steppe-tundra environments were replaced by increasingly wooded landscapes. The persistence of a stable dietary signal alongside changing environmental proxies points towards ecological disequilibrium rather than rapid dietary adaptation.

These findings are interpreted in relation to equid digestive physiology. As hindgut fermenters, equids can process high volumes of relatively low-quality forage, an effective strategy in extensive open habitats, but one requiring sustained access to abundant vegetation. As suitable grazing areas became smaller and increasingly shared with ruminant herbivores, this physiological strategy may have reduced the capacity of *E. ferus* to respond to resource fragmentation and competition. The study therefore supports a multicausal model in which climate-driven habitat restructuring, physiological constraints, competition and human pressures interacted over time. More broadly, it demonstrates the value of combining multi-isotope analysis with biological and spatial perspectives to investigate perissodactyl resilience, extinction vulnerability and the long-term ecological consequences of environmental change.

Keywords: Equus ferus*; stable isotopes; isotopic niche; digestive physiology; Late Quaternary*
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Reassessment of *Olbitherium*, the "perissodactyl-like archaic ungulate" from the early Eocene Wutu Formation, China

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Next to the numerous perissodactyls described from the famous early Eocene Wutu Formation in Shandong, China was the genus *Olbitherium*, originally described by Tong et al (2004) as a 'perissodactyl-like' archaic ungulate. The material consists of partial dentaries with lower cheek teeth, isolated upper molars, and an isolated upper premolar. Subsequent collaborative fieldwork by Belgian and Chinese paleontologists at Wutu coal Mine allowed to discover a partial skull associated with the anterior portion of the dentary and a few postcranial bones. The specimen comes from the middle coal-bearing Member of the Wutu Formation around the seventh coal layer about 250 meters deep. In their general form, the skull and postcrania are similar to those of early perissodactyls. The anterior dentary demonstrates the presence of three lower incisors and a large canine, both ancestral features for perissodactyls. The morphology of the teeth shows a moderate lophodonty, double rooted P1 and P2 and the presence of an extra cusp near the metaconule on the P4. The upper molars are not very transverse, giving a relatively square shape to the teeth. Two independent phylogenetic analyses are performed to test the affinities of *Olbitherium*. The first one is a matrix of 321 characters and 72 taxa of placental mammals emphasizing perissodactyls and other ungulates (Rose et al, 2020). The second one is a matrix more focused on early perissodactyls (Tissier and Smith, 2026), which includes 101 characters and 69 taxa (71 terminals). In Rose et al's analysis, *Olbitherium* is the sister-taxon to all perissodactyls except *Ghazijhippus*. Tissier and Smith's analysis provides the same results except that *Hallensia* and *Hyracotherium* are more basal to *Olbitherium*. The new material not only supports the identification of *Olbitherium* as a basal perissodactyl, but it also suggests that it is significant for understanding the ancestral perissodactyl morphotype.

***Keywords**: Perissodactyla, Phylogeny, early Eocene, Wutu coal Mine.*
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Inferences on the paleoecology of the elusive hornless rhinocerotid *Eochilotherium samium* (Perissodactyla, Rhinocerotidae) through the examination of dental mesowear and microwear

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Although modern rhinocerotids (Perissodactyla, Rhinocerotidae) display the strongest dietary variability among the extant perissodactyls, the paleoecology of the fossil representatives of the family remains to be thoroughly examined. Under this scope, the present work aims on the examination of the paleodiet of the elusive hornless rhinocerotid *Eochilotherium samium*, a relatively basal aceratheriine described from the Neogene of the Southern Balkans. The material we examine comes from the early Vallesian site Pentalophos in Northern Greece, the Turolian site Kromidovo in Bulgaria and the middle Turolian site Mytilinii in Samos Island, Greece.

In order to examine the paleodietary regime of *E. samium*, we opted for the application of a multi-proxy approach, combining short-term Dental Microwear Texture Analysis (DMTA) using the TRIDENT Software, and long term dental mesowear scoring using the Mesowear Ruler. Dental microwear is caused by microscopic damage to the enamel and records a short period before the animal's death, an effect known in literature as the "Last Supper" phenomenon; conversely, dental mesowear records the cummulative record of a lifetime of chewing and can be observed by the classification of the tooth cusps into shape and relief categories.

