Memòria especial 9

Paleontologia i Evolució

Abstract Book & Fieldtrip Guide

NOW 25th Anniversary Meeting

Sabadell (Barcelona), 16–18 November 2022

Institut Català de Paleontc
Miquel Crusafont

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PALEONTOLOGIA I EVOLUCIÓ, MEMÒRIA ESPECIAL 9

ABSTRACT BOOK & FIELDTRIP GUIDE
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EDITORS

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David M. Alba

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Institut Català de Paleontologia
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Prologue: From Crusafont to NOW

It is with great pleasure that we write this prologue for the Abstract Book & Fieldtrip Guide of the NOW 25th Anniversary Meeting. This is because of several reasons. Above all, because despite the delay in the celebration (owing to the pandemic) we will finally be able to meet in person with friends and colleagues to celebrate that the NOW database has come of age while being more lively than ever. Furthermore, the attendance to the meeting has been a success that surpassed our initial expectations, not only in terms of the number of contributions but also regarding their quality. This meeting will undoubtedly be an exceptional opportunity for junior and senior vertebrate paleontologists from multiple countries to meet, discuss, and continue collaborating. We hope that this will be a most enriching experience for everyone involved. As far as we are concerned, we are also particularly glad about this meeting because, in some sense, it represents the re-establishment of a practice established by Miquel Crusafont-Pairó (Sabadell, 1910–1983)—the founder of our institution and the 'father' of the Catalan school of vertebrate paleontology (for a biography, see Crusafont i Sabater, 2019)—in the 1950s: to reunite in Sabadell a vast number of most renowned foreign paleontologists, as we explain in further detail below.

Crusafont played a major role in the modernization of Catalan paleontology since the end of the Spanish Civil War in 1939. The find of fossils during his teens directed his naturalist vocation toward vertebrate paleontology, while his early academic training as a pharmacist contributed to his modern views of paleontology as a discipline inextricably linked to evoution and framed well within life sciences—i.e., a paleobiological view that contrasted with the more stratigraphically-oriented paleontology performed by his predecessors in Spain. Crusafont was initially based at the Museum of Sabadell and soon acquired the required academic credentials to be recognized as a professional paleontologist. Well before finishing his PhD, he was appointed

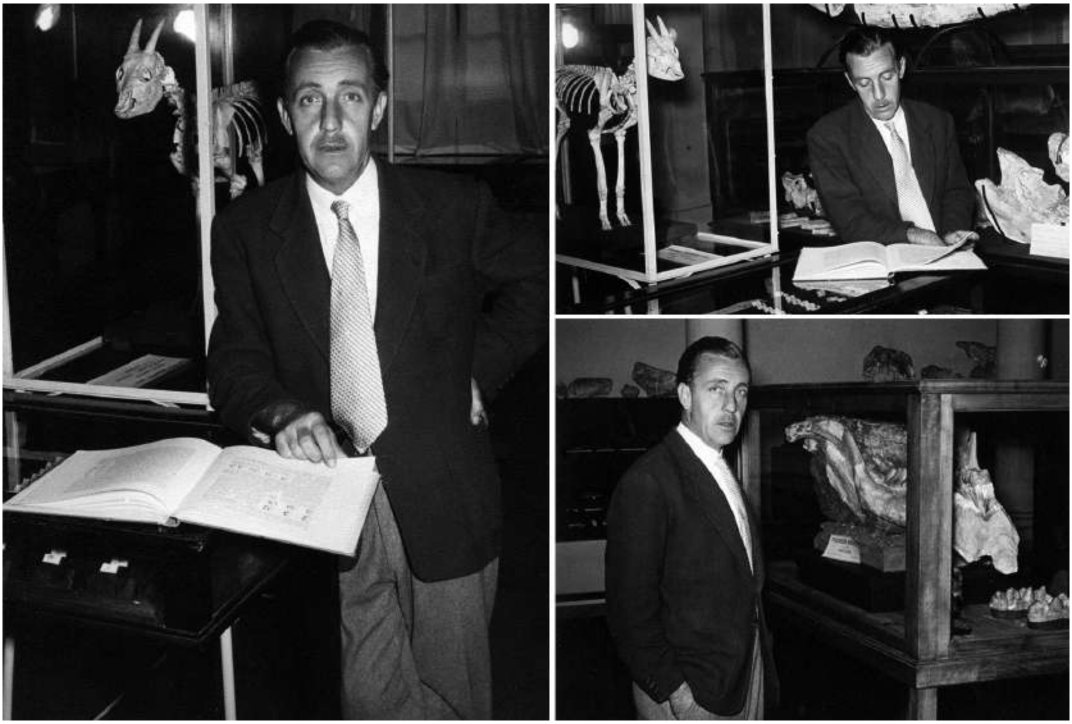

Figure 1. Miquel Crusafont-Pairó at the Paleontology Hall of the Sabadell Museum in 1952. Photographs © Arxiu Miquel Crusafont – Institut Català de Paleontologia Miquel Crusafont.

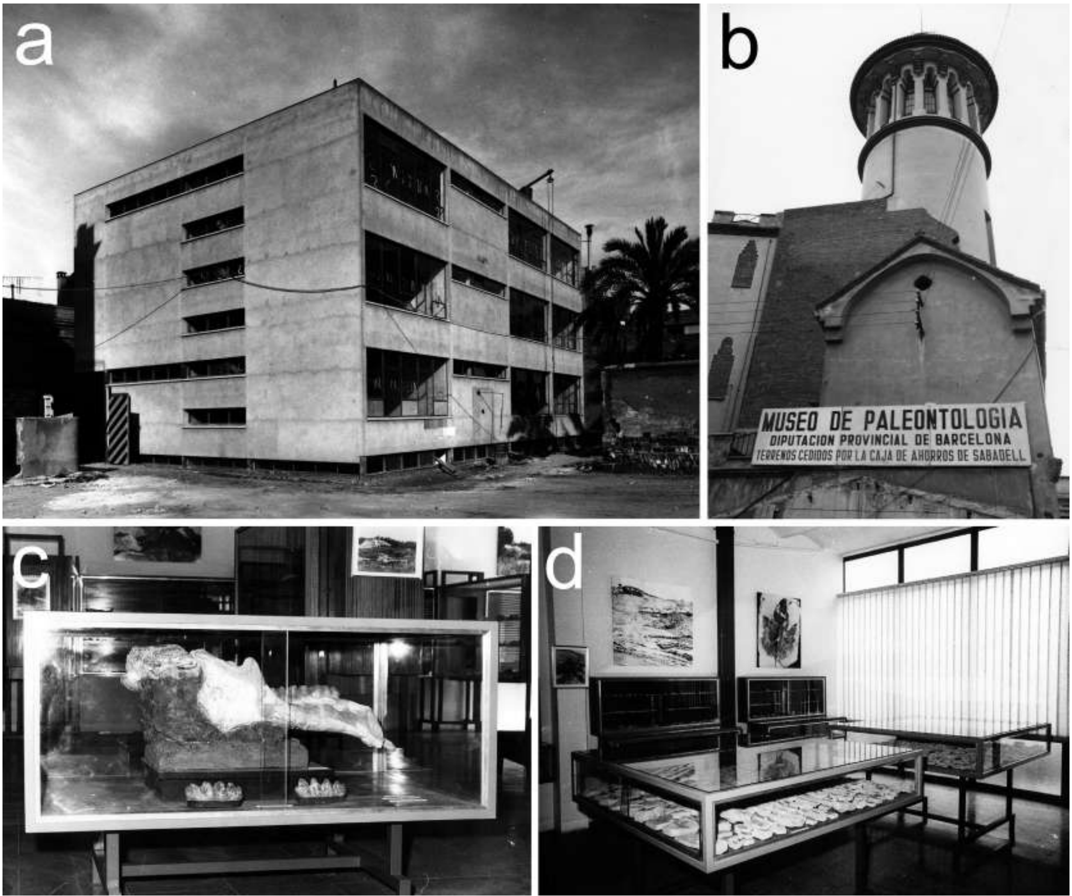

Figure 2. Construction of the Provincial Institute of Paleontology from Sabadell (a–b) and detail of the exhibits after its inauguration in 1969 (c–d). Photographs © Arxiu Miquel Crusafont – Institut Català de Paleontologia Miquel Crusafont.

curator of the Miocene Paleontology Hall (Fig. 1) of the museum and eventually became sponsored by the Consejo Superior de Investigaciones Científicas (CSIC), subsequently managing to create in the museum a Paleobiology Section—the germ of our current research center—ascribed to the Instituto "Lucas Mallada" of the CSIC (Crusafont Pairó, 1969). The large amount of fossils amassed by Crusafont and his collaborators during the 1940s and 1950s, together with his frantic research activity, as well as his charisma, stubbornness, and determination, ultimately culminated in the foundation in 1969 of the Instituto Provincial de Paleontología in Sabadell (IPS; Crusafont Pairó, 1969; Fig. 2). In the 1960s, he also became Chair of Paleontology, first in Oviedo and later in Barcelona, but due to health issues, and overwhelmed by bureaucratic and teaching duties, he ultimately resigned from the university in the 1970s but remained as IPS director until his death in 1983 (Truyols i Santonja, 1986).

In the 1930s, Crusafont started collaborating with Josep F. de Villalta-Comella, although it was not until the 1940s and 1950s that such collaboration gave most of its fruits. Although they essentially continued the work initiated by Josep R. Bataller, from the Geology Museum of the Barcelona Seminary, during the previous decades, Crusafont did so with unprecedented rigor and a clearly innovative character (Truyols i Santonja, 1986). Furthermore, the research performed by the tandem Crusafont–Villalta attained an exceptional international repercussion by the standards of the postwar period in Spain, when owing to the recent establishment of the Francoist dictatorial regime most of Spanish science remained

Figure 3. Josep F. de Villalta-Comella (left) and Miquel Crusafont-Pairó (right) at the Sabadell Museum in 1956, during the 3rd Cursillos Internacionales de Paleontología. Photograph © Arxiu Miquel Crusafont – Institut Català de Paleontologia Miquel Crusafont.

largely isolated. In contrast, Crusafont and Villalta first traveled abroad in 1946, establishing relationships with many foreign paleontologists—such as Viret, Piveteau, Hoffstetter, Ginsburg, Schaub, and Hürzeler, among others (Crusafont Pairó, 1969). This also led to the publication of a series of papers in the *Comptes Rendus de la Société Géologique de France*, which represented the beginning of Crusafont's international recognition (Truyols i Santonja, 1986).

To attain further international projection for the recently established Paleobiology Section of the Sabadell Museum, throughout the 1950s Crusafont organized in Sabadell several editions of the "Cursillos Internacionales de Paleontología" (in 1952, 1954, 1956, and 1958; Crusafont Pairó, 1969). These international paleontological courses (Figs. 3–4), equivalent to current scientific workshops, were very significant for Crusafont's recognition as a reputed paleontologist at the international level, being attended by many renowned foreign researchers such as Piveteau, Viret, Hürzeler, von Koenigswald, Kurtén, and Simpson. With the collaboration with Villalta interrupted during the 1950s, Crusafont increasingly established collaborations with other researchers during the 1960s and 1070s, such as Hürzeler and Kurtén, to cite only a couple of examples. Indeed, the prolific scientific production of Crusafont cannot be understood without taking into account his frequent collaboration with other researchers, from Villalta and Truyols to his later students and many foreign colleagues. This does not seem exceptional from our current perspective, but was much less frequent back then, thus emphasizing the modern views of Crusafont with regard to research.

Crusafont's main scientific contributions lie on the discovery and description of many fossil mammals from the Iberian Peninsula, as well as in the biostratigraphic work that led to the definition of the Vallesian and Turolian (Truyols i Santonja, 1985). However, from our current standpoint, even more important for the subsequent development of paleobiological research in Catalonia was the modernization of paleontological science during the mid-20th Century in Spain (from both methodological and theoretical viewpoints), as well as the establishment of a research center that is currently more active than ever and which has attained a dimension that Crusafont could have only dreamt

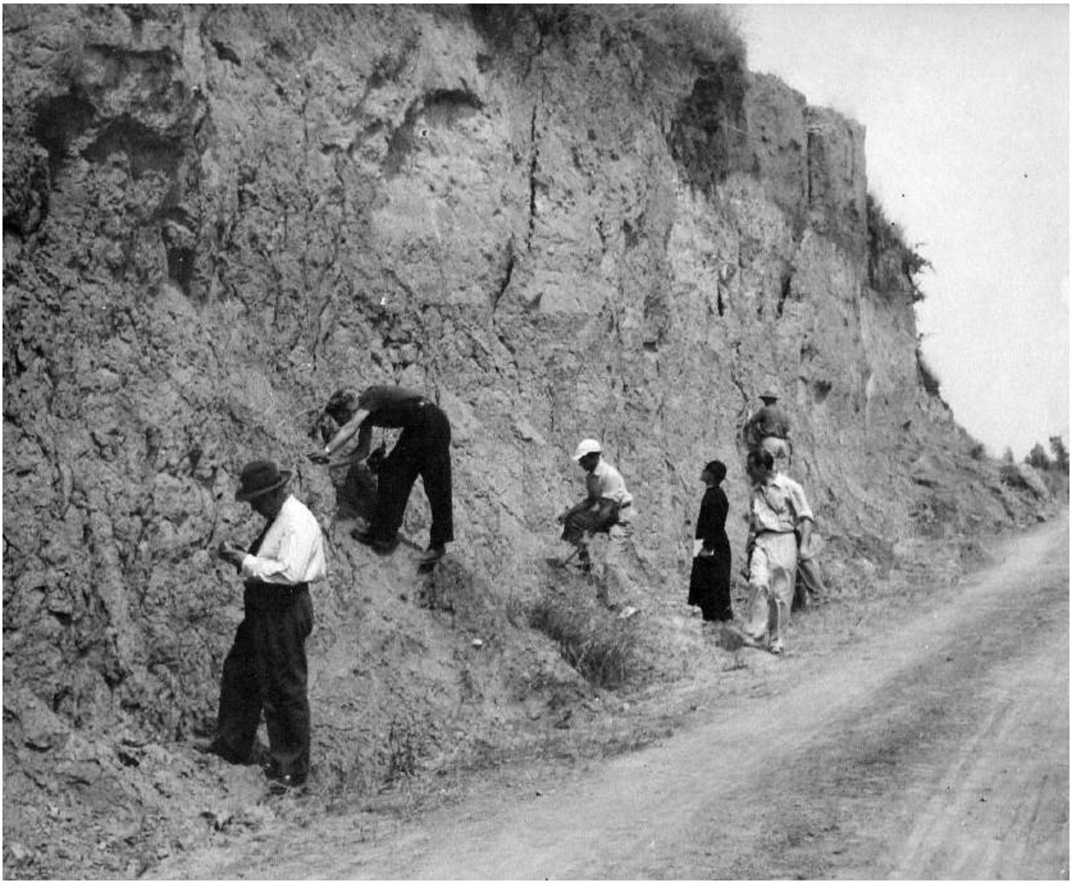

Figure 4. Miquel Crusafont-Pairó and other paleontologists during a visit to the Can Llobateres outcrop during the 'Cursillos Internacionales de Paleontología' in 1954. Photograph from Arxiu Miquel Crusafont, © Institut Català de Paleontologia Miquel Crusafont.

of. So, it is not by chance that we are celebrating this meeting in Sabadell, even though some subsequent developments were fortuitous and could not have been expected a priori.

