

Inventory and preliminary study of Lutetian fossil mammals from the “Oberbuchsiten” collection of the Olten Museum of Nature: focus on perissodactyls

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Abstract: The locality of Oberbuchsiten, situated in close proximity to the renowned Middle Lutetian site of Egerkingen (Solothurn, Switzerland), hosts a diverse and extensive fossil mammal assemblage. A project to inventory and update the so far unpublished fossil collection from Oberbuchsiten at the Olten Museum of Nature (Solothurn, Switzerland) was carried out as part of the SwissCollNet project in collaboration with the JURASSICA Museum (Jura, Switzerland). This recent collection is of interest due to its provenance from the same karst fill, which renders it homogeneous in comparison to the oldest collections of Egerkingen/Oberbuchsiten for which the origin of a significant part remains uncertain. The collection found in the second part of the 19th century (Stehlin, 1903) is more homogeneous as it was referred to specific quarries or lenses (e.g. “St. Verena” quarry for a large part of Stehlin collection in NMB), nevertheless the evolution of the quarries during the last century makes it difficult nowadays to identify the specific fissure filling which provided this collection. The fauna of Oberbuchsiten at the Olten Museum of Nature is predominantly composed of paleotheres (Perissodactyla, Mammalia), whose abundance demonstrates a high degree of morphological and dietary diversity, indicating adaptation to multiple strata and ecological niches. The composition of the assemblage confirms the correlation with MP14 reference level and indicates a dense forest environment in a humid tropical to subtropical climate. Further study of this collection, alongside a comparison with other assemblages from Egerkingen/Oberbuchsiten, will confirm whether there are any significant differences that could be attributed to the “Oberbuchsiten” collection at the Museum of Olten Nature.

Keywords: Collection, Mammalia, Perissodactyla, Eocene, Egerkingen, Oberbuchsiten, Switzerland.

Résumé : Inventaire et étude préliminaire des mammifères fossiles du Lutétien provenant de la collection « Oberbuchsiten » du Musée d'histoire naturelle d'Olten : focus sur les périssodactyles. - La localité d'Oberbuchsiten, située à proximité de la célèbre localité d'Egerkingen (Soleure, Suisse), datée du Lutétien moyen, abrite une faune de mammifères fossiles riche et variée. Un projet d'inventaire et de mise à jour de la collection fossile “Oberbuchsiten”, jusqu’à présent inédite, du musée d’histoire naturelle d’Olten (Soleure, Suisse) a été mené dans le cadre du projet SwissCollNet en collaboration avec le JURASSICA Museum (Jura, Suisse). Cette collection récente est intéressante par sa provenance d’un même remplissage karstique, ce qui la rend homogène par rapport aux plus anciennes collections d'Egerkingen/Oberbuchsiten dont l'origine reste pour une bonne partie incertaine. La collection trouvée dans la deuxième partie du 19ème siècle (Stehlin, 1903) est plus homogène car elle se réfère à des carrières ou des remplissages spécifiques (par exemple la carrière « St Verena » pour une grande partie de la collection Stehlin au NMB), néanmoins l'évolution des carrières au cours du siècle dernier rend aujourd'hui difficile l'identification des remplissages spécifiques qui ont fourni ces collections. La faune “Oberbuchsiten” du musée d’histoire naturelle d’Olten est majoritairement composée de périssodactyles, et en particulier de paléothères dont l’abondance manifeste une forte diversité morphologique et alimentaire, et donc d’une adaptation aux multiples strates et niches écologiques. La composition faunique de la collection confirme un âge MP14 et indique que l’environnement de forêts denses sous un climat tropical à subtropical humide. Une étude plus approfondie de cette collection et une comparaison avec les autres assemblages d'Egerkingen/Oberbuchsiten permettra à l’avenir d’indiquer si des différences significatives existent dans la collection “Oberbuchsiten” du musée d’histoire naturelle d’Olten.

Mots-clés : Collection, Mammalia, Perissodactyla, Éocène, Egerkingen, Oberbuchsiten, Suisse.

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1. INTRODUCTION

Egerkingen and Oberbuchsitzen are well-known Middle Lutetian fossil assemblages that have been the subject of numerous excavations, contributing to the gradual enrichment of the collections. The earliest collections were amassed by Robert Cartier between 1848 and 1874, originating from between the towns of Oberbuchsitzen and Egerkingen (more precisely on the Oberbuchsitzen commune territory, though the precise karst pocket is unknown), and donated in 1884 to the Natural History Museum of Basel (NMB). These collections were studied by Ludwig Rüttimeyer to complement his own excavations on the same area but on Egerkingen territory between 1861 and 1892. During this period, he described a number of new species, including: *Proviverra typica* Rüttimeyer, 1862; *Meniscodon europaeum* Rüttimeyer, 1888; *Caenopithecus pygmaeus* Rüttimeyer, 1890; *Dichodon cartieri* Rüttimeyer, 1891 and *Mixtotherium gresslyi* Rüttimeyer, 1891 (Rüttimeyer, 1862; Rüttimeyer, 1888; Rüttimeyer, 1890; Rüttimeyer, 1891; Costeur & Schneider, 2011). His disciple, Hans Georg Stehlin, also conducted research on the faunas of this locality, undertaking numerous excavations and publishing his findings between 1903 and 1916. Stehlin described the majority of the type specimens found at Egerkingen, such as the holotype of *Adelomys cartieri* Stehlin & Schaub, 1951; the syntypes of *Catodontherium fallax* Stehlin, 1910 and *Catodontherium buxgovianum* Stehlin, 1910; and the paratypes of *Palaeotherium ruetimeyeri* Stehlin, 1904; *Mixtotherium priscum* Stehlin, 1908 and *Haplobunodon solodurens*, Stehlin, 1908 (Stehlin, 1904; Stehlin, 1908; Stehlin, 1910; Stehlin & Schaub, 1951; Costeur & Schneider, 2011).

In addition to the aforementioned emblematic NMB collections, other collections from Egerkingen/Oberbuchsitzen can be found at the Natural History Museum of Solothurn (NMS) and the Natural History Museum of the University of Zurich (PIMUZ). In 1982, the Olten Museum of Nature (NMO) initiated new excavations in one of Oberbuchsitzen's Eocene fissures with the objective of developing a new collection (Fig. 1). The inventory and herein preliminary study of this so far unpublished collection is part of the SwissCollNet project "SCN207-JU: Restoration, revision and inventory of key fossil mammal localities in the north-eastern tip of the Jura mountains". This project was financed by the Swiss Academy of Natural Sciences (SCNAT) and has been carried out in collaboration between the NMO and JURASSICA Museum (MJSN) (Porrentruy, Switzerland).

The aim of this preliminary study is to present the first results of the project on the mammal fauna of the NMO's "Oberbuchsitzen" collection. It focuses on the record of perissodactyls and also aims at highlighting the importance and diversity of this fauna.