For the application of dental mesowear we opted for sampling the upper second molar, whereas we sampled both upper and lower second molars for the microwear analysis. Moreover, for the application of the DMTA, we sampled both the shearing (without Hunter–Schreger Bands) and the grinding (with Hunter–Schreger Bands) facets of the same enamel band on the lingual part of the protocone on upper second molars and on the distal part of the protoconid on lower second molars. Finally, in order to further elucidate the paleoecology of *E. samium*, we calibrated our results using data on the dental wear of of modern rhinocerotid species.

The microwear signature of *E. samium*, captured by high values of complexity, indicates the consumption of hard browse or dirt-contaminated vegetation due to low-ground foraging during seasonal dry spells. Moreover, the mesowear score of 2 points to mixed feeding or browsing paleodietary habits. The combination of the two complementary proxies describes the paleodiet of *E. samium* as a flexible mixed feeder, adapted to the fluctuating mosaic biomes and marked seasonality of the Balkan-Iranian Province.

***Keywords**: paleodiet, microwear, mesowear,* Eochilotherium samium*, Balkans*
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Systematics and evolution of early perissodactyls and earliest equoids

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The earliest known perissodactyls have been dated from the earliest Eocene (around 56 Ma), on three continents of the Northern Hemisphere: North America (with *Sifrhippus* and *Arenahippus*, both previously known as *Hyracotherium*), Europe (with *Cymbalophus* and a potential *Sifrhippus*, as well as *Pliolophus* and *Chowliia*) and Asia (with *Erihippus*, *Danjiangia*, *Orientolophus*, *Protomoropus*, and potentially *Cardiolophus*). They represent a diversity of up to 13 species and 9 genera, in just about 100 000 years, which is very unusual compared to other groups of modern placental mammals, which are usually represented by a single genus, on two or three continents. We have thus revised most of these taxa and included them in a new large-scale phylogeny, to better understand the relationships of these earliest known perissodactyls, and better understand their early diversification.

In addition, we also investigated two key taxa for the understanding of perissodactyl evolution, thanks to complete specimens from the UNESCO site of Messel (MP11, around 47Ma): *Hallensia matthesi* and *Eurohippus messelensis*, two early equoids. The anatomy of these two species was investigated through CT-scanning for the first time based on complete articulated skeletons from the collections of the Royal Belgian Institute of Natural Sciences (IRSNB), which permitted to observe the postcranial anatomy in three dimensions, as well as hidden morphological characters.

***Keywords**: Perissodactyla; Eocene; Phylogeny; Messel*
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Body mass, dietary flexibility and extinction vulnerability in the Pleistocene rhinoceros *Stephanorhinus hemitoechus*

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Perissodactyls repeatedly faced climatic and environmental shifts during the Pleistocene, yet the ecological mechanisms underlying their regional persistence and extinction remain unevenly understood. Here we synthesize anatomical and dietary evidence for the western European rhinoceros *Stephanorhinus hemitoechus* from Marine Isotopic Stage (MIS) 12 to MIS 3, testing whether body-size change, limb proportions and feeding strategy followed a single evolutionary trend or reflected regional responses. The dataset combines original and published observations from 57 cohorts from northern Europe (UK, Germany) and the Mediterranean area (France, Monaco, Italy, Spain and Portugal). Body mass was estimated from dental and tarsal measurements, limb conformation from metapodial gracility indices, and diet from dental mesowear and microwear, providing long- and short-term dietary signals.

The results argue against a simple continent-wide trajectory. Northern cohorts, mostly corresponding to interglacial range expansions, are generally heavier than Mediterranean contemporaries but show broad body-mass stability through time. In contrast, Mediterranean cohorts, representing the core range of the species, remain stable from MIS 12 to MIS 7, increase during MIS 6, and then plateau until MIS 3. Gracility indices show only limited variation, offering little support for the older scenario of successive gracile and robust chronotypes.

Dietary evidence reveals persistent mixed feeding across most of the record. Mesowear and microwear indicate regular incorporation of both monocots and dicots, with northern populations showing a slightly stronger grazing component. In the small subset of specimens with paired body-mass and mesowear data, increased grass intake is associated with lower body mass, suggesting that diet modulated, but did not drive, size variation. Near the last occurrences, assemblages from Axlor and El Castillo (Spain) depart from year-round mixed feeding and show seasonal specialization toward either grazing or browsing.

These patterns suggest that *S. hemitoechus* responded differently in its Mediterranean core range and northern peripheral incursions: climatic deterioration in the North likely led to local extirpation, whereas Mediterranean populations underwent anatomical adjustment but ultimately lost part of their dietary flexibility. This late ecological narrowing, combined with increased body mass, colder environmental conditions, and increased competitive pressure may have heightened extinction vulnerability.