After Crusafont's death, the IPS was renamed in his honor and the discovery and initial success of the Orce Man allowed a new generation of young researchers to become tenured at the IPS (Carandell Baruzzi, 2021; Alba, 2022). These included Jordi Agustí, who would soon become IPS director for the next couple of decades, as well as Salvador Moyà-Solà, who would eventually replace Agustí coinciding with the refoundation of the IPS in 2006 (see below). As explained elsewhere in greater detail (Fortelius et al., in press), Agustí was involved in the development of NOW database at various key stages, beginning with the coordination of the European Science Foundation network "Hominoid Evolution and Environmental Change in the Neogene of Europe" and the organization of its first workshop at Sant Feliu de Guíxols in 1996 (Agustí et al., 1998), which roughly coincided in time with the official launch of the database (Fortelius et al., in press). Agustí was also involved in the edition of a multiauthored book resulting from this network (Agustí et al., 1999) as well as in the organization of a meeting in Sabadell in 2001 in the framework of the European Science Foundation program "Environments and Ecosystem Dynamics of the Eurasian Neogene (EEDEN)", which nevertheless had less consequences for the development of the NOW database than that held during the previous decade (Fortelius et al., in press).

During this period, roughly comprised between the mid-1990s and the mid-2000s, Agustí was very active in compiling data for the NOW database, particularly from Iberian basins, and it is not exaggerated to say that NOW was in the air. Only this atmosphere can explain why one of us (D.M.A.), who had recently embarked in 1999 on his PhD focused on fossil primates under Moyà-Solà's supervision, performed by that time a NOW database-driven study in collaboration with Agustí (Alba et al., 2001). A few years later, however, the discovery of a hominoid partial skeleton at Abocador de Can Mata in 2002 and its subsequent description as a new genus and species (*Pierolapithecus catalaunicus*) by Moyà-Solà et al. (2004) drastically altered the subsequent course of events—at a time when the IPS had no apparent possibilities to grow and run the risk of becoming just a local museum (Alba, 2022). The great international repercussion of this discovery made the Catalan government (Generalitat de Catalunya) to realize the potential impact of paleontology, and eventually led to the refoundation of the IPS as a research center of the CERCA system (Research Centers of Catalonia) linked to the Universitat Autònoma de Barcelona—the Institut Català de Paleontologia Miquel Crusafont (ICP)—under the direction of Moyà-Solà in 2006 (Alba, 2022). This represented an unprecedented opportunity to boost vertebrate paleontology research in Catalonia in terms of personnel and infrastructure, ultimately enabling the recruitment and tenuring of a set of then young researchers that include the two authors of this prologue.

The discovery and publication of *Pierolapithecus* thus indirectly prompted the re-establishment of an active link between the Catalan school of vertebrate paleontology and the NOW database. In particular, I.C.V. was recruited as member of NOW's Advisory Board in 2010 (being in charge of rodents) and eventually became associate coordinator and member of the NOW Steering Group in 2021. In turn, D.M.A. joined the NOW's Advisory Board in 2018 to oversee the hominoid primates, while other ICP researchers or research associates (Marc Furió, Eric Delson, Raef Minwer-Barakat) also joined the Advisory Board at some point. Mainly as a result of NOW's influence over the years, during the last decade the two of us have been actively involved in the design and compilation of an ICP in-house database of Miocene vertebrates from the Vallès-Penedès Basin, which is still underway but was already presented during the NOW meeting held in Bratislava in 2018 (Casanovas-Vilar et al., 2018). Although this database is compiled at the specimen level and currently of internal use only, we hope to progressively upload the updated species-locality occurrences to the NOW database, thereby contributing to its overall development regarding our main area of study (the Vallès-Penedès Basin) beyond the two taxonomic groups (rodents and primates) in which we specialize.

Besides our personal involvement in the NOW database throughout the years, we would like to stress that, as members of the Catalan school of vertebrate paleontology, we feel obliged by the Crusafontian tradition to emphasize team working and international collaboration—and nothing epitomizes the ideals of such a tradition better than the NOW database. Indeed, the collaborative effort represented by The NOW Community is probably one of the best examples that we can offer to our students (and society in general) to illustrate that science is a collective enterprise after all—despite academia being often perceived (not without reason) as an exceedingly competitive and aggressive environment. Perhaps not surprisingly, the history of the NOW database (Fortelius et al., in press) shows interesting parallelisms to those of our own institution, which go beyond the fortunate consequences of unpredictable and serendipitous events such as those mentioned above (Alba, 2022). Without prejudice of the latter, their respective histories highlight the importance of tenacious (and sometimes even audacious) determination coupled with collaborative joint efforts—particularly when trying to build, from a very humble but ambitious origins, something bigger that is aimed to remain as a legacy for generations of paleontologists-to-be. Whatever the reasons, the NOW database managed to find its way to become one of the most important paleontological databases, while the ICP has never been in better position to consolidate itself as a benchmark center for vertebrate paleontology research. Our respective paths have progressively converged during the last years until arriving to this meeting, so let's hope that, from now onward, they will remain inextricably intertwined with one another in years to come. The best path to follow is always uncertain, but it is always important to bear in mind where we aim to go and, especially, that there is no need to walk alone.

To conclude, as ICP researchers and members of The NOW Community, we do not see the organization of this meeting as the culmination of anything but rather as the beginning of a beautiful friendship. So, welcome to the ICP and long live the NOW database!

ACKNOWLEDGMENTS

We cannot finish this prologue without mentioning all the institutions and people that have made it possible to organize this meeting. First of all, we are grateful to The NOW Community for having entrusted the ICP with this responsibility, as well as the ICP (the Generalitat de Catalunya and the Universitat Autònoma de Barcelona) for recognizing the importance of organizing international meetings. Second, this meeting is part of R+D+I project PID2020-117289GBI00 ("Paleobiodiversidad y paleoecología de las faunas de vertebrados miocenas durante intervalos de alta resolución en la cuenca del Vallès-Penedès), funded by the Agencia Estatal de Investigación of the Spanish Ministerio de Ciencia e Innovación (MCIN/AEI/10.13039/501100011033/). Third, the fieldwork reflected in the fieldtrip has benefited from OSIC grants CLT009/18/00068 and CLT009/18/00071 (Departament de Cultura, Generalitat de Catalunya). Fourth, we would like to thank the various additional sponsors of this meeting, namely: Ajuntament de Subirats (https://subirats.cat/), Ajuntament de Sabadell (https://web.sabadell.cat/), CERCAGinys (CERCA's platform of scientific and technical services; https://ginys.cerca.cat/), Cafès Pont (https://www.cafespont.com), and La MicroCervesaria (https://educamtap1.wixsite.com/lamicro). Finally, we are also grateful to the ICP personnel that has contributed in any way to the meeting's organization, including Roc Olivé (author of the logo's drawing) and, especially, the two other members of the Organizing Committee (Pere Figuerola and David Basanta), without whom this would have never been possible.

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David M. Alba & Isaac Casanovas-Vilar
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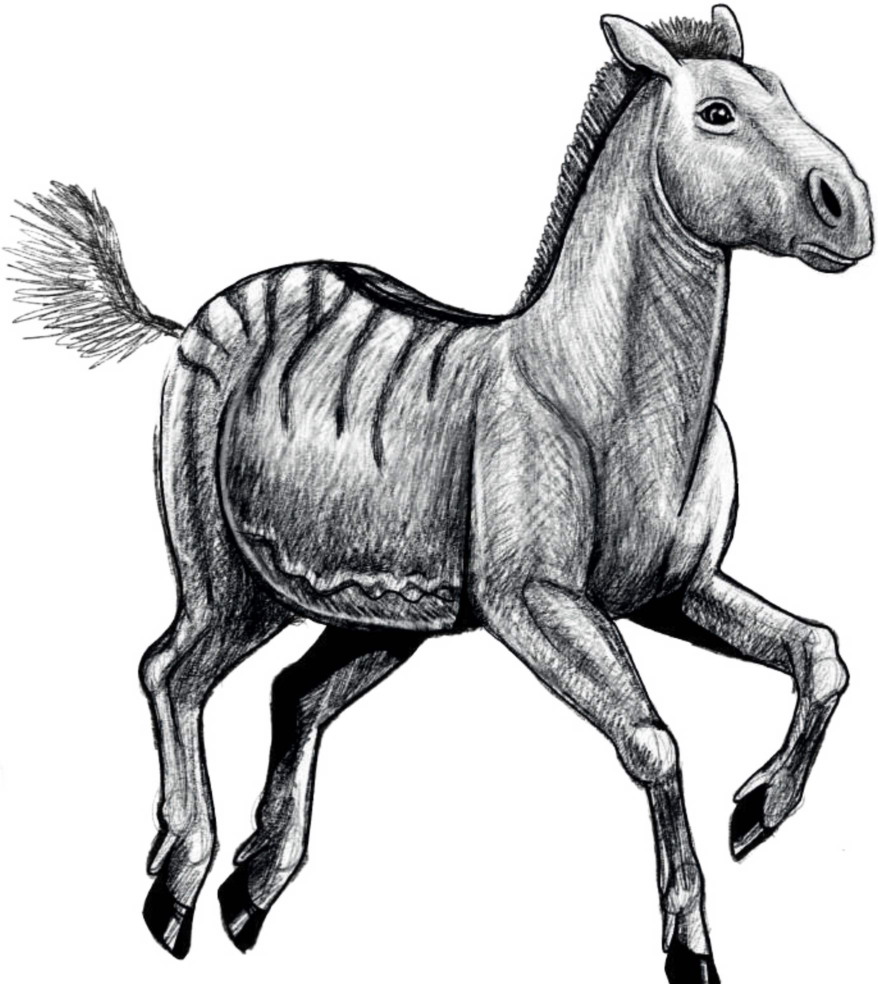
Bellaterra, October 2022

BOOK OF ABSTRACTS



NOW as it happened: The first decades

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ABSTRACT

The advent of computers accessible to ordinary academics very quickly generated widespread interest in systematic computational analysis of observational data that had been developing for a long time, in some disciplines for centuries. One of the first attempts to harness the scattered paleontological information for computational analysis, and arguably still the most widely known, was Jack Sepkoski's "compendium" from the later 1970s, of first and last occurrences of known marine metazoan taxa of the Phanerozoic (Sepkoski, 2002). For terrestrial vertebrates an early manifestation of this trend was the "Workshop on Computerization" organized by the Society of Vertebrate Paleontology in 1989 and the resulting Guidelines and Standards for Fossil Vertebrate Databases (Blum, 1991).

Against this background the emergence of the NOW database of fossil mammals during the early 1990s seems natural, if not inevitable. But how exactly it came together is a long and strange story, littered with coincidences and lucky breaks—and not devoid of passion. One might think that databases are just neutral repositories of primary data, necessary but boring. Instead, they seem to call forth strong personal ambitions, emotions and impulses, including the darker urges related to possession and ownership. At the end of the story there is a moral: a public database is fundamentally really a kind of museum collection. And, like all museum collections, it needs dedicated care and curation to deliver its potential for discovery, insight, beauty, and wonder.

The NOW database as we know it today came to be through a confluence of several interlinked initiatives spanning multiple decades (Fig. 1). The structure of what would become NOW was originally cloned from the ETE database of the Smithsonian Institution and the first NOW version accessible over the Internet was in fact a node of the ETE database. The first public version of NOW database was released in 1996 and the first Advisory Board was established the year after. In many ways, the invitation letter sent to prospective members of the Advisory Board may be regarded as the founding document of the NOW database as an entity in the public realm. It was dated October 15, 1997 and signed "With our highest hopes and best wishes" by Mikael Fortelius, Ray Bernor, Hans de Bruijn, Sevket Sen, and Lars Werdelin. Apart from Hans, whom we sadly lost in 2021, all of these 'founding fathers' are still alive and active NOW participants today.

The first standalone, online version of NOW was launched in 2005 and the first formal steering group was established in 2009. Originally, NOW stood for Neogene of the Old World but with the gradual expansion of the database in space and time the acronym was eventually reassigned to stand for New and Old Worlds. During its existence, NOW has been funded, directly or indirectly, by several organizations but fundamentally it has always been an unfunded community effort, dependent on voluntary work by the participants. Paradoxically, this seemingly limiting circumstance may in fact have contributed to its long endurance and lasting vitality.

KEYWORDS: Fossil mammal; Species list; Stratigraphic age; Functional trait; Database.

ACKNOWLEDGMENTS

I thank each and all of my 27 coauthors of the NOW history chapter in the 25 years of NOW anniversary volume (Fortelius et al., in press) that this contribution relies on entirely.