Fig. 1. Location of the fissure filling that yielded the NMO "Oberbuchsitzen" collection on the jurassic calcareous cliff at the north-east of Oberbuchsitzen town. The entrance of the fissure filling is protected by a metal grid. It is indicated by an arrow on the photo (photo by Pia Geiger-Schütz).

ABBREVIATIONS

Institutions

MJSN, Jurassica Museum (former « Musée Jurassien des Sciences Naturelles »); NMB, Naturhistorisches Museum Basel; NMO, Olten Museum of Nature; NMS, Natural History Museum of Solothurn; PIMUZ, Natural History Museum of the University of Zurich; SCNAT, Swiss Academy of Natural Sciences.

Anatomy

Px, upper premolar n°x; DPx, upper deciduous premolar n°x; px, lower premolar n°x; dpx, lower deciduous premolar n°x; Mx, upper molar n°x; mx, lower molar n°x. Statistics: N, total number of specimens.

2. MATERIAL AND METHODS

The material initially consisted of unprepared fossiliferous boulders, vertebrate dental, cranial and postcranial remains, and a few invertebrate shells. It was delivered to the MJSN in the summer of 2023 and consisted at the time of 655 fossils, 430 of which had already been pre-inventoried. The boulders were prepared

with sandblasters and air tools to extract new fossils, and previously isolated specimens were restored and/or reconditioned as needed. Each specimen was then identified/reviewed and assigned an inventory number. All systematic and anatomical data were recorded in an NMO database in February 2024.

3. GEOLOGICAL AND BIOCHRONOLOGIC FRAMEWORK

The localities of Egerkingen and Oberbuchsiten are situated respectively between the towns of the same name in northeastern Switzerland, within the Canton of Solothurn. They are located approximately ten kilometres from the city of Olten (Fig. 2).



Fig. 2. Map showing the geographical location of Egerkingen and Oberbuchsiten.

These sites are situated within a siderolithic facies (Hartenberger, 1970; Becker, 2003; Bläsi *et al.*, 2018), in the form of multiple rock fissures (Hartenberger, 1969; Hartenberger, 1970) filled with karst deposits (Hartenberger, 1969; Becker, 2003). The deposits contain a plethora of fossils, including vertebrates and invertebrates dating from the Middle Eocene. Of particular note is the mammal fauna, which is regarded as one of the most diverse and rich in Europe (Hartenberger, 1970). In 1987, a portion of this notable fauna was designated a biostratigraphic reference for the Paleogene period in Europe: MP14, c. 42 Ma (Escarguel *et al.*, 1997; Schmidt-Kittler *et al.*, 1987; Solé *et al.*, 2020) and which correlates with the terminal portion of the Lutetian epoch (Speijer *et al.*, 2020) (Fig. 3).

For the Eocene-Oligocene of Europe, the biochronological framework is based on the European Land Mammal Ages (ELMA; Sen, 1997) which is subdivided into a succession of European mammal reference levels for the Palaeogene (MP; Schmidt-Kittler *et al.*, 1987; Biochrom'97, 1997), each of them being correlated with the Palaeogene geological time scale (Speijer *et al.*, 2020; Fig. 3).

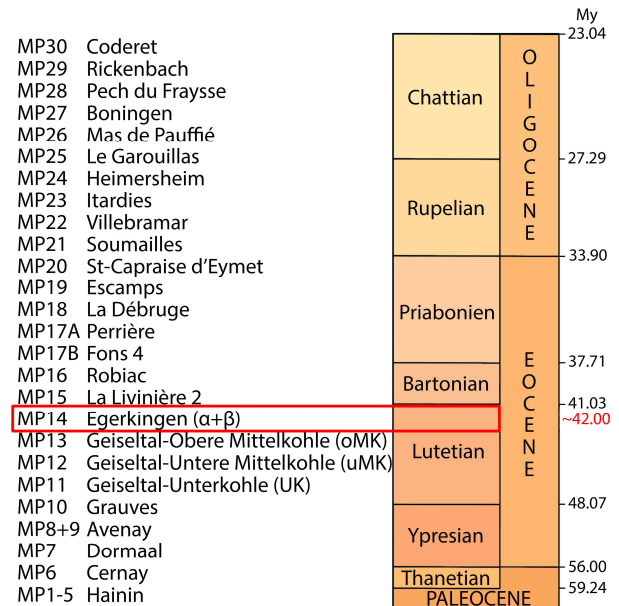


Fig. 3. Biostratigraphic position of Paleogene mammalian biochronological units in Europe and their reference localities (after Schmidt-Kittler *et al.*, 1987; Escarguel *et al.*, 1997; Speijer *et al.*, 2020; Solé *et al.*, 2020; Cohen *et al.*, 2023).

4. RESULTS

After preparation of the boulders, the NMO “Oberbuchsiten” collection now comprises 1222 fossils, which almost doubles the original number of specimens before study. It includes 20 undetermined specimens, 10 invertebrate specimens, 24 undetermined vertebrate specimens, 3 chondrichthyan specimens (probably reworked from the surrounding Late Jurassic sediment), 10 reptilian specimens, and 1155 mammalian specimens (Tab. 1).

Tabl. 1. Number of identified mammal specimens in the NMO's “Oberbuchsiten” collection.

| | N |
|-----------------|------|
| Perissodactyla: | 665 |
| Artiodactyla: | 113 |
| Creodonta: | 11 |
| Rodentia: | 36 |
| Primates: | 10 |
| Eulipotyphla: | 5 |
| Chiroptera: | 6 |
| Metatheria: | 7 |
| Mammalia indet. | 302 |
| Total: | 1155 |

Most of the mammal collection consists of dental remains, with up to 847 isolated teeth (sometimes fragmentary), 33 mandibular remains, and 13 maxillary remains. Perissodactyls are the most abundant mammals and are the focus of this preliminary study of the collection, representing 57.0% of the identified fauna (Fig. 4A). This percentage increases to 77.9% if we exclude the uncertain specimens identified as "Mammalia indet." due to insufficient preservation (Fig. 4B). In the NMO's "Oberbuchsitzen" collection, artiodactyls are much less

numerous than perissodactyls, representing between 9.7% (Mammalia indet. included) and 13.3% (Mammalia indet. excluded) of mammals (Fig. 4). Rodents, hyaenodonts, primates, metatherians, chiropterans, and eulipotyphans were least represented, with cumulative frequencies of less than 9%. No Carnivora were identified in the NMO "Oberbuchsitzen" collection, although they are known from older collections (Beaumont, 1966), such as *Quercygale helvetica* (Rütimeyer, 1882).