Keywords: Stephanorhinus hemitoechus*; Pleistocene; Rhinocerotidae; dental mesowear; dental microwear; body mass*

Mythbusting the Palaeobiology of 'Giant' Stenonid Horses from the Early Pleistocene

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The incursion of monodactyl horses (namely, *Equus* senso lato) from North America into the Old World during the onset of the Pleistocene glaciation cycles had profound impact in shaping modern mammalian herbivore communities. Rapid initial diversification of Old World *Equus* during the Early Pleistocene was achieved by the stenonid clade, from which emerged several challengers to the largest body size ever attained by equids, notably *Equus eisenmannae* and *E. sanmeniensis* from northern China, as well as *E. livenzovensis* and *E. major* from Western Eurasia. While adaptive response to harsh environments with seasonally fertile grassland flora is often invoked for evolution of large size in Pleistocene ungulates, findings from our ongoing palaeobiological synthesis of the biggest Eurasian stenonids do not confer to such ideas. Dental mesowear comparison and metapodial dimension-based body mass regression estimations indicate that across Pleistocene Northern Eurasia, maximum body size attainable to grassland ecomorphs of *Equus* is constrained at about 600 kg. This threshold was exceeded by *E. major* and *E. suessenbornensis* populations with mixed-feeding to browsing-dominated foraging ecology in relatively equable habitats. Intriguingly, despite boasting decisively the largest known complete skull of any equid (greatest sagittal length exceeding 70 cm), *E. eisenmannae* metapodials are surprisingly compact in their construction, allowing us to reconstruct a front-heavy, stocky animal surpassed in magnitude by *E. sanmeniensis*, *E. suessenbornensis* and *E. major*. Additionally, we tentatively consider the efficacy of the draught horse as potential modern analogue for the gross anatomical build of these large stenonids.

Keywords: Equus*; Pleistocene; palaeoecology, regression; body size*
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Posters

New remains of *Lophiodon* (Perissodactyla) from the Middle Eocene locality of La Vernière (Tarn-et-Garonne, France)

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New material of the tapiromorph perissodactyl *Lophiodon* Cuvier, 1822 from the Middle Eocene (MP16) locality of La Vernière (Tarn-et-Garonne, France) provides new insights into the taxonomy, biostratigraphic distribution, and palaeobiogeography of this characteristic European genus. Detailed morphological comparisons and metric analyses of the La Vernière specimens reveal close similarities with both *Lophiodon lautricense* Noulet, 1851 and *Lophiodon rhinocerodes* Rütimeyer, 1862. The morphological and metric characters examined provide no reliable criteria for distinguishing these two nominal species. We therefore propose *L. rhinocerodes* as a junior synonym of *L. lautricense*.

This taxonomic revision substantially modifies the biostratigraphic and palaeobiogeographic interpretation of *L. lautricense*. Under the revised taxonomy, the species ranges from MP14 to MP16 and displays a broad but palaeogeographically restricted distribution. All currently known occurrences are confined to a single large, isolated landmass within the Middle Eocene European archipelago, roughly encompassing present-day Spain, England, France, Switzerland, and Germany. *Lophiodon lautricense* thus appears to have been widely distributed across this insular landmass while remaining absent from the other palaeogeographic domains of the European archipelago.

As *L. lautricense* represents the last known and the largest (more than 2000 kg) species of *Lophiodon*, its disappearance after MP16 also marks the extinction of the genus and family. This extinction may have coincided with the Priabonian Oxygen Isotope Maximum (PrOM) event, inducing a major eustatic sea-level fall and an aridification phase. This scenario provides a new framework for interpreting the disappearance of Lophiodontidae. It also highlights the potential interplay between sea-level change, breakdown of insular isolation, biotic interactions and climatic change in shaping European mammalian faunal changes during the Bartonian-Priabonian transition.