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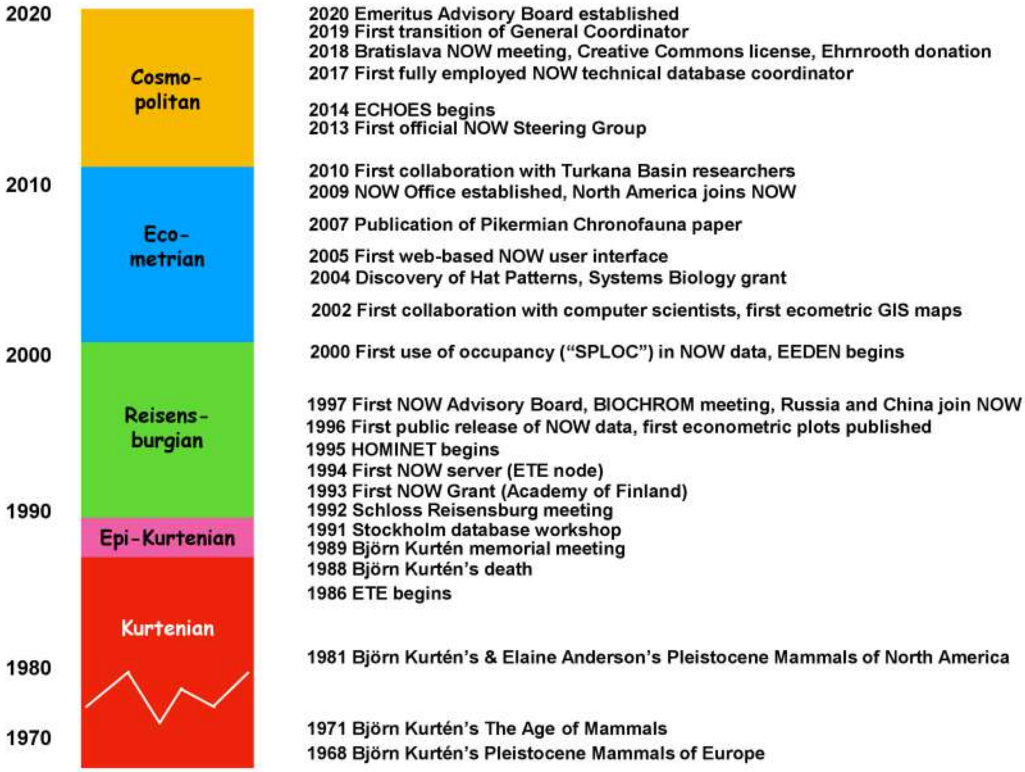

Figure 1. Timeline of the prehistory and history of the NOW database, showing the sequence and timing of key developments. The division into stratigraphic eras is heuristic and purely informal.

Teeth, limits and NOW: What can we expect from the Red Queen's perspective?

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ABSTRACT

How do we reason about living ecosystems through time from the fossil record? And how do we translate occurrences of fossil species into living ecosystems?

One of the main premises in geological research is that processes that operate today operated in the same way in the past, which allows us to reason scientifically about the current geological features and the past geological changes. At the same time a fundamental outcome of biological evolution is that ecosystems change. Thus, even if the change process is uniformitarian, the biological outcomes of this process may or may not be so.

Thus, we know that the present-day ecosystems present insufficient baselines for reasoning about the past. First, they present only a tiny fraction of the past diversity of life, even if we focus only on mammals. Moreover, patterns are often distorted due to excessive human activities on land. Thus, simply aligning structural patterns of mammalian communities today, such as how many species are expected to be found per locality, what body size distributions or predator to prey ratios can be expected in the past, does not quite work.

The NOW database (The NOW Community, 2022) reports a handful of Miocene localities from Africa and Europe that contain five or more genera of proboscideans, and even more localities that contain five or more genera of rhinoceroses, which is unimaginable in the ecosystems today. While wondering whether these animals could have lived at the same time and the same place and going through the NOW curatorial process, we often find that this is plausible, generalizing over such patterns without present-day baselines is challenging.

We can try to reason about the structure and completeness of fossil communities based on how the past ecosystems are expected to scale, which this talk is about. I will revisit metabolic scaling in relation to evolutionary theory. I will review the Red Queen hypothesis (Van Valen, 1973) and the associated evolutionary theory to connect them to scaling patterns known from macroecology (Brown, 2004) and outline expectations about the structure of the living mammalian communities from the perspective of energy acquisition and consumption, as well as expectations about the scaling of the dying and their fossilization processes.

I will illustrate the arguments with data analysis case studies of large herbivore communities from the NOW database as well as present-day observations, highlight the major empirical uncertainties and ways forward.

KEYWORDS: Red Queen hypothesis; Metabolic scaling; Mammalian fossil record; Large herbivores; NOW database.

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Eppelsheim—A key site for mammalian paleontology revisited

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ABSTRACT

The Eppelsheim fossil site is the type locality of the Eppelsheim Formation (Miocene). In current understanding, the latter comprises all sediments summarized under the historic term Dinotheriensande (Grimm et al., 2011). It consists of fluvial sediments, assignable to the so called 'Urrhein' that crossed the Mainz Basin during the Miocene and produced several famous historic mammal fossil sites.

Besides the eponymous *Deinotherium*, the Eppelsheim Formation yielded a diverse mammal fauna. In addition to many teeth and disarticulated bones of different large mammals, the first hominoid fossil find derives from Eppelsheim, found in 1835 (Franzen et al., 2003). Micromammals, in contrast, seem to be very rare; assumedly due to the sedimentologic and taphonomic conditions.

Despite the long scientific history, the temporal range represented by the sediments on the one hand and the faunal content on the other hand is still in debate. While sedimentary studies indicate a restricted time frame for fluvial sediments in single outcrops (comprising only a few thousand years or less), it is still not clear whether all sites can be correlated inside a narrow time frame and assigned to the Late Miocene, or that indeed some may at least contain also Middle Miocene fluvial deposits. The surprisingly rich, and unique record of Middle Miocene elements (e.g. *Prodeinotherium bavaricum*, *Heteroprox larteti*, *Dicrocerus elegans*) found in the same layers as Late Miocene representatives (e.g. *Hippotherium primigenium*, *Tapirus priscus*, *Aceratherium incisivum*) has been a matter of intense discussion for a long time: a more or less contemporaneous palaeocommunity at a Late Miocene Rhine River offering the last retreat for Middle Miocene taxa (e.g., von Königswald, 1929) or simply (and current state of understanding) a question of sedimentary reworking of older taxa (e.g. Klähn, 1929)?

Most of the fossils in the historic collections were discovered by chance during the time of sand mining for construction works. However, the sands were also excavated for their fossil content, ranging from professional fossil trade to more scientifically oriented collecting since the 19th century.

The scientific excavation at the Eppelsheim site, not only directed at retrieving fossils but also trying to capture the geologic framework, sedimentology and taphonomy, was initiated by the Senckenberg Gesellschaft für Naturkunde, Frankfurt in 1996. It then carried on as a joint venture with the Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz (nhm/LS). The current excavation is run by the nhm/LS in the scope of paleontologic field education for students. The combination of geoscientific and archaeological excavation techniques and field documentation aims at the best possible documentation and a comprehensive field education.

So far, three main fossil bearing layers could be identified in Eppelsheim, yielding a mixture of Middle and Late Miocene findings, with a clear dominance of the latter. The faunal list of mammals for the Eppelsheim site today consists of 37 taxa, including the first record of *Cainotherium* sp., a taxon that went extinct during the Middle Miocene. Twenty species were originally described from the site, making Eppelsheim their type locality (Table 1; data from The NOW Community, 2022, after Franzen et al., 2003).

KEYWORDS: Dinotheriensande; Miocene; Mainz Basin; Stratigraphy; Mammal biochronology.

ACKNOWLEDGMENTS

We thank the Bundesland Rheinland-Pfalz, the City of Mainz and of course the municipality of Eppelsheim for supporting our work in Eppelsheim, as well as the many students, technicians, and scientists, who have assisted in the excavations at Eppelsheim for so many years.

Table 1. Mammal faunal list for the fossil site Eppelsheim as reported in the NOW database (The NOW Community, 2022) with some additions after Franzen et al. (2003). *Cainotherium* added.

Order	Family	Species[1]
Artiodactyla	Bovidae	*Miotragocerus pannoniae*
Artiodactyla	Cervidae	*Amphiprox anocerus**
Artiodactyla	Cervidae	*Euprox dicranocerus**
Artiodactyla	Cervidae	*Euprox furcatus*
Artiodactyla	Tragulidae	*Dorcatherium naui**
Artiodactyla	Suidae	*Hippopotamodon antiquus**
Artiodactyla	Suidae	*Listriodon splendens*
Artiodactyla	Suidae	*Parachleuastochoerus steinheimensis*
Artiodactyla	Suidae	*Propotamochoerus palaeochoerus**
Artiodactyla	Cainotheriidae	*Cainotherium* sp.
Carnivora	Ailuridae	*Simocyon diaphorus**
Carnivora	Amphicyonidae	*Agnotherium antiquum**
Carnivora	Amphicyonidae	*Amphicyon major*
Carnivora	Felidae	*Machairodus aphanistus**
Carnivora	Felidae	*Promegantereon ogygia*
Carnivora	Hyaenidae	*Protictitherium crassum*
Carnivora	Mustelidae	*Limnonyx pontica*
Carnivora	Mustelidae	*Sivaonyx hessicus**
Eulipotyphla	Plesiosoricidae	*Plesiosorex roosi**
Eulipotyphla	Soricidae	*Crusafontina kormosi*
Eulipotyphla	Talpidae	*Talpa vallesensis*
Perissodactyla	Chalicotheriidae	*Chalicotherium goldfussi**
Perissodactyla	Equidae	*Hippotherium primigenium**
Perissodactyla	Rhinocerotidae	*Aceratherium incisivum**
Perissodactyla	Rhinocerotidae	*Brachypotherium goldfussi**
Perissodactyla	Rhinocerotidae	*Dicerorhinus steinheimensis*
Perissodactyla	Rhinocerotidae	*Dihoplus schleiermacheri**
Perissodactyla	Tapiridae	*Tapirus priscus**
Primates	Hominidae	cf. *Dryopithecus* sp.
Primates	incertae sedis	*Paidopithex rhenanus**
Primates	incertae sedis	*Semnopithecus eppelsheimensis**
Proboscidea	Deinotheriidae	*Deinotherium giganteum**
Proboscidea	Deinotheriidae	*Prodeinotherium bavaricum*
Proboscidea	Gomphotheriidae	*Gomphotherium angustidens*
Proboscidea	Gomphotheriidae	*Tetralophodon longirostris**
Rodentia	Castoridae	*Chalicomys jaegeri*
Rodentia	Castoridae	*Euroxenomys minutus*

[1] An asterisk denotes when Eppelsheim is the type locality.

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Updated Early Miocene biochronology of Anatolia

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ABSTRACT

Fossil small mammals, especially rodents, are known as a very useful tool for dating terrestrial sediments, biogeographical studies, and paleoenvironmental reconstructions. Anatolia, the Asian part of Turkey, is rich in small mammal localities, including many fossils from the Early Miocene. During that time period, Anatolia formed, with the Balkans, a bioprovince separated from western Europe, leading to correlation problems between the two areas. Therefore, creating a local zonation system was an important step to monitor faunal development in the region.

Ünay et al. (2003) constructed a preliminary zonation system of the Anatolian Neogene based on Muroidea, which are the best stratigraphic markers because of their rich and continuous record. This allowed them to provide accurate relative age estimates based on changes in the Anatolian rodent assemblages. For the correlation with the Mammal Neogene (MN) system, Ünay et al. (2003) took a straightforward approach, correlating the regional zones almost completely one on one to the MN units (Zone B = MN 1, Zone C = MN 2, etc.). However, MN units, as well as Anatolian local zones are biochronologic systems that are based on faunal content. As such, they can be diachronous in time, as has been shown for the MN system based on late Early and Middle Miocene sections in Western Europe (Van der Meulen et al., 2011).

Since 2003, several new localities have been discovered. A taxonomic description of the small mammal faunas of the new localities allows us to present an updated biostratigraphy and chronology of the Early Miocene of Anatolia. The new studies in the area focus on the correlation with the time scale using old radiometric and magnetostratigraphic studies (Krijgsman et al., 1996) combined with the new data from Gökler section, Belenyenice section, and Beydere 3 locality (Lüdecke et al., 2013; Bilgin et al., 2022). This implies that, if we follow the correlation to the MN units by Ünay et al. (2003), these units are clearly diachronic. This is in line with earlier studies, such as the assessment that the MN4 locality of Aliveri should be dated between 17.5 and 18 Ma.

KEYWORDS: Small mammals; Stratigraphy; Turkey.

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Late Miocene habitat changes in the same section at Alsótelekes and Rudabánya (NE Hungary)

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ABSTRACT

Among the European Miocene great ape sites, Rudabánya (N 48° 23’ 40”, E 20° 38’ 39”, 262 m a.s.l.) is one of the most exstensively studied locality systems and has yielded the hominoid *Rudapithecus* and the pliopithecoid *Anapithecus* (Bernor et al., 2005; Kordos, 2021). The open pit at Alsótelekes (N 48° 25’ 23”, E 20° 39’ 33”, 226 m) is close to Rudabánya. Primate remains, assigned to *Anapithecus* and probably a new species of *Rudapithecus*, were discovered in the lower swampy sediments (Kordos, 1977; Begun & Kelley, 2018).

At Alsótelekes the lower layers by erosional discordancy are covered by fluviatile-lacustrine layers without lignite. The sediments of the two localities were deposited only 3 km apart, in the same tectonic unit, in the pre-Pannonian depressions of the Rudabánya mountain range, at almost the same altitude. In both places, the lignite series is followed by lacustrine-fluvial sediments in clear discordant contact. In Rudabánya, the younger sediments of the lignite series were eroded and the crushed bones accumulated in the depressions of the karstic surface that formed at the same time. In Alsótelekes, the lower, lignite layers are separated from the upper lacustrine-fluviatile sediments by a fluviatile erosion surface. Paleomagnetic studies indicate a gap of about 2 Myr between the two lithostratigraphic units.

The faunal and plant fossil content of the lignite layers and the overlying lake-swamp layers is essentially the same. In the upper layers at Alsótelekes, anurans, birds, and different types of mammalian tracks have been found and are currently under study.

Three environmental and biotic changes likely forced by global and regional (related to Lake Pannon dynamics) events can be detected in the Rudabánya–Alsótelekes Late Miocene sediments. The environment corresponding to the lignite complex (10.5–10 Ma), rich in forest elements and animals and plants linked to water environments, shows a two-episode cycle. Later on, fluviatile erosion and karstification was high and occurred in a probably less forested, more open habitat between about 10 and 8 Ma. Plant remains of the upper fluviatile-lacustrine series as well as animal tracks indicate the presence of a temperate open

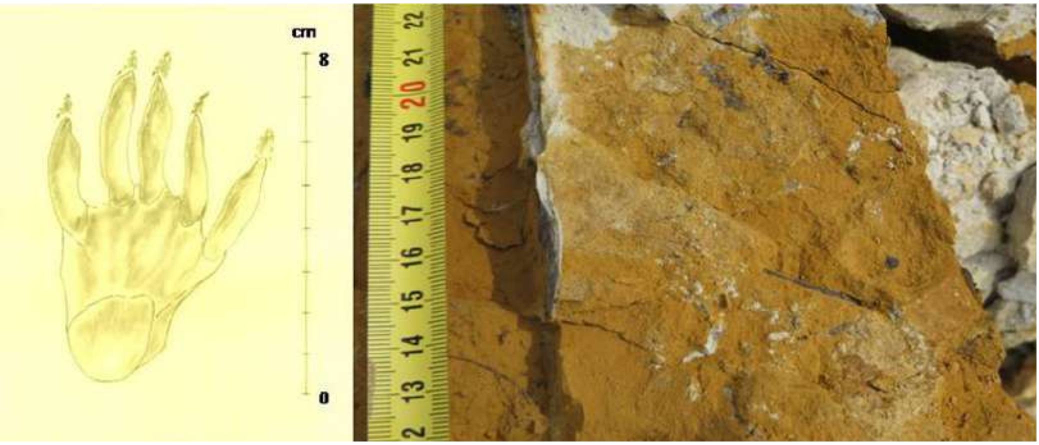

Figure 1. Original left hand track and its graphic interpretation of an enigmatic mammal trackmaker from the upper layers of Late Miocene sediments at Alsótelekes.

woodland periodically covered by water. These environmental changes can probably be correlated to the Vallesian/Turolian boundary.