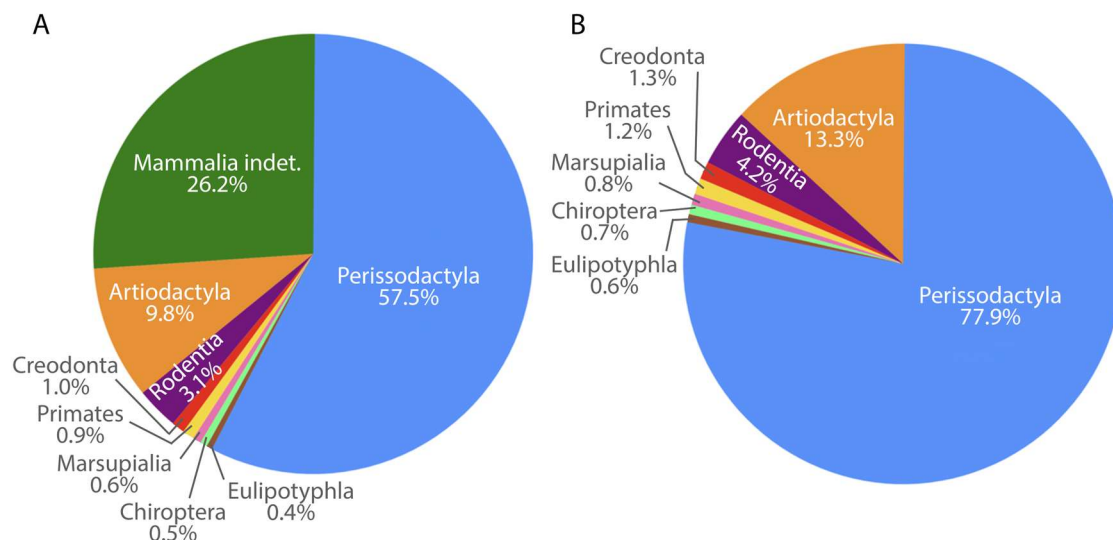


Fig. 4. Pie diagrams showing the statistical distribution of each mammal group in the NMO's "Oberbuchsitzen" collection, inventoried in the frame of the SwissCollNet project. A, Specimens identified as "Mammalia indet." are included in the analysis; B, Specimens identified as "Mammalia indet." are excluded from the analysis.

Among the 663 perissodactyl specimens are 2 *Chasmodon cartieri* Rütimeyer, 1862 (Fig. 5B & C); 23 unidentified *Lophiodon* Cuvier, 1822 (Fig. 5A); 1 *Metanchilophus depereti* (Stehlin, 1905); 1 unidentified *Pachynolophus* Pomel, 1847; 1 *Palaeotherium castrense* Noutlet, 1863; 3 unidentified *Palaeotherium* Cuvier, 1804 (fig. 5D); 3 *Plagiolophus cartieri* Stehlin, 1904 (fig. 5G); 16 unidentified *Plagiolophus* Pomel, 1847 (fig. 5E & F); 2 *Propalaeotherium isselanum* Cuvier, 1824; 2 *Eurohippus parvulus* (Laurillard, 1849); 1 *Propalaeotherium sudrei* Remy, Krasovec & Marandat, 2016 and 2 unidentified *Propalaeotherium* Gervais, 1849 (fig. 5J & K). 519 specimens are identified at the family level "Palaeotheriidae indet." (Fig. 5H & I) and 88 specimens are identified at the ordinal level "Perissodactyla indet.". The 113 artiodactyls include 2 *Hyperdichobune* sp. Stehlin, 1910; 4 *Mixtotherium* sp. Filhol, 1880 (Fig. 6C); 2 *Dichodon cartieri* Rütimeyer, 1891 (Fig. 6A & B); 2 large-sized *Haplobunodon* sp. Depéret, 1908 (Fig. 6D & E); 1 *Catodonthidium fallax* Stehlin, 1910 (Fig. 6F); 1 "Gervachoerus" suillus

(Gervais, 1859) (Fig. 6G) and 1 *Mouillacitherium* sp. Filhol, 1882 (Fig. 6H). The remaining 100 specimens are more fragmentary and classified as "Artiodactyla indet.". The 11 Hyaenodonta include 5 specimens of *Proviverra typica* Rütimeyer, 1862 (Fig. 7A & B) and 1 unidentified specimen of *Cynohyaenodon* Filhol, 1873. The other 5 specimens are identified as "Hyaenodonta indet.". Of the 36 rodent specimens, 19 belong to the species *Protadelomys cartieri* Stehlin & Schaub, 1951 (Fig. 7D, E & F) and 17 are identified to the order as "Rodentia indet.". The Metatheria include 1 specimen of *Amphiperatherium bastbergense* Crochet, 1979 (Fig. 7G) and 6 identified as "Metatheria indet." (Fig. 7H). Finally, of the 11 primates, only 2 specimens could be specifically identified: *Necrolemur zitteli* Schlosser, 1887 (Fig. 7I). The other 8 specimens were identified at the ordinal level "Primates indet.". 1 Amphilemuridae indet. (Fig. 7J) and 1 *Stehlinia* sp. Revilliod, 1919 (Fig. 7C) have also been identified, the other 4 Eulipotyphla specimens and the 5 Chiroptera specimens are unidentified, referred as "Eulipotyphla indet." and "Chiroptera indet."

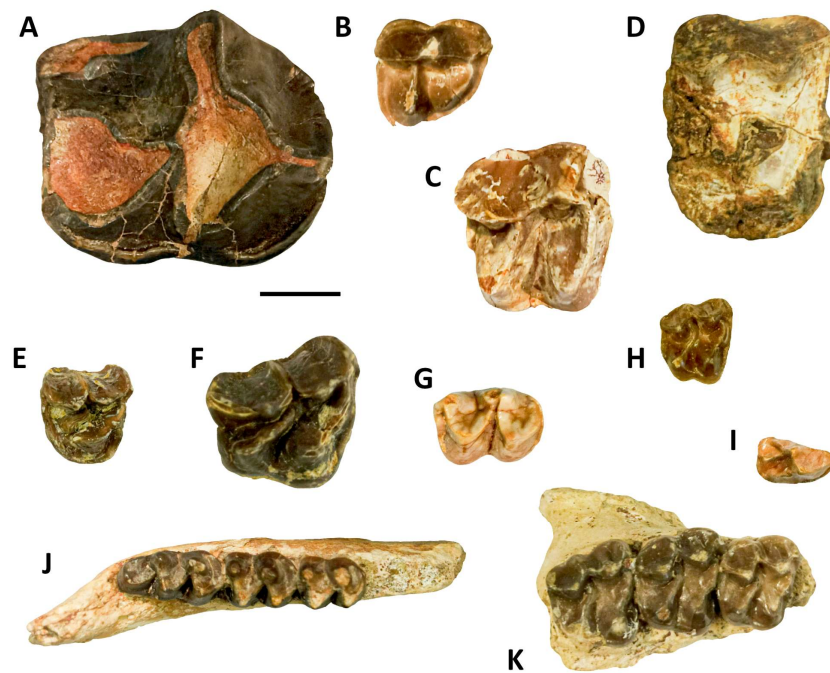


Fig. 5. Perissodactyla specimens in the NMO's “Oberbuchsitzen” collection, inventoried as part of the SwissCollNet project. A, *Lophiodon* sp., right p4 (NMO-27390); B, *Chasmotherium cartieri*, left DP4 (mirror view) (NMO-27378); C, *Chasmotherium cartieri*, right M1/2 (NMO-27379); D, *Palaeotherium* sp., left P4 (mirror view) (NMO-23256); E, *Plagiolophus* sp., left P4 (mirror view) (MNO- 27547); F, *Plagiolophus* sp., left M1/2 (mirror view) (NMO-27571); G, *Plagiolophus cartieri*, left m1/2 (mirror view) (NMO- 27674); H, Palaeotheriidae indet., left M3 (mirror view) (NMO-26504); I, Palaeotheriidae indet., right p3 (NMO-26276); J, *Propalaeotherium* sp., right hemi-mandible with m1-m3 (NMO-27704); K, *Propalaeotherium sudrei*, left maxilla with M1-M3 (mirror view) (NMO-26497). Scale bar = 1 cm.