***Keywords**:* Lophiodon lautricense*, Systematics, Biostratigraphy, Paleobiogeography*
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The late Cenozoic Rhinocerotidae from the sandpits in Nakhon Ratchasima, Northeastern Thailand and its biostratigraphical implication

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The Rhinocerotidae were among the most diverse terrestrial mammal groups during the early part of the Neogene. Since the Miocene, there has been a dramatic increase in speciation within this family in Eurasia, Africa, and North America. In Asia, abundant rhinocerotid fossils have been mainly described from China and Indo-Pakistan, and their fossil records have been systematically documented. In contrast, the fossil record of Southeast Asia, especially in Thailand, is unclear due to the lack of their detailed descriptions, although abundant rhinocerotid fossils have been collected from the several late Cenozoic localities. More than ten sandpits are located along the Mun River in the Chaloem Phra Kiat District, Nakhon Ratchasima in Northeastern Thailand, and various rhinocerotid fossils have been reported from there. These records will contribute to discussing the terrestrial mammalian biostratigraphy in Thailand. Here, we review the rhinocerotid fossil assemblages from these sandpits and discuss their biostratigraphic ranges.

Among the sandpits in Northeastern Thailand, rhinocerotid fossils have been recovered from six localities: Tha Chaing sandpits Nos. 4, 8, and 10 as well as the Phra Phut, Sin Charoen, and Khok Sung sandpits. The Teleoceratini (*Brachypotherium perimense*, *Brachypotherium* sp.), Aceratheriini (*Alicornops complanatum*, *Aceratherium porpani*, *Acerorhinus palaeosinensis*, and *Acerorhinus* sp.), and Rhinocerotini (*Rhinoceros unicornis* and *Rhinoceros sondaicus*) have been collected from these sandpits.

Nagaoka and Nakaya (2014) noted that *Brachypotherium* sp. was collected from the Sandpit No. 4, although its detailed description is lacking. Sandpit No. 8 has yielded abundant fossil mammals that include a hominoid *Khoratpithecus*. Four species have been reported from the lower deposits of this sandpit, namely *B*. *perimense*, *Al*. *complanatum*, *Acero*. *palaeosinensis* by Chimanee et al. (2004, 2006), although no descriptions were provided. Later, Deng et al. (2013) described a skull identified as *Acera*. *porpani*. Handa et al. (2021) described additional specimens of *B*. *perimense* collected from the sandpit. We investigated the fossil mammal remains from Sandpit No. 10, resulting in a few specimens of *B*. *perimense*. We also described four taxa from Phra Phut Sandpit (*B*. *perimense*, *Al*. *complanatum*, *Acera*. *porpani*, and *Acerorhinus* sp. indet.). Suraprasit et al. (2016) described *R*. *sondaicus* and *R*. *unicornis* from Khok Sung Sandpit. Naksri et al. (2023) summarized the vertebrate fauna from Sin Charoen Sandpit, which includes *B*. cf. *perimense*, cf. *Rhinoceros* sp. indet. and Rhinocerotidae gen. et sp. indet.

Sandpit No. 4 that yielded *Brachypotherium* sp. is correlated with the Middle Miocene based on the mammal fauna from there such as cf. *Protanancus chinjiensis*, *Gomphotherium* sp., and *Prodeinotherium* sp. (Nagaoka and Nakaya, 2014). The genus *Brachypotherium* has also been yielded from the Middle Miocene localities in Europe and South Asia. Thus, this finding is consistent with the estimated geological age.

B. *perimense*, *Al*. *complanatum* and *Acero*. *palaeosinensis* from Sandpit No. 8 are mainly found from the Late Miocene localities in South and East Asia. The co-occurrence of *B*. *perimense* and *Al*. *complanatum* at Phra Phut Sandpit along with *B*. *perimense* at Sandpit No. 10 and Sin Charoen suggests a predominantly Late Miocene age for these mammalian fossil assemblages.

Pleistocene rhinocerotid taxa (e.g. *Rhinoceros* spp.) have been collected from the upper deposits of Sin Charoen and Khok Sung sandpits. A small number of possibly Pleistocene taxa have been also recorded from Sandpit No. 8 (e.g. bovid *Duboisia*; Nishioka and Vidthayanon, 2018), although no Pleistocene rhinocerotids have been found from the associated fossil assemblage.

In conclusion, the rhinocerotid fossil assemblages from Northeastern Thailand suggest that the estimated a geological age ranging from the Middle Miocene to the Pleistocene. The fossil assemblages represented by Sandpits Nos. 8 and 10, as well as Phra Phut and Sin Charoen sandpits, are positively correlated with the Late Miocene fauna, whereas that from Sandpit No. 4 includes at least one rhinocerotid taxon consisted with the Middle Miocene fauna from this sandpit. Furthermore, the upper horizons of the Khok Sung and Sin Charoen sandpits are composed preliminarily of Pleistocene deposits characterized by the presence of Pleistocene *Rhinoceros*.