KEYWORDS: Late Miocene; Rudabánya; Alsótelekes; Primates.

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The soricids (Eulipotyphla, Mammalia) of Gran Dolina (Early–Middle Pleistocene, N Spain): Systematics and biochronological implications

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ABSTRACT

Members of the family Soricidae (Eulipotyphla, Mammalia) are commonly retrieved from Pleistocene sites in Europe. On the Iberian Peninsula, soricids of the post-Jaramillo Early–Middle Pleistocene are mainly indeterminate species of *Sorex*, *Neomys*, and *Crocidura*. The identified species of the post-Jaramillo Early Pleistocene are *Dolinasorex glyphodon*, *Sorex minutus*, *Crocidura russula*, and *Crocidura kornfeldi*, while in the Middle Pleistocene the species are: *S. minutus*, *Sorex* gr. *araneus–coronatus*, *C. russula*, *C.* aff. *russula*, and *Crocidura suaveolens* (see references in Moya-Costa, 2020).

Gran Dolina (Burgos, Spain) is one of the cave infills in the karstic complex of Sierra de Atapuerca (Atapuerca Hill), with sediments dated as post-Jaramillo Early Pleistocene and Middle Pleistocene. The Sierra de Atapuerca is located in the north of the Iberian Peninsula.

We analyzed the soricid remains recovered from Gran Dolina in the field campaigns of 1991–2017. From this assemblage, we selected 200 fragmented mandibles coming from the Early and Middle Pleistocene levels of the site. These mandibles were identified after washing and sieving the sediments and picking/sorting the fossils. The analysis included taking images of all the mandibles in different orientations with a trinocular magnifier, measuring the specimens using tpsDig2, and describing and comparing the morphology and measurements to specimens of the rest of Europe (Moya-Costa, 2020). We performed univariate and bivariate diagrams and canonical variate analysis to refine the identifications using the software PAST v3.21 (Hammer et al., 2001)

Nine soricid taxa were identified in Gran Dolina. In the post-Jaramillo Early Pleistocene levels: *S. minutus*, *Sorex* gr. *runtonensis–subaraneus*, *Sorex* (*Drepanosorex*) gr. *margaritodon–savini*, *D. glyphodon*, *Asoriculus gibberodon*, *Neomys* cf. *newtoni*, and *C. kornfeldi*. In the Middle Pleistocene levels: *S. minutus*, *S.* gr. *runtonensis–subaraneus*, *Neomys* cf. *fodiens*, Neomyni cf. *Macroneomys*, and *C. kornfeldi* (Fig. 1).

The identification of this assemblage adds notably to the previously known biochronology and biogeography of the aforementioned taxa, contributing: (a) the first Iberian post-Jaramillo Early Pleistocene record of *S.* gr. *runtonensis–subaraneus*, *S.* (*D.*) gr. *margaritodon–savini*, *A. gibberodon*, and *N.* cf. *newtoni*; (b) the first and the last record of *S.* gr. *runtonensis–subaraneus* in the Middle Pleistocene of the Iberian Peninsula; (c) the second record of cf. *Macroneomys* in the Iberian Peninsula; (d) the first account of *N.* cf. *newtoni* in the Iberian Peninsula; (e) the youngest record of *A. gibberodon* in the world; and (f) the youngest record of *S.* (*D.*) *margaritodon–savini* in the Iberian Peninsula.

KEYWORDS: Morphology; Morphometry; Mandible; Post-Jaramillo; Soricidae.

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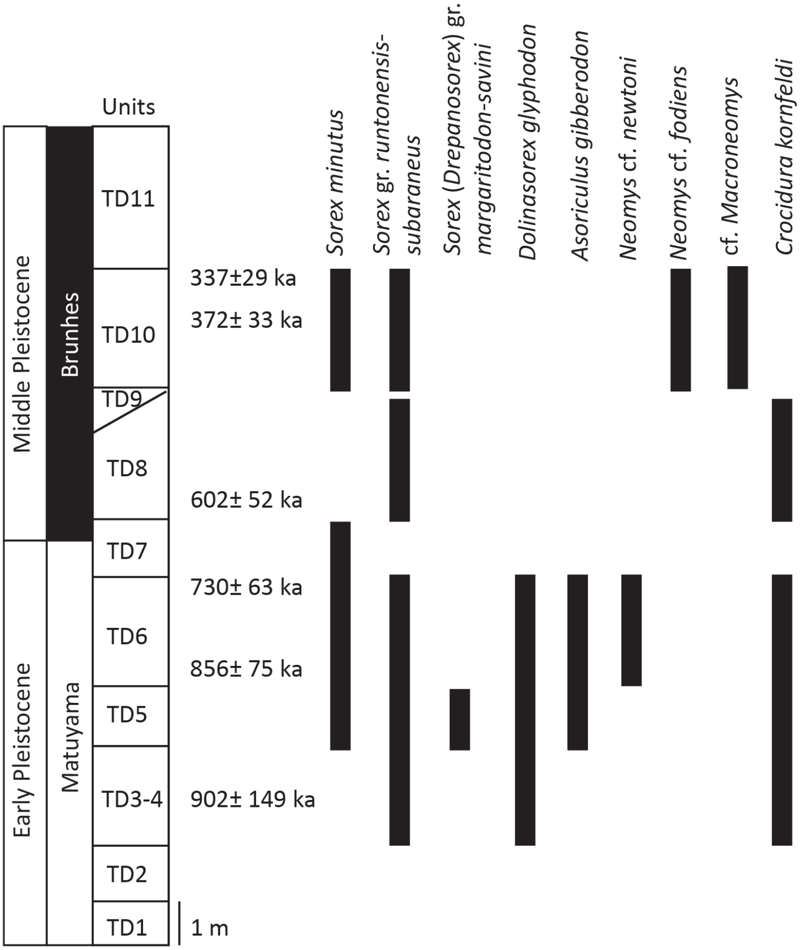

Figure 1. Distribution of the soricid species identified in the stratigraphic units of Gran Dolina. Dates summarized in Campaña et al. (2017) with additions of Álvarez-Posada et al. (2018).

La Piquera: A new early Ruscinian karstic site from central Spain

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ABSTRACT

In this work, we introduce the new vertebrate site of La Piquera (Duero Basin, central Iberian Peninsula) by presenting a preliminary faunal list. The faunal diversity and abundance of La Piquera is extraordinary. Among the material, there are representatives of urodeles (Salamandridae), anurans (Alytidae, Pelodytidae, Bufonidae), lizards (Agamidae, Lacertidae, Anguidae, Scincidae, Blanidae), snakes (Erycidae, Colubridae/Psammophiidae), artiodactyls (Bovidae), insectivores (Soricidae, Erinaceidae), bats (Vespertilionidae, Rhinolophidae, Megadermatidae), rodents (Cricetidae, Gerbillidae, Muridae, Gliridae, Sciuridae), and lagomorphs (Leporidae, Ochotonidae). The faunal assemblage suggests a basal, Early Pliocene age, lower part of the MN14 unit (early Ruscinian), with the presence of *Myosorex meini*, *Debruijnimys* sp., *Castillomys gracilis*, *Stephanomys dubari*, *Apodemus gorafensis*, *Paraethomys meini*, *Occitanomys alcalai*, *Apocricetus* cf. *barrierei*, and *Ruscinomys lasallei*, among others. The new locality has an intermediate biostratigraphic position between the sites of Sifón-413 (at about 5.33–5.23 Ma; Piñero & Agustí, 2019) and Botardo-D (4.79–4.63 Ma; Piñero & Agustí, 2020; Fig. 1). The ecological affinities of the identified small vertebrates suggest the presence of a landscape dominated by open herbaceous meadows in central Spain during the earliest Pliocene, with the occasional presence of woodland patches and stable water bodies under relatively dry and warm environmental conditions. La Piquera, therefore, enhances our knowledge on the association of fossil vertebrates recorded in the central Iberian Peninsula during the basal Pliocene. With more than 1200 remains, the La Piquera collection represents the richest sample of small vertebrates from the beginning of the Pliocene documented to date in the Iberian Peninsula. Thus, it becomes a key locality for the Early Pliocene of Southwestern Europe, in a region, central Spain, where this timespan is poorly represented (Luengo et al., 2009).

KEYWORDS: Duero Basin; Early Pliocene; Vertebrates; Biochronology; Paleoecology.

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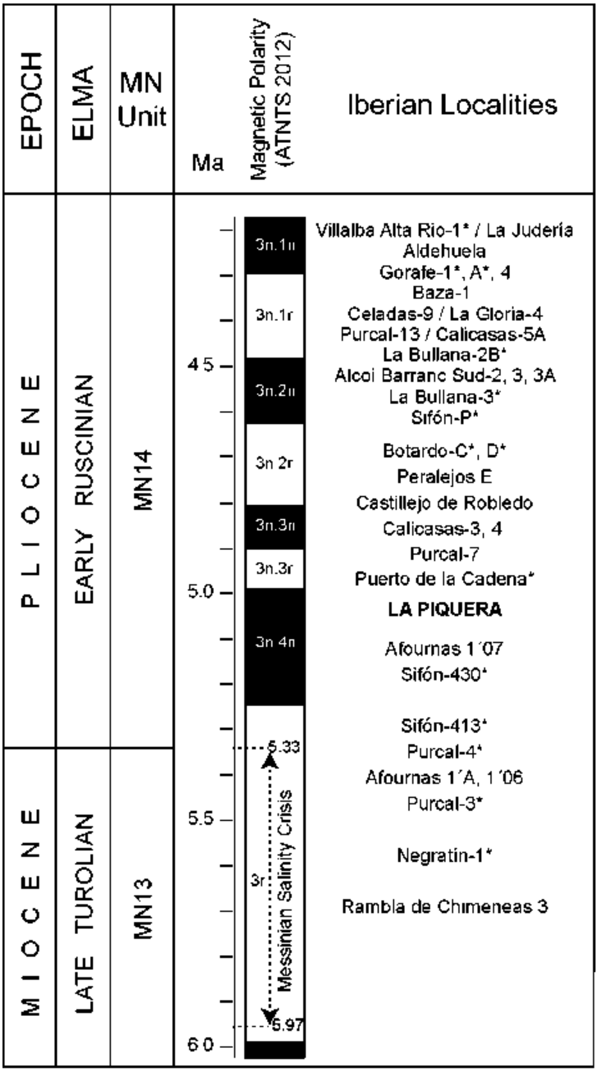

Figure 1. Biostratigraphic position of the La Piquera locality as compared to other Spanish sites. The localities marked with an asterisk are calibrated with paleomagnetic data. Abbreviations: ATNTS = Astronomically Tuned Neogene Time Scale; ELMA = European Land Mammal Ages; MN = Mammal Neogene.

Evolutionary history and dispersal of Holarctic ground squirrels (Rodentia, Xerinae, Marmotini)

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ABSTRACT

Holarctic ground squirrels (Marmotini) are the most diverse tribe of sciurids occurring in Eurasia and North America throughout arctic and temperate habitats, extending as far south as the tropics of southern China (Thorington et al., 2012). Extending back to the Oligocene, marmotins are also among the most ancient groups of living rodents with a rich fossil record and complicated evolutionary history (Black, 1963). Uncertainties over the phylogenetic status of extant forms and the lack of reliable osteological synapomorphies have all contributed to the tribe's status as a poorly defined repository for various fossil sciurids and sciurid-like taxa. In the last twenty years, molecular-based phylogenetic analyses have stabilized the extant members of the tribe, now known to comprise 13 living genera with about 97 species of marmots, prairie dogs, chipmunks, and rock squirrels (Thorington et al., 2012). However, the relationships between the extinct taxa, as well as the origin and biogeography of the clade, remain poorly understood while the fossil record insufficiently incorporated.

To address these problems, key Eurasian ground squirrel taxa were revised, with particular attention to cranial features. A series of phylogenetic analyses of 257 craniodental characters coded for 51 xerine taxa and 10 non-ground squirrel sciurids revealed monophyletic Xerinae clades Protoxerini (African tree squirrels), Xerini (African ground squirrels), and Marmotini (Holarctic ground squirrels) as successive sister taxa to tree squirrel clades Callosciurinae and Sciurinae (Sinitsa, 2018; Sinitsa et al., 2019, 2022). Several well substantiated phylogenetic relationships emerged from the analyses: (1) a monophyletic subtribal clade Sciurotamiina composed of the basal Oligo-Miocene ground squirrels *Palaeosciurus*, *Csakvaromys*, and *Protospermophilus*, together with living *Sciurotamias*, assumed a basal position; (2) the Holarctic genus *Miospermophilus* (including eastern Asian *Plesiosciurus*) and Eurasian *Sinotamias* are robustly grouped in a basal position with derived Holarctic ground squirrels, the Marmotina; (3) chipmunks, the subtribe Tamiina, are found nested within stem ground squirrels, as the sister to Sciurotamiina; and (4) the early Pleistocene European ground squirrel species traditionally attributed to *Urocitellus* are placed within *Spermophilus*.

Although the early ground squirrels, exemplified by the Paleogene species of *Palaeosciurus*, are first documented in western Europe at 32 Ma, the results of the biogeographic analysis suggest an early Oligocene dispersal event from North America to Eurasia, possibly via the North Atlantic Land Bridge. This major event was followed by at least two separate migration events via the Bering Land Bridge that occurred during the late Oligocene and the Early Miocene, and resulted in a sudden appearance of *Miospermophilus*, *Marmota*, and *Spermophilus* in the Eurasian fossil record (Sinitsa, 2018; Sinitsa et al., 2022). This result is consistent with current hypotheses of rodent, ungulate, and 'carnivoran' dispersals from the Nearctic to the Palearctic during these intervals.