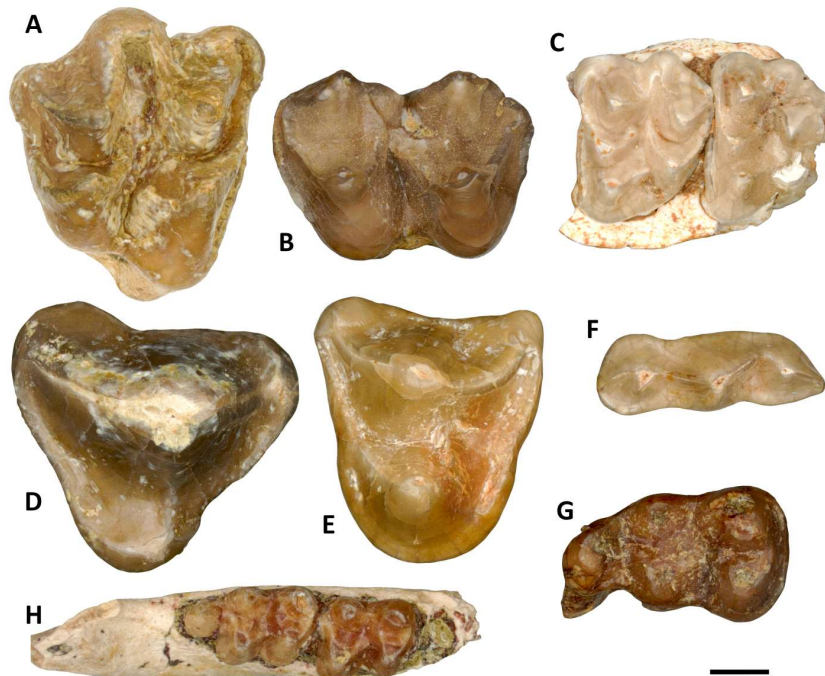


Fig. 6. Artiodactyla specimens in the NMO's “Oberbuchsitzen” collection, inventoried as part of the SwissCollNet project. A, *Dichodon cartieri*, right M1/2/3 (NMO-27188); B, *Dichodon cartieri*, left m1/2 (mirror view) (NMO-27301); C, *Mixtotherium* sp., left maxilla with M2-M3 (mirror view) (NMO-27247); D, *Haplobunodon* sp., right P3 (NMO-27239); E, *Haplobunodon* sp., right P4 (NMO-26550); F, *Catodontherium fallax*, left p3 (mirror view) (NMO-27295); G, “*Gervachoerus*” *suillus*, left m3 (mirror view) (NMO-26472); H, *Mouillacitherium* sp., left hemi-mandible with m2-m3 (mirror view) (NMO-27290). Scale bar = 2 mm.

5. DISCUSSION

5.1. A homogeneous fauna

The various karst fills between the cities of Egerkingen and Oberbuchsiten have always given rise to uncertainties as to the exact origin of the mammalian assemblages that they yielded. In fact, the exact provenance of the first collections by Cartier and Rütimeyer has never been determined. Based on colors of the bones, on the sedimentary residues present on the specimens, and on his expertise in the field, Stehlin began in 1916 to differentiate facies between "Huppersand", "Marnes grises", and "Faciès aberrant", and referred them to different fissures that he named α , β , and γ (Stehlin, 1916;

Hartenberger, 1970). The fossil assemblages of fissures α and β are dated from the late Lutetian (Hartenberger, 1969; Schmidt-Kittler *et al.*, 1987; Biochrom'97, 1997), and it is these that make up the fauna of the type locality MP14 "Egerkingen $\alpha+\beta$ " (Schmidt-Kittler *et al.*, 1987; Biochrom'97, 1997) (Fig. 3). The γ assemblages are older, dated to the Lower to Middle Lutetian (Hartenberger, 1969; Biochrom'97, 1997) and brought closer to the level MP13 (Biochrom'97, 1997). Since the NMO "Oberbuchsiten" collection was excavated recently from a single well-identified fissure filling (Fig. 1), there is no ambiguity as to its origin. The specimens form an essentially homogeneous fauna, both in terms of geographic origin and stratigraphic age (Fig. 3).

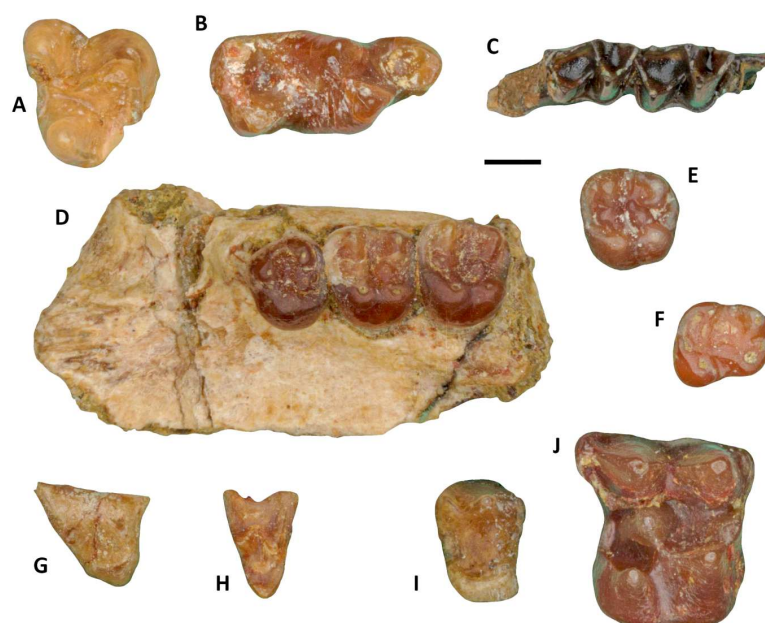


Fig. 7. Specimens of hyaenodontans, chiropterans, rodents, metatherians and primates in the "Oberbuchsiten" collection of the NMO, inventoried as part of the SwissCollNet project. A, *Proviverra typica*, right m1/2/3 trigonid (NMO-27738); B, *Proviverra typica*, right m1/2/3 (NMO-27735); C, *Stehlinia* sp., right hemi-mandible with m2-m3 (NMO-23312); D, *Protadelomys cartieri*, right maxilla with M1-M3 (NMO-26493); E, *Protadelomys cartieri*, left M2 (mirror view) (NMO-27722); F, *Protadelomys cartieri*, left m1/2 (mirror view) (NMO-27732); G, *Amphiperatherium bastbergense*, left M1 (mirror view) (NMO-26505); H, Metatheria indet., left M2 (mirror image) (NMO-27751); I, *Necrolemur zitteli*, right P4 (NMO-26252); J, *Amphilemuridae* indet., left M1/2 (mirror image) (NMO-27744). Scale bar = 1 mm.