***Keywords**: biostratigraphy, Cenozoic, Nakhon Ratchasima, Rhinocerotidae, Thailand*
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First discovery of a skull of *Urtinotherium* Chiu, 1962 from the Late Eocene of Altyn Tagh (Xinjiang, China)

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Paraceratheriidae are a Eurasian group of giant rhinoceroses (Rhinocerotoidea), that first appeared in the late Middle Eocene of China with the genus *Juxia*. Later genera such as *Urtinotherium*, *Paraceratherium* and *Turpanatherium* are characterized by their gigantic size, as well as a typical anterior dentition retaining the first lower and upper incisors. The genus *Urtinotherium* is of particular importance with regard to the early diversification of this clade, as it is one of the earliest representatives of this group and the first to have reached a gigantic body mass (> 2 tons). Two species are currently accepted: the type species *Urtinotherium intermedium*, as well as the smaller-sized *U. parvum*. The large-sized *U. intermedium* is only known by a complete lower jaw (type specimen), a few isolated bones, and a broken maxilla with P2-M3, whereas *U. parvum* is only known by a maxilla with P1-M3, as well as a few isolated bones and teeth. The skull thus remained unknown so far for this genus.

Here, we report the first sub-complete skull of the genus *Urtinotherium* (IVPP V20108), recently discovered in a new locality of the Suerkuli Basin of Altyn Tagh (Xinjiang, PR China) which has been dated from the Late Eocene based on the characteristic mammalian assemblage. Part of the skeleton was also discovered alongside this skull, but will be described in another study to follow. It is referred to the smaller-sized *U. parvum*, and presents a complete dental formula with a reduced canine (size equivalent to I2 and I3), and a notably larger I1, differing from *Juxia*. It also differs from *Juxia* by its nasal notch further backwards (above P4) and more posterior anterior border of the orbit (above M2). This configuration is intermediate with *Paraceratherium*, which shows a nasal notch above P4/M1 and an anterior border of the orbit above M2/M3. Finally, it also differs from *U. intermedium* by the presence of a large postcanine diastema (assuming that upper and lower diastema mirror each other). We replaced this new skull of *Urtinotherium parvum* as well as all other referred specimen in a phylogeny for the first time, based on the matrix from Deng et al. (2021). The results show that *Urtinotherium* may not be monophyletic, although the material available to compare the two species is limited. The future inclusion of new postcranial elements in this matrix could prove essential for better understanding the early diversification of this group.

***Keywords**: Paraceratheriidae;* Urtinotherium*; phylogeny; gigantism*
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From tooth to food: a multiproxy approach to infer dietary preferences in Lophiodontidae (Mammalia, Perissodactyla) from Southern France

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The first occurrence, taxonomic diversification, and last occurrence of Lophiodontidae, all happened during the early to middle Eocene within the confines of the European landmass. In the span of approximately 20 million years, the group experienced an increase in body mass and a tendency towards the molarisation of the premolars, two phenomena often related with dietary changes. Although being amongst the largest herbivores of their communities, these perissodactyls have rarely been investigated from an ecological perspective. This work is the first dive into the temporal evolution of dietary preferences of lophiodontids using several proxies, all based on teeth. We studied both the internal organisation through enamel microstructure, which reflect biomechanical properties and capacity of the tooth element, and the external wear at different scales. The signal given by dental mesowear and microwear (DMTA) is directly linked to how the teeth were used during the mastication process both at the life-long scale for the former and in a shorter time-window of a couple of weeks before the death for the latter. The results obtained were put in relation to body mass.

We studied Lophiodontidae (188 specimens) from seven Southern France localities dated from the early Ypresian (Mammal Palaeogene levels]MP7–8 + 9[interval, Palette), middle Ypresian (~MP8 + 9, La Borie, Sainte-Eulalie), late Ypresian (~MP10 Naples 2;]MP10–11[interval, Aumelas), Lutetian (?MP11–12, Saint-Martin-de-Londres) and late Bartonian (MP16, Robiac; Last Appearance Datum of the family). Only the enamel microstructure of *Lophiaspis maurettei* from Palette can be discriminated by its Schmelzmuster, with a large proportion of inner radial enamel, low decussation and straight Hunter-Schreger bands. The three oldest and smallest lophiodontids (85–350 kg) present mesowear suggesting similar browsing preferences, while the DMTA and microstructure exclude the consumption of abrasive and hard items. All proxies indicate tough foliage browsing, contrasting with the traditional view of frugivory for all stem perissodactyls. Our results suggest that the younger and giant-sized *Lophiodon lautricense* (~ 2300 kg) consumed more abrasive and harder items. The relative reduction in enamel thickness, coupled with increased molarization, may have facilitated a dietary transition before the extinction of the family, in relation to the MECO event.