KEYWORDS: Ground squirrels; Evolution; Phylogeny; Biogeography; Holarctic.

ACKNOWLEDGMENTS

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Enamel free areas, the key to unlock Arvicolinae taxonomy

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ABSTRACT

The fossil molars of voles (Arvicolinae) play an important role in the study of Plio-Pleistocene localities. They are excellent index fossils because of their high crown prismatic molars, which show a clear evolutionary trend in the increase in hypsodonty over time. However, it was only in the early 1980s when Rabeder (1981) came up with an effective way to quantify hypsodonty in rooted voles, based on the linea sinuosa. He defined indices based on measurements of the enamel free areas, demonstrating these can be used to distinguish species. However, the detailed description of arvicoline enamel free areas is often lacking, particularly in older literature. The importance of this method is well illustrated by the research history of the species *Mimomys hassiacus*, *Mimomys hajnackensis*, *Mimomys occitanus*, and *Mimomys stehlini*. They have all been recognized as separate species, but some authors synonymize some (e.g., Fejfar and Storch, 1990) or even all of them (Ruiz Bustos & Sesé, 1985; Ruiz Bustos, 1987). We used the method of Rabeder (1981) to distinguish various *Mimomys* species during the Pliocene. Particularly, we determined whether or not *M. hajnackensis* should be considered a synonym of *M. hassiacus*.

Apart from the length of the occlusal surface, the following measurements were taken: HSD = height of the hyposinuid; and HSLD = height of the hyposinulid. To compare the different arvicoline species, we calculated the HH-index = (HSD2 + HSLD2)1/2 (Rabeder, 1981), and correlated it with the maximum length of the occlusal surface. We measured the m1 of *M. hassiacus* from Afşar 2, Gundersheim 1 (holotype), and Hajnáčka; *M. stehlini* from Hajnáčka, Deutsch Altenburg DA20; *M. occitanus* from Sète; and *M. gracilis* from Afşar 2 and Escorihuela A. The measurements from *M. hassiacus* from Hambach, Tollo de Chiclana-1B; *M. hajnackensis* from Shirokino and Negavskaya; *M. stehlini* from Deutsch Altenburg DA9 and Tollo de Chiclana-13; *Mimomys gracilis* from Zverinogolovskoye; *Mimomys davakosi* from Çalta; and *Mimomys polonicus* from Kushkuna, were retrieved from the literature.

Our results show the presence of four main groups (Fig. 1). The first one includes the species with the lowest enamel free areas, *M. gracilis* and *M. occitanus*. The second group includes the species *M. hajnackensis* and *M. hassiacus*, including their holotypes from Hajnáčka and Gundersheim-1, respectively. Based on these results we support the decision of Fejfar and Storch (1990) to synonymize *M. hassiacus* with *M. hajnackensis* because, besides their morphological similarities, they overlap in the measurements. The paratype of *M. hassiacus* from Hajnáčka should be transferred to *M. stehlini*. In addition, we show that *M. hassiacus* from Hambach as well as *M. hajnackensis* from Negavksaya and Shirokino also belong to the *M. stehlini* group.

The NOW data on fossil voles are compiled in part from old literature. The method of Rabeder was not available before 1981, and it has not been followed by all later authors. Therefore, our study shows that these data need to be considered with caution.

KEYWORDS: HH-index; Rodentia; *Mimomys*; Linea sinuosa; Data validation.

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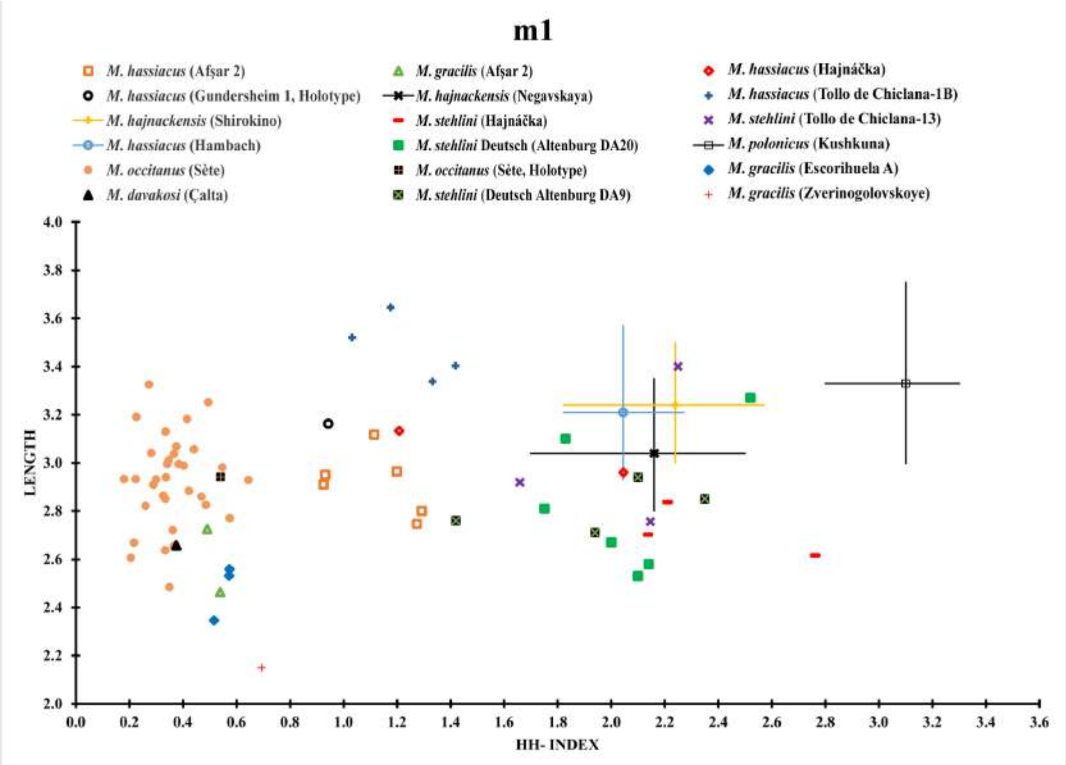

Figure 1. HH-index/L scatter plot of the m1 from *Mimomys hassiacus* (Afşar 2, Gundersheim 1, Hambach, Hajnáčka and Tollo de Chiclana-1B), *Mimomys hajnackensis* (Shirokino and Negavskaya), *Mimomys stehlini* from (Hajnáčka, Tollo de Chiclana-13, Deutsch Altenburg), *Mimomys occitanus* (Sète), *Mimomys gracilis* (Afşar 2 and Escorihuela A), *Mimomys davakosi* (Çalta), and *Mimomys polonicus* (Kushkuna). HH-index = hyposinuid-hyposinulid height (Rabeder, 1981); L = maximum length of the occlusal surface. For *M. hajnackensis* (Shirokino), *M. hassiacus* (Hambach), *M. hajnackensis* (Negavskaya), and *M. polonicus* (Kushkuna), mean, maximum, and minimum measurements are indicated instead. All measurements are in mm.

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Between local zones and MN units: A new inter-basinal rodent zonation for the late Neogene of Spain

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ABSTRACT

Since the appearance of the first major magnetostratigraphic studies covering the late Neogene of Spain (e.g., Opdyke et al., 1997; Garcés et al., 1998) the number of Spanish continental sections with a correlation to the Geomagnetic Time Scale has steadily grown. Nonetheless, well-calibrated sections with a dense record are still rare, between-basin biostratigraphic correlation is not straightforward, and ages of uncalibrated sites are poorly constrained. Given the overall similarity of rodent assemblages between Iberian basins during the interval MN11–MN17 (9–2 Ma), the definition of a system of Iberian rodent zones for this interval is a logical and necessary step leading to improved correlations. Our revision thus entails the integration of local biozonations into a single Iberian biostratigraphic framework. The inferred series of zone boundary ages are used to improve the age estimates for most Iberian micromammal sites.

The chronological backbone in our approach is formed by the available Iberian magnetochronologic records (Teruel, Cabriel, Júcar, Jumilla-La Celia, Fortuna and Guadix-Baza Basins). After analyzing similarities in taxonomic composition and turnover across basins with a defined biozonation (Teruel, Bajo Segura, Alcoy, Granada and Guadix-Baza Basins), 15 Iberian biozones were defined for the 9–2 Ma interval. Age uncertainty intervals for each boundary and for most Iberian micromammal sites were inferred using additional information on local sedimentation and/or evolutionary rates.

Among our results are new ages for the latest Tortonian and earliest Messinian (MN12–MN13 transition, 8–7 Ma), a thus far poorly dated interval on the Iberian Peninsula. The new chronology for this interval is based on the integrated stratigraphic records of the Jumilla-La Celia and Teruel Basins. Sections in the Jumilla-La Celia basin (eastern Betic Cordillera; Van Balen et al., 2015) were sampled paleomagnetically, further constraining the ages of various MN12-correlative sites (Van Dam et al., 2014). Finally, regular bedding patterns in sections near Concud in the Teruel Basin (eastern Central Spain) were interpreted cyclostratigraphically and used as a tool in addition to magnetostratigraphy for dating several classical and newly sampled MN12-correlative mammal sites in the area.

KEYWORDS: Neogene; Spain; Rodentia; Biostratigraphy; Geochronology.

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An updated range chart for the Oligocene to recent west Eurasian Suoidea. Variation in species richness

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ABSTRACT

The first intent to publish a complete range chart for the European Suoidea was over 30 years ago (Van der Made, 1990). There have been important advances in dating and many papers have dealt with the systematics, nomenclature, and temporal distribution of these Suoidea. Here, this information is united, and an update is presented. This range-chart also shows in a compact way the taxonomy and nomenclature as used in the NOW database.

The ages of the MN and MP units and a Spanish biozonation follow Hilgen et al. (2012) and Van Dam et al. (2006). Where the boundaries are drawn obliquely, this reflects the range of their uncertainty for the Spanish biozones, but only partially so for the MN units, because many of the criteria used for the correlation of the MN units are diachronic. In most cases, presence in a MN unit is marked as in the whole unit, while in other cases additional information (local biostratigraphy, magnetostratigraphy) shows a taxon to be present only in part of a MN unit. This is also the case when two chrono(sub)species of a lineage occur in the same biozone. These problems are dealt with as by Van der Made (2020). Localities in Anatolia are included (as also in the earlier range-chart), as well as from Kazakhstan and Israel, parts of west Eurasia that are not Europe.

The differences with the range chart from 1990 are shown in red (Fig. 1). A name written in red was not applied in 1990. A red line indicates that the species was not recognized as a distinct species. A red oblique line indicates a newly proposed ancestor-descendant relationship. Corrections to temporal ranges are not indicated. Most of these differences and those with publications of colleagues are discussed elsewhere (e.g., Van der Made, 2020).

In 1990, I followed Ginsburg (1974) for the Palaeochoeridae. Recently, many new names have been proposed for the Palaeochoeridae, but see the discussion by Van der Made (2020). There are two types of Oligocene Palaeochoeridae. *Doliochoerus* (=*Propalaeochoerus*) has narrow upper molars with convergent lingual roots and with the distal cusplet on the m1–m2 close to the hypoconid and includes *Doliochoerus leptodon* (=*Doliochoerus quercyi*) and its likely descendant *Doliochoerus elaverensis*, which has a longer third molar. *Palaeochoerus* has wide upper molars with divergent lingual roots that are connected with a bony plate and m1–m2 with the distal cusplet in the middle. It includes *Palaeochoerus aquensis* and its likely smaller descendant *Palaeochoerus typus*.

Whereas the range chart of 1990 had just over 40 species and subspecies, the updated one has over 60. The diversity is lower in the Oligocene than in the Middle Miocene, but the temporal ranges are longer. This could reflect the lesser density of fossils, a slower rate of evolution, or lower temperatures and atmospheric pCO_2. Species diversity parallels that of the Plio-Pleistocene, when temperatures and pCO_2 declined.

KEYWORDS: Range chart; Suoidea; Palaeochoeridae; Suidae; Biostratigraphy.

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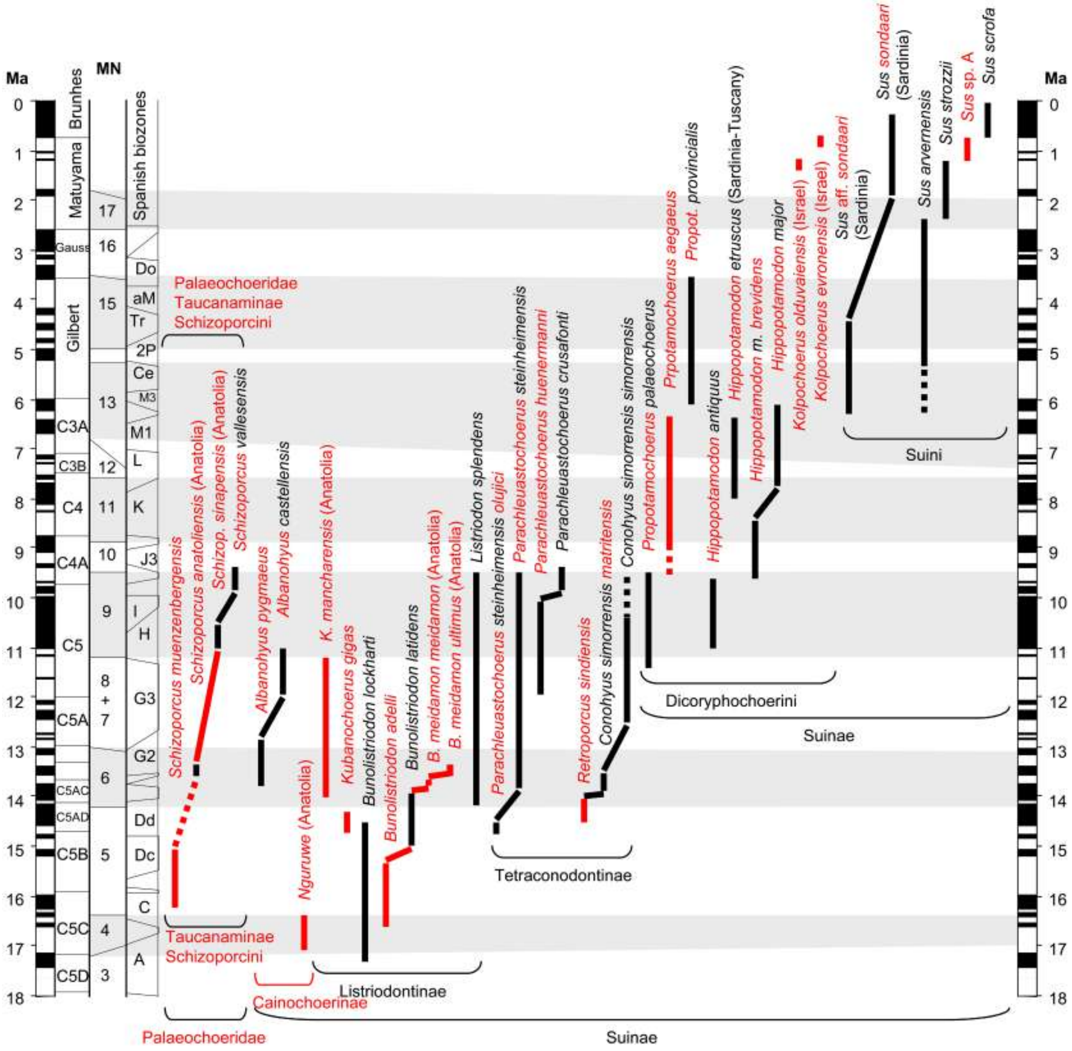

Figure 1. Range chart of the west Eurasian Suoidea.