5.2. Age of the NMO "Oberbuchsiten" assemblage

As this collection is a novel assemblage, the question of its age arises. The first observation is that 13 species are common with the Egerkingen α and β assemblages but not with γ (Table 2). These species include *Palaeotherium castrense*, *Metanchilophus depereti* and *Dichodon cartieri* which are characteristic of the MP14 biochronological unit (Biochrom'97, 1997). Only 4 taxa are common with Egerkingen γ (*Cynohyaenodon* sp., *Proviverra typica*, *Necrolemur zitteli*, *Protadelomys cartieri*), but these species are also present in Egerkingen α and β and therefore do not provide any additional information to specify the age of the NMO

"Oberbuchsiten" assemblage. The strong similarity with the Egerkingen α and β assemblages therefore suggests an equivalent biochronological age, i.e. MP14, whereas Egerkingen γ is generally considered to be slightly older, i.e. MP13 (Biochrom'97, 1997). However, one species, *Propalaeotherium sudrei*, was found in the NMO "Oberbuchsiten" collection, which is not present in any of the other Egerkingen/Oberbuchsiten assemblages. This species was first described by Remy *et al.* (2016) from the locality Aumelas (Hérault, France) dated from MP13 based on its fossil assemblage (see Remy *et al.*, 2016 for a summary of studies on this locality). Remy *et al.* (2016) also indicate that *Propalaeotherium sudrei* is rare in the fossil record and only found in another locality, Saint-

Martin-de-Londres, also dated from MP13. The specimen NMO-26497 is tentatively referred to this species based on the following diagnostic characters: very deeply notched centrocrista, elongated conules, and absence of hypostyle on M3. The presence of this species in the NMO “Oberbuchsiten” assemblage may therefore represent its third occurrence to date in the European fossil record.

This species could indicate a slightly older age of the NMO “Oberbuchsiten” assemblage compared to Egerkingen α and β . However, given the strong similarities with Egerkingen α and β and the rarity of *Propalaeotherium sudrei* in the fossil record, we rather interpret for now this new occurrence of the species as an extension of its biochronological duration to MP14.



Fig. 8. Simplified map of the Lutetian paleogeographic context of Europe (modified from Palcu & Krijgsman, 2023). The red star indicates the location of Egerkingen/Oberbuchsiten.

The Palaeotheriidae are known almost exclusively from Europe, from the Ypresian (MP8+9) to the late Rupelian (MP25) (Remy, 1995; BiochroM'97, 1997; Remy, 2017). They are generally considered to be sister groups to the Equidae Gray, 1821 (Franzen, 1989; Froehlich, 1999; Froehlich, 2002; Rose, 2006), which are grouped within the superfamily Equoidea Hay, 1902 (Franzen, 1989; Froehlich, 1999; Rose, 2006). In the type locality "Egerkingen $\alpha+\beta$ " eight different paleotheres genera were identified: *Pachynolophus*; *Propalaeotherium*; *Palaeotherium*; *Anchilophus* Gervais, 1852; *Metanchilophus* Remy, 2012; *Eurohippus* Franzen, 2006; *Plagiolophus* and *Lophiotherium* Marsh, 1871 (Hartenberger, 1970; Schmidt-Kittler *et al.*, 1987; BiochroM'97, 1997), six of which are present in the NMO “Oberbuchsiten” collection (Tab. 2). Only the genera *Lophiotherium* and *Anchilophus* were not found in the NMO “Oberbuchsiten” collection. In contrast, the species *Propalaeotherium sudrei* occurs in the NMO collection but was never identified in other Egerkingen/Oberbuchsiten assemblages, possibly due to the recent recognition of this new species by Remy *et al.* (2016).

Most small-sized paleotheres (Tab. 3) such as *Pachynolophus*, *Propalaeotherium* and *Eurohippus* display brachyodont teeth, moderate lophodonty, and unmolarized premolars (Danilo *et al.*, 2013; Remy *et al.*, 2016; Remy *et al.*, 2019). These dental characteristics, typical of a folivorous/frugivorous diet (Janis, 1995), are corroborated by the discovery of remains of fruits and tender leaves of a plant in the Lauraceae family in the stomach of a specimen of *Propalaeotherium hassiacum*

Haupt, 1925 from Messel (Sturm, 1978; Koenigswald & Schaarschmidt, 1983; Blondel, 2001). The other small-sized paleothere *Metanchilophus* is the only one in this size category to display a more lophodont morphology indicating a rather browser diet (*sensu* Janis, 1995). Conversely, medium and large-sized paleotheres (Tab. 3) all have high-crowned teeth, more pronounced lophodontia, and molarized premolars such as *Plagiolophus* and *Palaeotherium* (Remy, 2015), which were adapted to a browser diet (*sensu* Janis, 1995). They fed not only on tougher leaves, but also on young shoots and branches of trees and shrubs. Dental microwear analyses in *Plagiolophus* confirm a browsing diet (Collinson & Hooker, 1991; Janis, 1995; Blondel, 2001; Perales-Gogenola *et al.*, 2022), consuming leaves of both monocotyledon and dicotyledon plants (Perales-Gogenola *et al.*, 2022).

Additionally, the NMO “Oberbuchsiten” collection encompasses specimens of the tapiromorph such as *Chasmodon* Leidy, 1871. The chasmodons are poorly documented, known from the mid Lutetian (MP 13) to the late Bartonian (MP 16) (Remy, 2015), and of ambiguous systematic status. In some studies, they have been regarded as belonging to the Helaeidae (Radinsky, 1967) or the Lophodontidae (McKenna & Bell, 1997). However, they are more commonly associated with the Hyrachyidae (Savage *et al.*, 1966; Hooker & Weidmann, 2000; Becker, 2003; Remy, 2015) in the superfamily Rhinocerotidae (Savage *et al.*, 1966; Hooker, 1989; Remy, 2015). Their size and weight are comparable to those of a modern-day American tapir (Depéret, 1904; Becker, 2003). Two specimens of *Chasmodon*

cartieri are represented in the collection: a DP4 and a M1/2 (Fig. 5B and C). While the M1 is generally well preserved, its parastyle is broken off and only a fragment of the developed cingulum remains on the distal edge of the tooth. However, other characters specific to the genus *Chasmothierium* are present, including the absence of conules on transverse lophs, a highly developed paracone, and a flattened metacone (Remy, 2015). Its brachyodontia suggests a folivorous and/or frugivorous diet (Janis, 1995).