***Keywords**: Eocene; Perissodactyla; body mass; enamel microstructure; dental wear*
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A new elasmotheriine species in the European Early Miocene, description and paleobiogeographic implications

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A new species of Rhinocerotidae from Benken (Zurich Canton, Switzerland) of the Early Miocene has been identified. *Victoriaceros* sp. nov. is represented by two almost complete skulls, some isolated upper cheek teeth and a few postcranial remains. The main diagnostic characters are the concave dorsal profile of the skull, the high zygomatic arches and a U-shaped nasal notch. The third molar (M3) has a pinched protocone and hypocone and a developed antecrochet. The presence of *Victoriaceros* sp. nov. in Benken expands the geographical distribution of the genus as it is the first recognized mention of *Victoriaceros* outside of Africa. It may also represent the earliest occurrence of a Rhinocerotidae with African affinities in Europe. This is compatible with the first spread of Eurasian rhinos toward Africa during the early Miocene.

***Keywords**: Perissodactyla, Rhinocerotidae, Elasmotheriinae, Paleobiogeography, Miocene*
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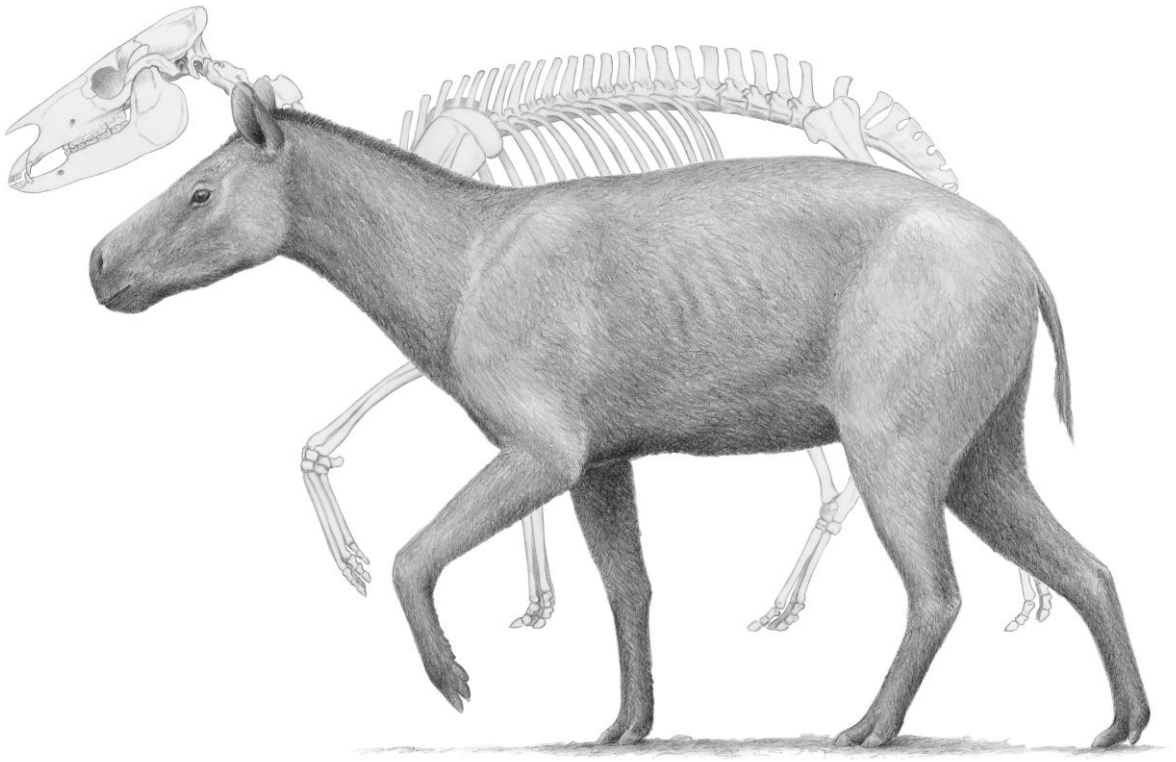

Reconstruction of the Early Oligocene paleothere *Plagiolophus huerzeleri* by Patrick Röschli (© JURASSICA)

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