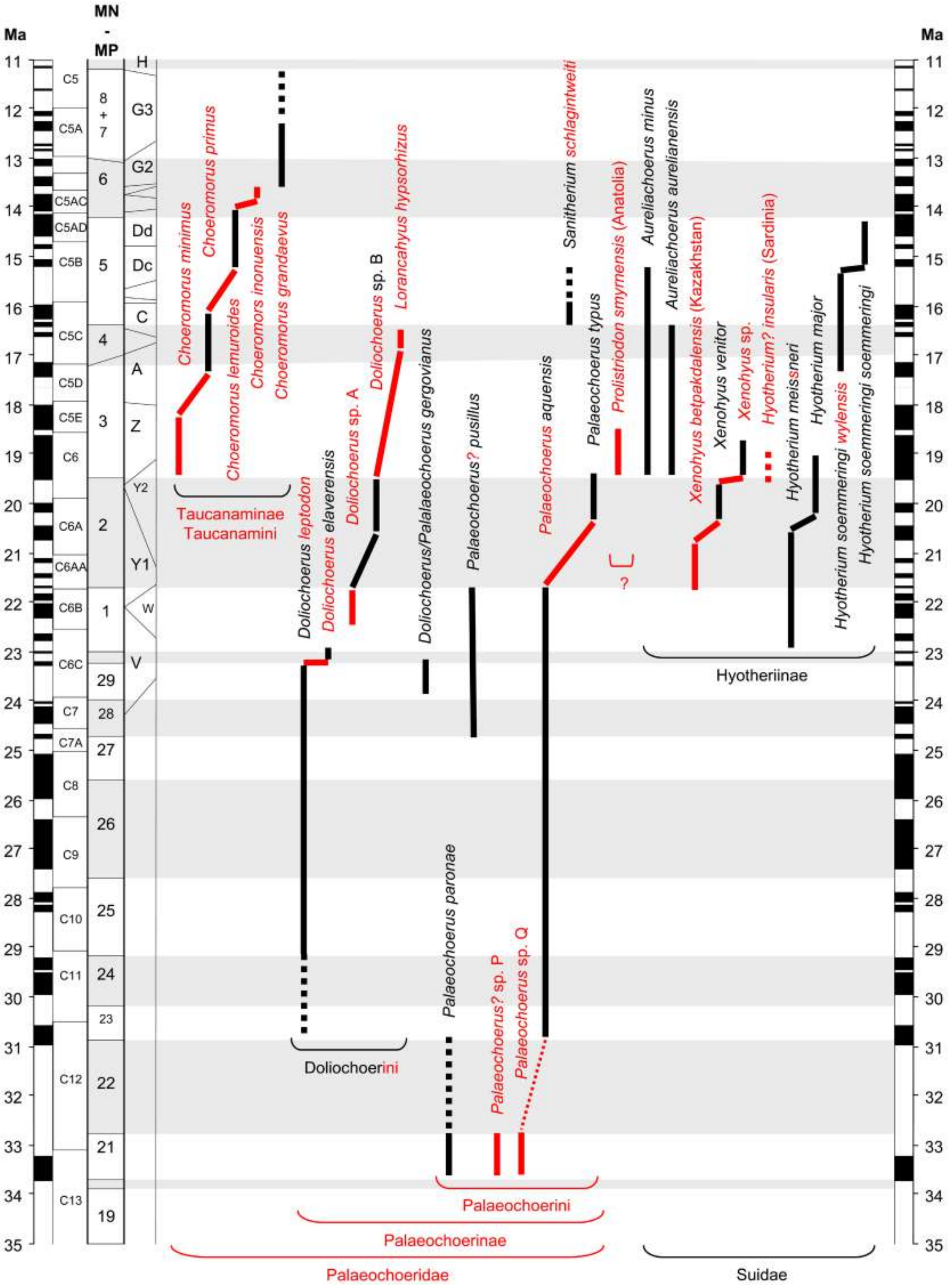

Figure 1 (Continuation). Range chart of the west Eurasian Suoidea.

Middle Eocene aridification drove a drop in Asian mammal biodiversity that preceded the Eocene–Oligocene Transition

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ABSTRACT

The Eocene–Oligocene Transition (EOT; 34 Ma) marks the onset of the icehouse world and is characterized by global cooling, growth of the Antarctic ice sheet, sea-level drop, aridification, and mammal turnovers. In Asia, previous studies have shown a transition from communities dominated by large-bodied perissodactyls to those dominated by smaller-bodied Glires (rodents and lagomorphs) better adapted to a dry environment with limited resources (Barbolini et al., 2020). However, more recent paleoenvironmental records show that drying was already occurring during the middle Eocene due to global cooling, the growing Tibetan Plateau, and the retreating inland Paratethys Sea. With fossil mammal occurrence records combined from the NOW database (The NOW Community, 2022), the Paleobiology Database (PBDB, 2022) and supplemented with data collected from the literature, we use a common sampling standardization technique (shareholder quorum subsampling, SQS; Alroy, 2010; Chao & Jost, 2012) to reconstruct the Paleogene evolution of mammal biodiversity across Central and East Asia. Our results show high total mammal species richness during the hothouse climate of the early and middle Eocene, followed by substantially lower diversity throughout the late Eocene and Oligocene. Although mammal communities became dominated by Glires in the aftermath of the EOT, sampling corrected species richness of Glires show a decrease concurrent to the one seen for total mammals, despite an increase in their raw abundance. This drop precedes the EOT. Sampling of mammal fossils from the Cenozoic of Asia is particularly uneven and may warrant further attention. Despite these limitations in the data, we suggest that the middle Eocene drying of the Asian interior may have affected levels of species diversity and set the stage for the subsequent mammal turnovers (Mongolian Remodeling and Grande Coupure) during the abrupt paleoenvironmental changes of the EOT.

KEYWORDS: Mammals; Diversity; Asia; Eocene-Oligocene Transition; Aridification.

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Old World Equidae dispersals, evolutionary radiations, and biogeographic extensions since 11.1 Ma

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ABSTRACT

Representatives of the family Equidae made three main biogeographic extensions from North America into Eurasia during the Early Miocene with the genus *Anchitherium*, at the beginning of the Late Miocene (MN9) with *Cormohipparion* (11.4–11.1 Ma), and at the beginning of the Pleistocene with the genus *Equus* (~2.58 Ma). In this contribution, we present the main biogeographic extensions and evolutionary radiations of the three (11.4 Ma) and one toed (2.58 Ma) equids into Eurasia and Africa. We correlate these dispersal events with paleoclimatic maps of critical time frames showing the paleoenvironmental changes and evolution in the Late Miocene, Pliocene, and Pleistocene. We report the most recent outcomes of Bernor et al. (2021) and Cirilli et al. (2022) on the subject matter for three and one toed equids, respectively.

Bernor et al. (2021) integrated nearly five decades study on the origin and evolutionary radiation of Old World hipparionin equids and their North American ancestors. *Cormohipparion* was the founding Old World population (Bernor et al., 2021, 2022). Within MN9, Eurasian hipparions diversified into *Hippotherium* and *Sivalhippus*. By the end of the Vallesian *Cremohipparion* and *Hipparion* s.s. appeared in Eurasia and *Sivalhippus* extended into Africa. The Turolian witnessed several speciation events in these lineages with MN12 recording dispersion of hipparions across Eurasia and Africa with the addition of new lineages *Eurygnathohippus*, *Plesiohipparion*, *Shanxihippus*, *Proboscidipparion*, and *Baryhipparion*. Hipparionins sharply declined during the early Pliocene and by the earliest Pleistocene were restricted to isolated populations in Europe. Yet, they persisted in China until 1 Ma, and even later in Africa.

Cirilli et al. (2022) reviewed the origin and evolution of *Equus* including Plio-Pleistocene fossil and living species from the Americas, Eurasia, and Africa, recognizing 114 valid species of fossil and living Equinae across this range. They showed that the decline of archaic Equinae lineages and the origin of *Equus* coincided with the expansion of more arid environments in North America, and the arid conditions which favored *Equus* dispersal in Eurasia did not occur before the Early Pleistocene. Currently *Equus* is clearly recognized as a single clade by both morphological and molecular phylogenetic analyses (Jonsson et al., 2014; Cirilli et al., 2021), including modern zebras, asses, and horses. At the present time, two main dispersal events of *Equus* from North America to Eurasia have been identified: an earlier biogeographic extension at ~2.58 Ma involving the North American *Equus simplicidens* which led to the evolution of the stenonine equids (including zebras and asses), and a later dispersal involving early representative of the caballine horses during the Middle Pleistocene. This last event has not been well documented. More studies on the morphology, alpha taxonomy, morphometrics, paleoecology, and phylogeny of Old and New World *Equus* are needed in particular to better understand the origin of extant *Equus* species.

KEYWORDS: Equids; Paleoecology; Evolution; Dispersal events.

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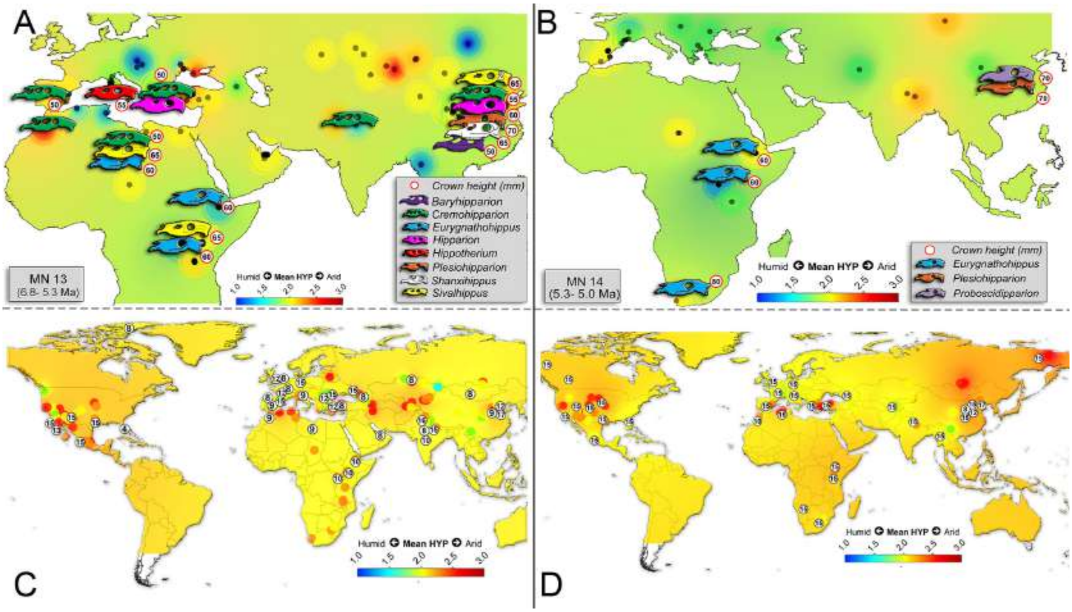

Figure 1. Mean hypsodonty maps (Bernor et al., 2021; Cirilli et al., 2022) showing the paleoclimatological conditions from most humid (blue) to most arid (red), representing the Old World hipparions diversity and the global *Equus* distribution during the Plio-Pleistocene: **A**, MN13; **B**, MN14; **C**, 4–2.5 Ma; **D**, 2.5–1.5 Ma.

Paleopathologies and bite marks: The last stand of the Miocene gymnure *Galerix stehlini* (Mammalia, Eulipotyphla)

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ABSTRACT

Ends are delicate times. The nature of fossilization and geological record make the recognition of ongoing extinction processes hard. The decline of a taxa is a priori identifiable through change in local abundance and comparisons of large datasets. Nevertheless, these ways are unsuitable in some particular cases and do not inform us about the process of decline itself. A clue may be found in the increased number of peculiar variabilities resulting from smaller populations.

Here, we report clinical cases of dental anomalies in fossils of Eulipotyphla, found in permanent dentitions belonging to the endemic gymnure *Galerix stehlini* from its type locality La Grive-Saint-Alban, fissure M (late Middle Miocene, France).

Several double-teeth anomalies are identified and attributed to a fusion process stricto sensu. The observed malformations are frequent in the rich material, suggesting developmental troubles in a significant percentage of the population.

In addition, we found a mandibular trauma on the inner flank of a mandible attributed to G. stehlini and interpreted as bite marks caused by the first upper incisors (I1) of an erinaceid. Comparative allometric data have been extracted from extant species to estimate the distance between I1 of fossils taxa based on several dental measurements. The only erinaceid from La Grive M whose size is coherent with our estimation is *Parasorex socialis*. The reconstruction based on these marks fit perfectly with the social behavior of modern-day gymnures (Gould, 1978). Such behavior is much more likely related to territorial competition rather than predation.

If we consider the distribution of the genus in the Middle Miocene (The NOW Community, 2022), it is clear that at the time of La Grive M, *Galerix* was already hardly surviving in Europe with only two representatives. *Galerix exilis* was cornered in the Iberian Peninsula during the late Middle Miocene, with the exception of a peculiar occurrence from the German locality of Hammerschmiede (*G.* cf. *exilis*) showing great dental variation (Prieto et al., 2011) and suggesting a reverse migration at the very end of its time distribution. *Galerix stehlini* is only known from La Grive-Saint-Alban, a site that preserved favorable environmental conditions and might have constituted a relict area for some Middle Miocene lineages. The developmental troubles occurring in *G. stehlini* are identified as a direct consequence of habitat fragmentation, increasing competition, constraining population size and reducing genetic viability in a way similar, although less brutal, to the insular introduction hypothesis of Brockie (1964).