Tabl. 2. Comparison of the Egerkingen α , β and γ faunal lists (after Beaumont, 1966; Hartenberger, 1969; Hartenberger, 1970; Biochrom'97, 1997; Costeur & Schneider, 2011; Solé & Mennecart, 2019; Vianey-Liaud & Marivaux, 2021) with the NMO "Oberbuchsiten" faunal list. The lists take into account taxa identified at generic or specific levels only. ✓ = species present.

| Order | Family | Species | α | β | γ | NMO |
|----------------|-----------------|--|----------|---------|----------|-----|
| Perissodactyla | Hyrachyidae | <i>Chasmothierium cartieri</i> | ✓ | ✓ | | ✓ |
| | | <i>Hyrachyus minimus</i> | ✓ | | | |
| | Lophiodontidae | <i>Lophiodon rhinoceros</i> | ✓ | ✓ | | |
| | | <i>Lophiodon tapiroides</i> | ✓ | ✓ | | |
| | | <i>Lophiodon cuvieri</i> | ✓ | ✓ | | |
| | | <i>Lophiodon tapirotherium</i> | ✓ | | | |
| | | <i>Lophiodon</i> sp. | ✓ | ✓ | | ✓ |
| | Palaeotheriidae | <i>Pachynolophus</i> sp. | ✓ | ✓ | | ✓ |
| | | <i>Eurohippus parvulus</i> | ✓ | ✓ | | ✓ |
| | | <i>Propalaeotherium helveticum</i> | ✓ | ✓ | | |
| | | <i>Propalaeotherium rollinatti</i> | | ✓ | | |
| | | <i>Propalaeotherium sudrei</i> | | | | ✓ |
| | | <i>Propalaeotherium</i> sp. | ✓ | ✓ | | ✓ |
| | | <i>Palaeotherium eocaenium</i> | ✓ | ✓ | | |
| | | <i>Palaeotherium ruetimeyeri</i> | ✓ | ✓ | | |
| | | <i>Palaeotherium castrense</i> | ✓ | ✓ | | ✓ |
| | | <i>Palaeotherium</i> sp. | ✓ | ✓ | | ✓ |
| | | <i>Metanichilophus depereti</i> | ✓ | ✓ | | ✓ |
| | | <i>Anchilophus desmaresti</i> | ✓ | ✓ | | |
| | | <i>Plagiolophus cartieri</i> | ✓ | ✓ | | ✓ |
| | | <i>Plagiolophus</i> sp. | ✓ | ✓ | | ✓ |
| | | <i>Lophiotherium pygmaeum</i> | ✓ | ✓ | | |
| Artiodactyla | Dichobunidae | <i>Dichobune langi</i> | ✓ | ✓ | | |
| | | <i>Dichobune robertiana</i> | ✓ | ✓ | | |
| | | <i>Hyperdichobune nobilis</i> | ✓ | ✓ | | |
| | | <i>Hyperdichobune</i> sp. | ✓ | ✓ | | ✓ |
| | | <i>Meniscodon europaeum</i> | ✓ | ✓ | | |
| | | <i>Mouillacitherium cartieri</i> | ✓ | ✓ | | |
| | | <i>Mouillacitherium</i> sp. | ✓ | | | ✓ |
| | | | | | | |
| | Cebochoeridae | <i>Cebochoerus ruetimeyeri</i> | ✓ | ✓ | | |
| | | " <i>Gervachoerus</i> " <i>suillus</i> | ✓ | ✓ | | ✓ |
| | | <i>Choeromorvus jurensis</i> | ✓ | ✓ | | |
| | Mixtotheriidae | <i>Mixtotherium gresslyi</i> | ✓ | ✓ | | |
| | | <i>Mixtotherium priscum</i> | ✓ | | | |
| | | <i>Mixtotherium infans</i> | ✓ | ✓ | | |
| | | <i>Mixtotherium</i> sp. | ✓ | ✓ | | ✓ |
| | Choeropotamidae | <i>Haplobunodon solodurens</i> | ✓ | ✓ | | |
| | | <i>Haplobunodon mulleri</i> | ✓ | ✓ | | |
| | | <i>Haplobunodon</i> sp. | | | | ✓ |

The fauna of Oberbuchsiten does not include any perissodactyls with a grazer diet (*sensu* Janis, 1995). These animals consume a more abrasive diet, either due to the presence of harder plants or to dust deposition in an open environment (e.g. Simpson, 1944; Janis, 1988; MacFadden, 2000; Williams and Kay, 2001). Indeed, they are found exclusively in the mid-Oligocene interval, between MP23 and MP26, and are entirely absent throughout the remainder of the Paleogene (Blondel, 2001).

| | | | | | | |
|-----------------|------------------|--------------------------------------|---|---|---|---|
| | | <i>Rhagatherium kowalevskyi</i> | ✓ | ✓ | | |
| Anoplotheriidae | | <i>Catodonthierium buxgovianum</i> | ✓ | ✓ | | |
| | | <i>Catodonthierium fallax</i> | ✓ | ✓ | | ✓ |
| | | <i>Dacrytherium elegans</i> | ✓ | ✓ | | |
| Tapirulidae | | <i>Tapirulus depereti</i> | ✓ | ✓ | | |
| Xiphodontidae | | <i>Leptotheridium traguloides</i> | ✓ | ✓ | | |
| | | <i>Dichodon cartieri</i> | ✓ | ✓ | | ✓ |
| | | <i>Haplomeryx egerkingensis</i> | ✓ | ✓ | | |
| Amphimerycidae | | <i>Pseudamphimeryx schlosseri</i> | ✓ | ✓ | | |
| Hyaenodonta | Hyaenodontidae | <i>Prototomus torvidus</i> | ✓ | | ✓ | |
| | | <i>Eurotherium theriodis</i> | ✓ | ✓ | ✓ | |
| | | <i>Prodissopsalis eocaenicus</i> | ✓ | ✓ | | |
| | | <i>Cynohyaenodon trux</i> | ✓ | ✓ | ✓ | |
| | | <i>Cynohyaenodon ruetimeyeri</i> | ✓ | ✓ | | |
| | | <i>Cynohyaenodon</i> sp. | ✓ | ✓ | ✓ | ✓ |
| | | <i>Cartierodon egerkingensis</i> | | | | ✓ |
| | | <i>Incertain sedis</i> | | | | |
| | | <i>Proviverra typica</i> | ✓ | ✓ | ✓ | ✓ |
| | | <i>Allopteronodon torvidus</i> | ✓ | ✓ | | |
| Carnivora | Querzygalidae | <i>Querzygale helvetica</i> | ✓ | ✓ | | |
| Primates | Adapidae | <i>Adapis priscus</i> | | | | ✓ |
| | | <i>Adapis sciureus</i> | | | | ✓ |
| | | <i>Adapis ruetimeyeri</i> | ✓ | | ✓ | |
| | | <i>Caenopithecus lemuroides</i> | | | | ✓ |
| | | <i>Leptadapis ruetimeyeri</i> | ✓ | ✓ | | |
| | | <i>Simonsia lynnae</i> | ✓ | ✓ | ✓ | |
| | | <i>Incertain sedis</i> | | | | |
| | | <i>Chasselasia eldredgei</i> | | | | ✓ |
| | | <i>Plesiarctomys spectabilis</i> | ✓ | ✓ | | |
| | | <i>Paradelomys</i> sp. | ✓ | ✓ | | |
| Rodentia | Pseudosciuridae | <i>Pseudosciuridae</i> sp. | ✓ | | ✓ | |
| | | <i>Treposciurus</i> sp. | ✓ | ✓ | | |
| | | <i>Incertain sedis</i> | | | | |
| | | <i>Protadelomys cartieri</i> | ✓ | ✓ | ✓ | ✓ |
| | | <i>Ailuravus picteti</i> | ✓ | ✓ | | |
| | Apatotheria | <i>Heterohyus europaeus</i> | | | | ✓ |
| | | <i>Heterohyus gracilis</i> | | | | ✓ |
| | | <i>Heterohyus fortis</i> | ✓ | ✓ | ✓ | |
| | Chiroptera | <i>Vespertilionidae</i> | | | | |
| | | <i>Stehlinia gracilis</i> | ✓ | | | |
| | | <i>Stehlinia pusilla</i> | ✓ | | | |
| | | <i>Stehlinia ruetimeyeri</i> | | | ✓ | |
| | | <i>Stehlinia</i> sp. | | | | ✓ |
| Eulipotyphla | Amphilemuridae | <i>Amphilemuridae</i> indet. | | | | ✓ |
| Metatheria | Herpetotheriidae | <i>Amphiperatherium bastbergense</i> | ✓ | ✓ | | ✓ |

Tabl. 3. Size categories of perissodactyl genera found in NMO “Oberbuchsitzen” based on the length of upper and lower molars (in mm). Measurements are taken from Franzen (2006), Remy (2004, 2012, 2015) Remy *et al.* (2016), Savage *et al.* (1965), Stehlin (1903) and Sudre (1971).

| | M1 | m1 | M2 | m2 | M3 | m3 | References |
|------------------------------------|-------|-------|------|------|-------|------|-----------------------------|
| Size category : small | | | | | | | |
| <i>Pachynolophus livinierensis</i> | 7.2 | 7.0 | 8.2 | 7.8 | 9.4 | 12.7 | Savage <i>et al.</i> , 1965 |
| <i>Pachynolophus duvali</i> | - | 8.0 | 9.0 | 9.0 | 8.9 | - | Savage <i>et al.</i> , 1965 |
| <i>Eurohippus parvulus</i> | - | 8.2 | 9.0 | - | 9.5 | 12.2 | Franzen, 2006 |
| <i>Metanchilophus depereti</i> | 10.1 | 9.3 | 11.8 | 10.9 | 11.5 | 14.7 | Remy, 2012 |
| <i>Propalaeotherium sudrei</i> | 10.4 | 10.2 | 11.9 | 11.4 | 12 | 16.4 | Remy <i>et al.</i> , 2016 |
| Size category : medium | | | | | | | |
| <i>Plagiolophus cartieri</i> | 14.6 | 13.1 | 16.3 | 14.8 | 19.5 | 22.0 | Remy, 2004 |
| <i>Chasmotherium cartieri</i> | 20-22 | 19-20 | 23 | 21 | 18-21 | 24 | Stehlin, 1903 |
| Size category : large | | | | | | | |
| <i>Palaeotherium castrense</i> | 30.3 | 28.2 | 34.1 | 31.4 | 38.1 | 44.6 | Remy, 2015 |
| <i>Lophiodon lautricense</i> | 48 | 43 | 58 | 53 | 56 | 71 | Sudre, 1971 |

5.3. Paleoenvironment and specificities of the perissodactyls assemblage

The assemblage is notable for its abundance of perissodactyl specimens, particularly paleotheres. This can be attributed to the gregarious nature of these animals and their ability to adapt to diverse ecological niches. The assemblage reveals indeed an over-representation of Equoids (comprising various sizes of Palaeotheridae) compared to Tapiromorphs (*Lophiodon* and *Chasmotherium*; Fig. 9A).

An analysis of the identified taxa, at least at the generic level, whose ecology and size can be estimated (Tab. 3; Fig. 9B & C), corroborates the preservation bias. Indeed, the intermediate and large sized perissodactyls are well represented, indicating that they are minimally affected by potential preservation bias (Fig. 9C). The considerable number of unidentified paleotheres (Fig. 9A vs. 9B) precludes further paleoecological interpretation. Nevertheless, a few observations can be made. For the assemblage as a whole, despite the probable under-representation of small perissodactyls (*Pachynolophus*, *Propalaeotherium* and *Metanchilophus*) and the lack of data on all paleotheres, folivorous/frugivorous feeders account for 58% of the remains found (Fig. 9). Folivorous/frugivorous paleotheres are mostly small-sized taxa whereas medium and large-sized paleotheres are all browser. The only medium to large-sized folivorous/frugivorous taxa are the tapiromorphs *Chasmotherium* and *Lophiodon*.

A greater proportion of folivorous and frugivorous taxa in comparison to other diets assemblages may suggest the dominance of a more closed and humid environment. However, this percentage is not fully reliable without further study of the whole faunal assemblage. Additionally, small and large taxa are dominated by folivorous and frugivorous diets whereas medium size

taxa are dominated by browser (mostly due to the abundance of *Plagiolophus*) which may indicate a partitioning of resources in a complex mosaic landscape in the context of a general warm and humid climate. It is in this opposition between folivorous/frugivorous and browser that we may find a confirmation of a potential specific environmental context of NMO “Oberbuchsitzen”. Further study and comparison with other assemblages from the Egerkingen/Oberbuchsitzen historical collections will likely confirm whether significant ecological differences contribute to the particularities of the NMO “Oberbuchsitzen” collection, in addition to the preservation bias already observed.