In the current biodiversity crisis, conservationists point out the risks of habitat fragmentation and the resulting reduced gene flow. The record of *Galerix* indicates that these processes also played a role in the demise of species in the past; and it shows that, ultimately, it will lead to extinction.

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Siwalik rodent relative abundances and recognition of metacommunities

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ABSTRACT

Miocene small-mammal assemblages of the Indian Subcontinent display relatively high endemism (Flynn et al., 2020), and recovered fossil taxa represent local communities of the past. To overcome the difficulty of recognizing and defining past community structure, we have analyzed well-dated richer assemblages that sample relative abundances of species in paleocommunities. The composition of successive samples through time is stable, and the broad geographic species ranges throughout the northern Indian Subcontinent yield confidence that the assemblages of fossil elements we observe constitute metacommunities that approximate biological communities of the past. We recognize small-mammal metacommunities for the middle and late Miocene Siwaliks of the Potwar Plateau, Pakistan, that is, those observed in the Chinji, Nagri, and Dhok Pathan formations of the Potwar.

To avoid bias in interpretation due to samples that are small, we concentrate our study on single, richer, well-dated localities. Given demonstrable superposition of strata and long paleomagnetic sections, we are confident in their dating relative to one another to the precision of 10^5 years (Barry et al., 2013). Productive sites that are in sections have been assigned to 100 kyr time bins. We examined Middle to early Late Miocene age Siwalik microfaunas and recognized an *Antemus* metacommunity in the mid-Chinji Formation, which was replaced by a crown-murine metacommunity after about 12.5 Ma (Flynn et al., in press a). The *Antemus* metacommunity, rich in that genus, was replaced by a metacommunity heavily dominated by derived murines that represent the origins of extant murine tribes. The basal crown-murine metacommunity persisted to at least 10.1 Ma.

Here we extend this study in time, and now recognize a distinct subsequent metacommunity. Selected samples (Fig. 1) fall into the time bins of 9.4, 9.2, 8.7, 8.2, and 8.0 Ma. A few older, but poorly represented sites at 9.7 Ma probably pertain to the same metacommunity. This Late Miocene metacommunity is constrained at its younger end by different assemblages dated to 7.8 and 7.3 Ma. From about 9.7 Ma to 8.0 Ma, the microfauna remains dominated by murines, especially the abundant species *Karnimata darwini*. This *K. darwini* metacommunity also contains the mouse *Progonomys debruijni* and the abundant scratch-digger *Kanisamys sivalensis*. The less common burrower *Miorhizomys* occurs at many sites, but the gundi *Sayimys* is absent. A gerbil or hamster is found at some sites. A younger metacommunity beginning by 7.8 Ma is dominated by arvicanthine mice more derived than *Karnimata* (Flynn et al., in press b).

Successive Neogene small-mammal communities of the Indian Subcontinent were distinct from those of temperate Eurasia at higher latitudes. The Siwalik assemblages sampled on the Potwar Plateau show resilience through time as metacommunities, until replacement after 1 to 2 Myr, sometimes by new cohorts that differ at the family level. The timing of replacement and paleobiology of the taxa involved may provide clues to the paleoecological history of the Siwalik fauna and how its metacommunities interacted and responded to extrinsic physical forcing (Fortelius et al., 2014).

KEYWORDS: Siwaliks; Pakistan; Rodent; Metacommunity; Miocene.

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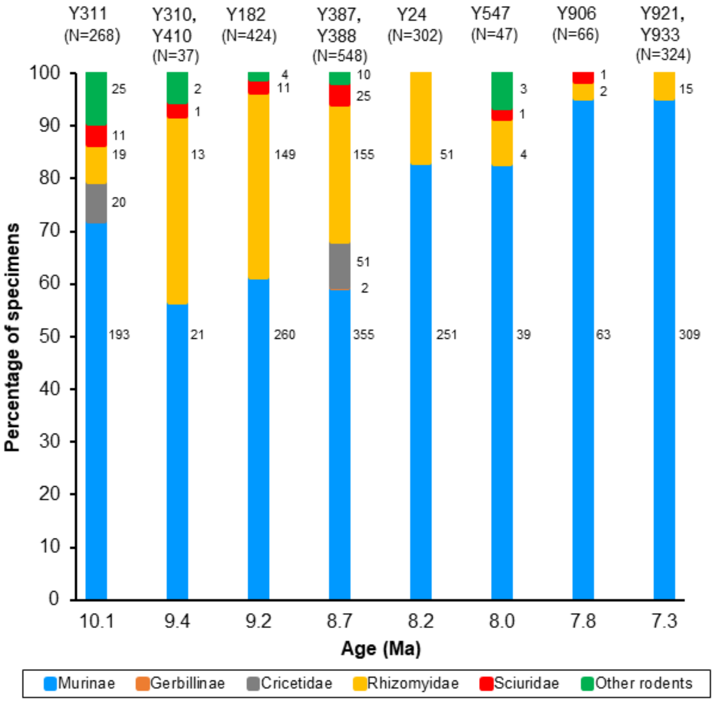

Figure 1. Relative abundances of major rodent groups in key Late Miocene deposits of the Potwar Siwaliks. Time bins (columns) are dominated by one or two fossil sites (top). The six rodent groups occur also in older deposits; small numbers are specimen counts. Bins 9.4–8.0 record the *Karnimata darwini* metacommunity.

Computational ecoregions in Asia in the present and the past

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ABSTRACT

Asia is one of the most complex zoogeographical regions in the world. Except for a north-south gradient (Palearctic-Oriental realms) along the southern rim of the Tibetan Plateau and its lateral extensions, a west-east gradient driven by the Asian monsoon is also prominent. Studying the evolution of ecoregions in this area is crucial to understand climatic changes and the topographic evolution of the Tibetan Plateau. However, there has been a shortage of studies on ecoregions in the geological past in this area.

We apply a recently developed data mining method called redescription (a hybrid of cluster analysis and regression; Galbrun et al., 2018) to investigate the associations between mammalian communities and the climatic contexts. The faunal community is analyzed using herbivore dental traits. Each herbivorous species is scored with 7 dental traits based on its tooth morphology. A faunal community can thus be described by mean values of the 7 dental traits of all herbivores that coexist in the fauna. Present day species occurrence data come from the list of the International Union for Conservation of Nature (IUCN, 2014). The mammalian fossil occurrence data for this study have been downloaded from the NOW database (The NOW Community, 2022). We include 19 standard climatic variables in our analysis, the present climatic variables come from WorldClim2 observations and paleoclimatic variables are derived from paleoclimatic models.

A total of 17 most accurate computational modern ecoregions (redescriptions) with dental traits and climate constraints were selected and investigated. Our two most accurate redescriptions capture the temperature gradients in East Asia, comparable with the Oriental and Palearctic realms. The third most accurate redescription captures the west-east precipitation gradient (monsoon pattern) in Asia and indicates that East China, India, and Southeast Asia differ from the Tibetan Plateau and the Xinjiang-Mongolia steppe by their higher precipitation.

The 17 computational modern ecoregions can be further clustered into five computational biomes that compare well with the map of established biomes (Olson et al., 2001). These are: the Tibetan montane grasslands and shrubland ecoregion; temperate broadleaf and mixed forests and temperate conifer forests in East China; temperate steppes in Xinjiang and Inner Mongolia; dry broadleaf forests in India; and tropical and subtropical moist broadleaf forests in Southeast Asia (including East and south India and the narrow band of forest along the southern slope of the Himalayas).

Neogene fossil data are analyzed from five intervals: Early Miocene, Middle Miocene, early Late Miocene, late Late Miocene, and Pliocene. We find that a north-south temperature gradient in Asia already existed in the beginning of Miocene. The boundary between the south and north realms shifted northward to higher latitudes during the Middle Miocene Climate Optimum, but retreated southward due to the Middle Miocene climate cooling (Flower and Kennett, 1994), and began to match the modern Palearctic-Oriental pattern. The east-west monsoon precipitation gradient emerged around the late Late Miocene when East China shifted from arid to humid conditions.

KEYWORDS: Redescription data mining; Ecometrics; Ecoregion; Asia; Neogene.

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The earliest ruminants from Western Europe, two different stories, two different Asiatic origins

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ABSTRACT

Ruminants are the clade comprising today's pronghorns, giraffes, deer, bovids, musk deer, and chevrotains. They are currently one of the most diverse groups of large mammals with more than 200 species. They colonized environments from rainforest to desert. Their deep time evolution is currently poorly known, even if environmental and geographical events associated with their unique physiology may have fostered this success. The oldest known ruminant is *Archaeomeryx optatus* from the middle Eocene of China. Asia hosted the first radiation of undisputable ruminants with four different families (including crown Ruminantia) already present during the late Eocene (Mennecart et al., 2021). In contrast, due to its geographical isolation, no ruminant is known until the beginning of the Oligocene in Western Europe. The discovery of new fossils and the reassessment of formerly known ones led to the description of the oldest European ruminant and two diachronic dispersal paths into Europe, with two different Asiatic origins.

Original and reinterpreted fossil specimens come from Bulgaria (NMNHS, Sofia, Bulgaria), Mongolia (MPC, Ulaanbaatar, Mongolia; NHMW, Vienna, Austria; AMNH, New York, USA), China (IVPP, Beijing, China), and Serbia (this specimen being lost and based on an illustration; Mennecart et al. 2018a).

The oldest Western European ruminants belong to the Gelocidae and the Lophiomerycidae (aka *Lophiomeryx*). They arrived as guild members of the Grande Coupure 33.9 Ma. In relation to the Terminal Eocene Event (TEE), the glaciation of the South Pole led to a sea level drop forming new land bridges between Asia and Europe. The species *Lophiomeryx angarae* is well known in Central Asia (Mongolia) during the late Eocene. Direct relationships are supposed between the Mongolian *Lophiomeryx* and the European ones. However, other *Lophiomeryx* species are mentioned in the late Eocene deposits from Southeastern Asia. The reassessment of these specimens led to the conclusion that no *Lophiomeryx* is known in this area during the Eocene and that two different Asiatic paleobioprovinces may be already distinguished during the late Eocene (Mennecart et al. 2021). The reattribution of *Lophiomeryx*? *gracilis* to the tragulid *Iberomeryx miaoi* led to the description of the oldest known crown Ruminantia (36 Ma). Similarly to the genus *Bachitherium*, *Iberomeryx* is known in Western Europe starting from ~31 Ma. Nevertheless, two *Bachitherium* mandibles have been described from the late Eocene of the Balkans (Mennecart et al., 2018a, 2018b). The description of this oldest known European ruminant (*Bachitherium thraciensis*), associated to a specific micromammal fauna, supposed the occurrence of an isolated Balkano-Anatolian faunistic province from the late Eocene until 31 Ma (Mennecart et al., 2018a), further confirmed by tectonic data (Licht et al., 2022). *Iberomeryx* and *Bachitherium* could reach Western Europe once the closure of the Tethys was accomplished through the Alpine orogeny ~31 Ma, a faunal event known as the "*Bachitherium* dispersal event" (Mennecart et al., 2018b).

The early colonization of Western Europe by ruminants has been achieved by two successive dispersal waves (Grande Coupure vs. *Bachitherium* dispersal event) of different tectonic (TEE vs. Tethys closure) and location (Central vs. Southeastern Asia) origins (Fig. 1).

KEYWORDS: Paleobiogeography; Eocene–Oligocene transition; Grande Coupure; *Bachitherium* dispersal event.

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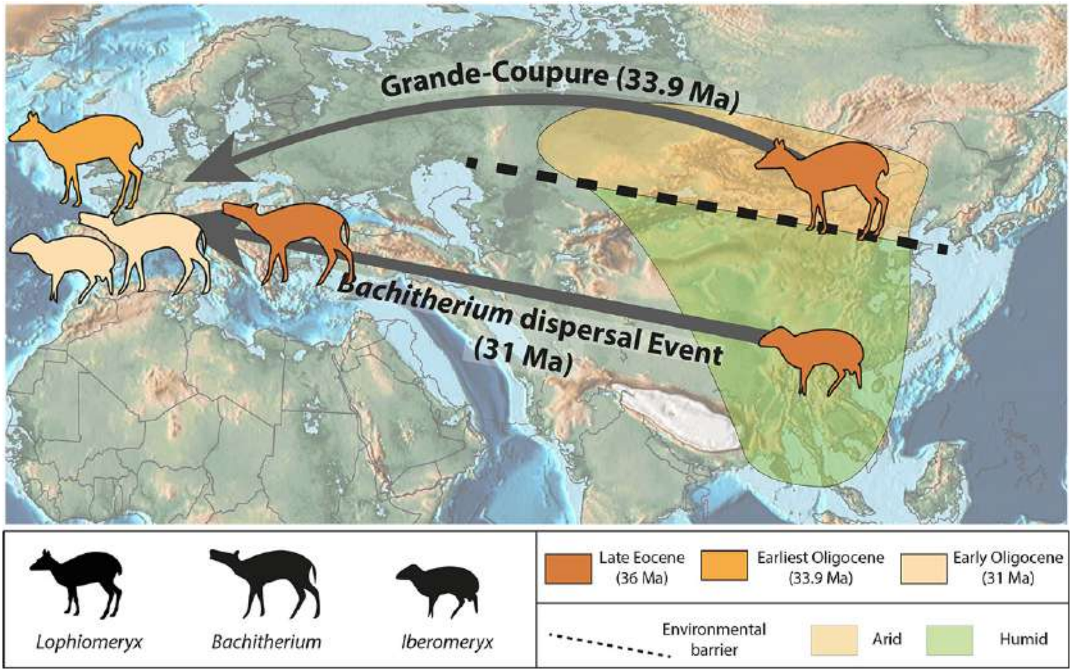

Figure 1. Paleobiogeography of the Eocene and early Oligocene *Lophiomeryx*, *Bachitherium*, and *Iberomeryx* with associated faunal event (modified after Mennecart et al., 2021). The palinspastic map is modified from Scotese (2014).