The intrinsic composition of the siderolitic karst filling, comprising clay deposits enriched in kaolinite and iron pisolites (Becker, 2003), already indicates the presence of wetlands and a tropical climate (Becker, 2003; Thiry, 2000; Vernet, 1963). Additionally, several species provide insights into the paleoenvironment of this locality. The presence of *Necrolemur zitteli*, a small arboreal primate, indicates the development of a significant forest environment around the karst fill during the period of sediment deposition. Additionally, the massive postcranial morphology of *Lophiodon* (Holbrook, 2009) indicates an adaptation to a wet habitat. Indeed, contrary to many Eocene perissodactyls, *Lophiodon* had a pentadactyl manus, and a tridactyl pes (Depéret 1907), in addition to a tibia that was much shorter than the femur (Holbrook 2009), indicating a lack of adaptation to cursoriality. These palaeoecological features are further supported by its dentition, which is suited to a non-abrasive diet of soft, low-growing plants, leaves, or fruits (Remy, 2015). In contrast, the presence of medium-sized and large paleotheres with high-crowned teeth, more pronounced lophodontia, and molarized premolars indicates a browsing diet. This could suggest a more open and potentially also less

humid component in the environment, although their postcranial anatomy suggests otherwise (Remy, 1992: 211). Indeed, Remy (1992) noted that the vertebral column and head posture of *Palaeotherium* were not adapted to grazing, and that their short hindlimbs were not adapted to cursoriality, thus indicating a closed environment instead. Remy (2015) suggested that some palaeotheres with semi-hypsodont crowns could have fed

on the leaves of some phytolith-rich angiosperms that are found in mangroves such as *Arecaceae* (palms), which are strongly abrasive. The presence of semi-hypsodont palaeotheres is thus coherent with the other faunal components.

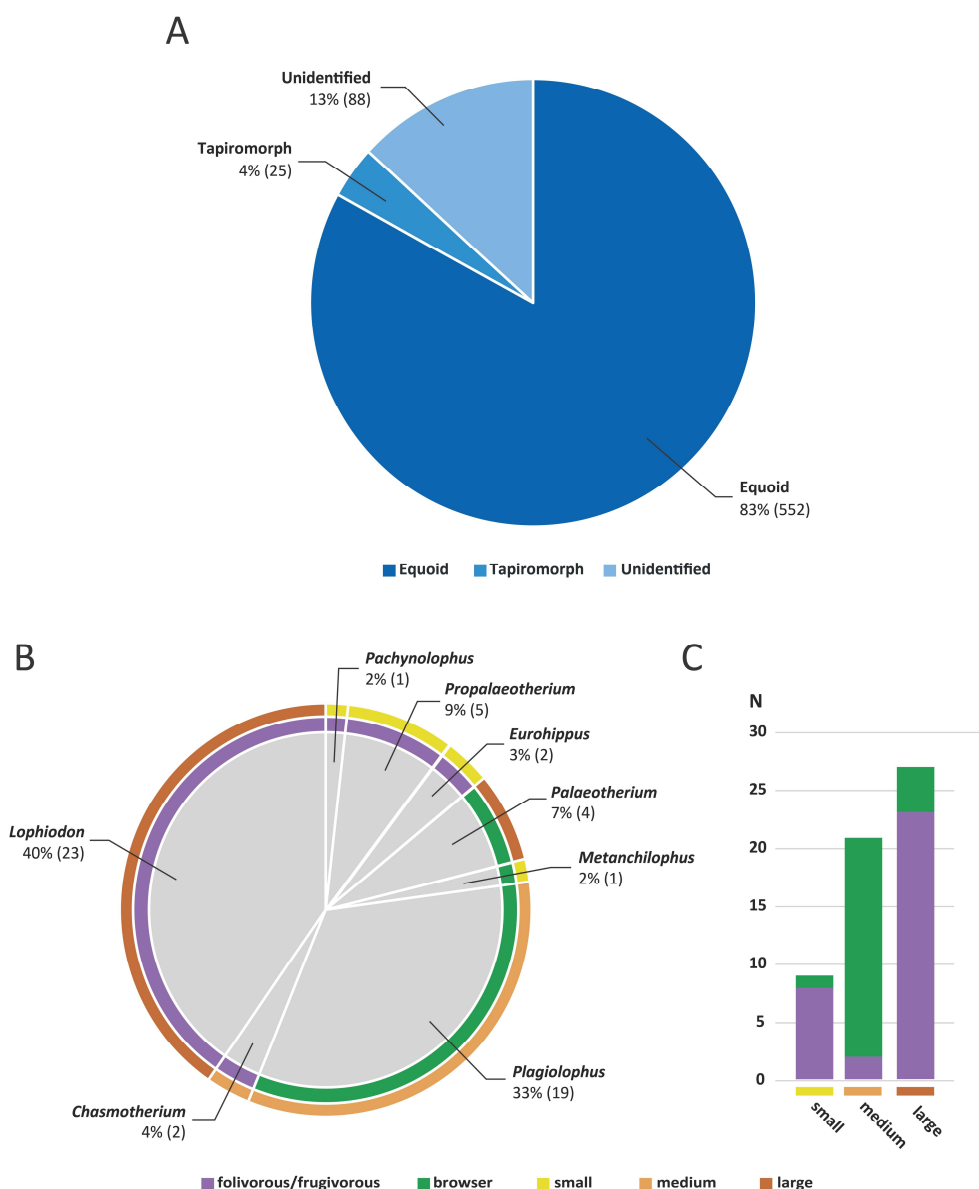


Fig. 9. Proportion of perissodactyls (number of specimens) in the NMO “Oberbuchsiten” collection. A, Proportion of the whole assemblage including incomplete identifications; B-C, Proportion of the specimens identified at minimal at generic level with their diet and size category; B, Ordered by systematic; C, Ordered by size. Of all Perissodactyla (N=665), 8.5% (N=57) could be determined at least at generic level. Size categories are defined in Table 3.

6. CONCLUSIONS

In conclusion, the NMO has acquired a significant collection from Oberbuchsiten, now comprising 1222 fossils. Originated from a unique fissure filling, it exhibits

a completely homogeneous fauna, in contrast to some historical Egerkingen/Oberbuchsiten collections, whose provenance (exact fissure filling) often remains uncertain. The inventory and preliminary study show that most of the collection is composed of mammalian remains (1155),

with up to 847 isolated teeth (often fragmentary), 33 mandibular remains, and 13 maxillary remains. The faunal list comprises so far 30 taxa, 24 of them being identified at least at generic level.

Despite the occurrence of *Propalaeotherium sudrei* in the NMO “Oberbuchsiten” assemblage, which is unknown in other Egerkingen/Oberbuchsiten collections, the strong similarities with Egerkingen α and β suggest a referral of this novel assemblage to the MP14 reference level. The assemblage is notable for its abundance of perissodactyl specimens, particularly paleotheres, leading to an overrepresentation of Equoids within perissodactyls. It is not possible for now to interpret further this dominance of Equoids. All sedimentary and paleontological data point to an environment dominated by forests in a general warm and humid climate. Nevertheless, a diversity of diets of perissodactyls and their uneven distribution among size-categories suggest an ecological partitioning reflecting a more fragmented landscape.

The completion of this collection's inventory will facilitate a more comprehensive investigation of the assemblage by specialists in the various mammal groups that comprise it, and potentially lead to the identification of new taxa. These future studies will likely assist in elucidating the particularities of the Oberbuchsiten assemblage of the NMO, thereby providing additional insights into the question of a potential environmental difference when compared to other Egerkingen/Oberbuchsiten collections.

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