An assessment of heterogeneity in hominin paleoecology through hypsodonty of mammalian communities

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ABSTRACT

We investigate how mean ordinated hypsodonty of large plant-eating mammals can be used to cross-compare paleoenvironments occupied by *Homo* species in the Early Pleistocene. In conducting a survey of early Pleistocene hominin environments it became clear that descriptions of paleovegetation are often context-dependent and specific to the study locality or time period. Meaningful comparison of paleoenvironmental reconstructions across sites or regions requires that reconstructions are converted into a 'common currency', to standardize descriptions of vegetation, or other paleoenvironmental variables. As the first step towards such descriptions, here we use the mean ordinated hypsodonty of large plant-eating mammals from the NOW database (The NOW Community, 2022) to investigate the environmental variability within and between the regions occupied by *Homo* during the Early Pleistocene. We particularly focus on whether hominin environments varied more outside than within Africa.

We use the mean ordinated hypsodonty of large mammal communities as this is a proxy for environmental aridity (Fortelius et al., 2002). Hypsodonty is a measure of tooth height and is an evolutionary response to increased dental wear. The increased wear associated with hypsodonty arises from several interrelated factors such as the proportion of grass in the food ingested, the occlusal pressure required to break the plant tissues, and the dust load on the vegetation. The higher the mean hypsodonty of an herbivore community, the more open, grass-dominated, and seasonal the environment tends to be (Fortelius et al., 2002; Liu et al., 2012; Žliobaitė et al., 2016). Our preliminary results show that the variance of mean hypsodonty across sites occupied by early *Homo* increased out of Africa, with the highest variance displayed in Asia. This supports the burgeoning hypothesis that *Homo* in this period was not constrained to the environmental limits of its African niche but was increasingly able to exploit a wider range of environments.

We plan to cross-compare these findings with data collected by some of us and use the analysis to develop a 'common currency' which can aid in the explicit comparison of diverse paleoenvironments. This would allow application of the hypsodonty data published in the NOW database (The NOW Community, 2022) to answer not only this specific question but other macroevolutionary questions requiring the application of paleontological data to characterize environmental heterogeneity across multiple locations.

KEYWORDS: Hypsodonty; Paleoecology; Hominin; Paleovegetation.

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Asymmetry of evolutionary patterns between Old World and New World equids

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ABSTRACT

Equids (family Equidae) were originally a North American radiation. The subfamily Equinae contains hypsodont forms, with mixed feeding and grazing diets. Equinae first appeared in North America ~17.5 Ma with three subfamilies: Equini (9–11 genera, ~45 species), Hipparionini (New World: 6 genera, ~37 species), and Protohippini (4 genera, 15 species). Hipparionins migrated to the Old World by ~11 Ma (10 genera, ~60 species), and equins (the extant genus *Equus*) at 2.58 Ma (Cantalapiedra et al., 2017; Bernor et al., 2021). Only the Equini survived past the Early Pleistocene, and became extinct in the New World at the end of the epoch. Members of the subfamily Anchitheriinae (brachydont browsers) were also present in the Middle to early Late Miocene of New and Old Worlds. Equini differed from other Equinae in: the tendency to evolve monodactyly, cheek teeth with more simple occlusal relief, the lack of dwarf lineages, and in general were morphologically more robust and less diverse than hipparions, and less species diverse until the Pleistocene (MacFadden, 1992).

While equids were a prominent component in all Miocene faunas, they had different patterns of locality occupancy in New World (=NW) and Old World (=OW) regions. Using the NOW database, I counted the number of equid species in individual localities through the Neogene and early Pleistocene (Fig. 1), creating seven time bins (each ~2.5–3 Ma) that broadly correlate across North American Land Mammal Ages and Old World Neogene Mammal Zones (Hilgen et al., 2012).

Figure 1 compares the most species-dense areas in NW and OW. In the late Early and Middle Miocene there was an average of five species in NW localities (Anchitheriinae and three tribes of Equinae), with only 1–2 Anchitheriinae in OW localities. By the early Late Miocene hipparionins were in the OW localities: there was a similar diversity of species in both regions (34 NW, 26 OW) but OW localities averaged only 1.7 species (comprising 17% of the ungulate fauna) while NW localities averaged 5.5 species (44% of the fauna). This disparate pattern continued, with slightly lower numbers in NW localities, through the later Miocene. Only in the Pliocene were the numbers similar (1–2 species in all localities), although in the NW equids still comprised a greater percentage of the fauna. Species of the tribe Equini were never numerous, rarely more than one per locality.

As the climate cooled through the later Neogene, equids became less species diverse but still maintained a higher locality occupancy in the NW. This difference may relate to equids being the original incumbents in North America, or to a difference in competition among ungulates in the faunas: NW equids had camelids as likely competitors (which were never highly numerous in localities), while OW ones had bovids (which were usually twice as numerous as the equids). Interestingly, species of the tribe Equini were never common, and only became species diverse with the genus Equus in the Pleistocene. The predominant equids in both NW and OW Miocene faunas were the hipparions.

KEYWORDS: Equidae; Neogene; Locality occupancy; Equini; Hipparionini.

ACKNOWLEDGMENTS

I thank Ray Bernor for advice on hipparion taxonomy; Jussi Eronen for providing the NOW database Excel files; and Nuria Melisa Morales-García (www.sciencegraphicdesign.com) for the artwork. Also thanks to many personal friends among the species *Equus caballus* over the years (despite its success being overrated).

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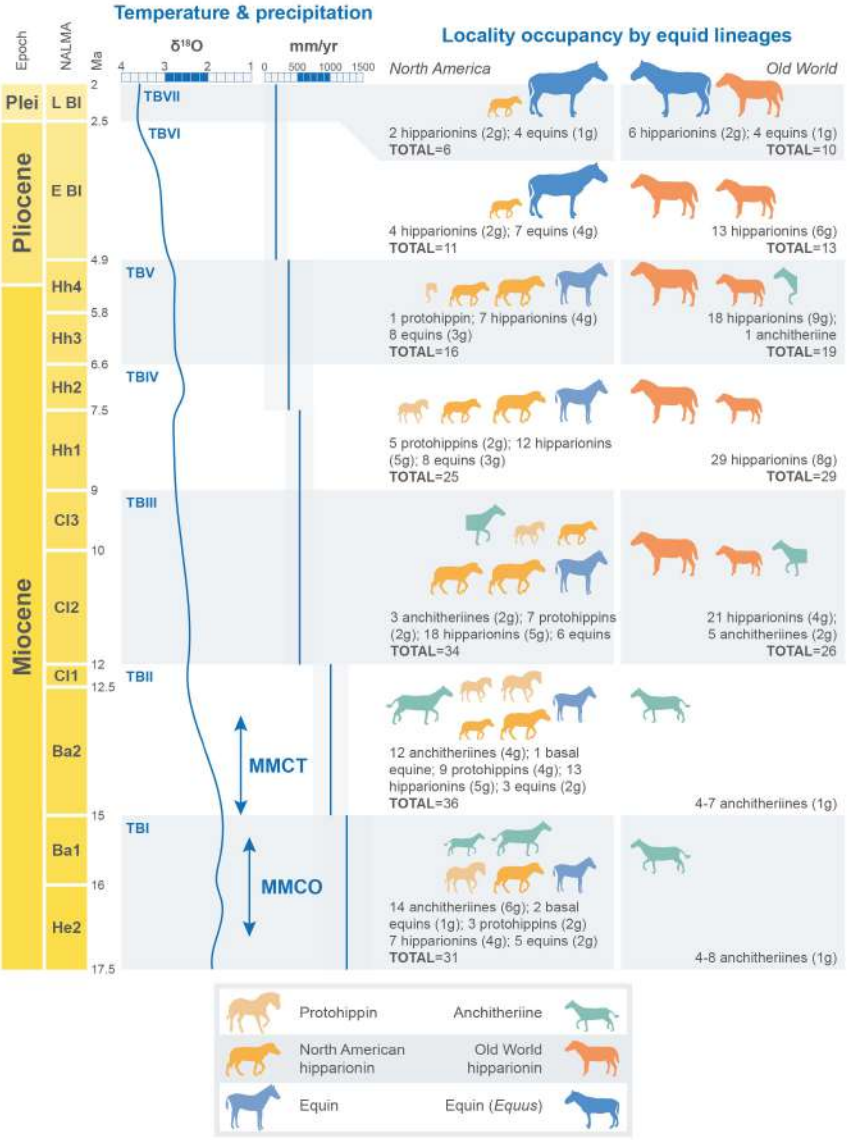

Figure 1. Locality occupancy by equid species in the most species dense areas in the New World (North American Central Great Plains) versus the Old World (Southern Europe/Western Asia—Greece, Iran and Turkey). Abbreviations: MMCO = Middle Miocene Climatic Optimum; MMCT = Middle Miocene Climatic Transition.

Elephants and environments—new developments in understanding the evolution and ecometrics of Proboscidea during the Cenozoic

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ABSTRACT

Proboscideans have been the largest terrestrial herbivorous mammals in most parts of the world during the Neogene, and in Africa during much of the Paleogene as well. Being large, they are typically relatively non-selective feeders and they respond to and interact with local vegetation structure in a profound way. Thus, it can be hypothesized that ecometric traits and dietary variation within proboscidean paleocommunities provide a signal of vegetation type and potentially other environmental and climatic properties of past environments.

Large datasets of proboscidean dental traits, mesowear angle data and postcranial bone measurements (for developing body mass estimation methods) were collected from various publications (Saarinen et al., 2015; Saarinen and Lister, 2016; Cantalapiedra et al., 2021; Huang et al., in press) to analyze how these ecometric and paleoecological aspects are related to paleoenvironmental proxy data obtained from literature (stable isotopes, dust accumulation, and paleobotanical proxies). Based on such analyses the hypothesis that proboscidean dental traits, diet, and body size can be used for estimating paleoenvironmental and paleoclimatic variables (especially vegetation type and precipitation) are tested.

According to mesowear angle analyses, the dietary signal of fossil proboscidean communities broadly reflects the estimated proportion of grass in associated fossil plant assemblages (Saarinen and Lister, 2016). Key dental functional adaptations (e. g., increase in hypsodonty and horizodonty) are more clearly associated with overall increase in the aridity of climate (and dust accumulation) during the Neogene in East Africa than with the shift from browse-dominated to grass-dominated diet. However, increasing length of exposed enamel ridges on worn molar surface seems to be primarily an adaptation for grazing.

New dental measurement-based body mass estimates allow us to analyze spatial differences in proboscidean body size at a population-level, opening the possibility to explore how variation in proboscidean body size is related to climate and vegetation. The evolution of proboscidean body size during the Neogene followed changes in global temperature, suggesting that phases of "harsh" (cold or dry) and seasonal climate favored large body size in proboscideans in Europe and Africa during the Neogene (Huang et al., in press).

KEYWORDS: Proboscidea; Mesowear; Dental ecometrics; Body size; Vegetation; Climate.

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Climate and habitat changes drove mammal community evolution through the Cenozoic of Oregon: Comparing community structures to paleoclimate data

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ABSTRACT

The John Day and Crooked River Basins of Oregon are well known for having an incredible record of Cenozoic life. That detailed, well-dated sequence of rocks and fossils documents evolution in floras and faunas in North America through approximately 50 Myr of time, most of the Cenozoic (Albright et al., 2008). Stratigraphic studies and more than 30 dated tuffs and lava flows provide a detailed chronology of events through time (e. g., Albright et al., 2008; Maguire et al., 2018). Paleosol data (Retallack, 2007), paleobotanical records (e.g., Dillhoff et al., 2009), and recent ecometric analysis of mammal teeth using data from the NOW database (Schap et al., 2021) provide independent evidence of climate and habitat changes through the sequence. Data from these proxies reveal a trend of cooling and increased aridity starting in the early Oligocene, at the same time habitats in the region became more open. Independent lines of evidence document warmer and more humid conditions during the Middle Miocene Climatic Optimum, a global event that may be attributable to volcanic activity in the region (Columbia River Flood Basalts).

These records of environmental change allow for detailed study of floras and faunas in Oregon, including the well-known record of fossil mammals spanning from the middle Eocene to the Late Miocene. Although assemblages vary in completeness, the John Day and Crooked River Basins include mammals from every North American Land Mammal age from the Uintan to Hemphillian, except the Clarendonian. Here, we use community structure analysis to examine the evolution of faunas in Oregon. For each of the 18 assemblages, mammal taxa (total 284) were coded into tooth crown height and locomotor categories using data from the NOW database. Our analysis included 8 mammalian orders (Rodentia, Lagomorpha, Primates, Carnivora, Creodonta, Artiodactyla, Perissodactyla, and Proboscidea) that represent the vast majority of species within these assemblages. Relative abundances of attributes were studied across assemblages and compared to records of paleoclimate and habitat conditions derived from paleosols, floras, and ecometric analyses.

Results document changes in structure of mammal communities that correspond to the timing of climate and habitat changes. Proportions of brachydont, mesodont, hypsodont, and cursorial mammals within assemblages show significant correlations with paleosol and ecometric estimates of annual precipitation and mean annual temperature. Following the Eocene–Oligocene transition, smaller herbivore communities (rodents and lagomorphs) shifted to be dominated by taxa with higher-crowned teeth, and the earliest cursorial rabbits and burrowing rodents appeared. In the late Oligocene and Early Miocene, high-crowned and cursorial ungulates appeared, as did running-adapted carnivorans and saltatory rodents. Open habitat specialists became more common through the Oligocene and Early Miocene, while forest dependent groups declined. In the early and Middle Miocene, low-crowned herbivores and arboreal mammals were still common, but open habitat specialist cursorial ungulates and burrowing rodents diversified greatly. In Late Miocene assemblages, both large and small herbivorous mammals were predominantly high-crowned taxa, similar to mammals inhabiting the Columbia Plateau today. Overall, the detailed record Oregon reveals dynamic relationships between climate, geology, and mammal communities.

KEYWORDS: Faunal Evolution; Hypsodonty; Locomotion; Eocene–Oligocene Transition; Middle Miocene Climatic Optimum.

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The life history of proboscidean functional diversity

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ABSTRACT

Large herbivores, and specifically megaherbivores (>1,000 kg), are keystone elements across Cenozoic terrestrial ecosystems. As a landmark example of megaherbivory, the study of the proboscidean fossil record poses a unique opportunity to frame the tempo and magnitude of recent megafauna extinctions against long-term macroevolutionary patterns. To test this, we attempted to reconstruct the entire proboscidean fossil history using a model-based approach. Our aim is to capture the evolutionary patterns behind the rise and demise of functional diversity (FD) of proboscideans over time.

First, we gathered a species-level occurrence dataset for proboscideans drawn from the literature, the New and Old World database (NOW), and the Paleobiology Database (PBDB). A total of 16 discrete functional traits were considered to quantify morphologies with a clear role in the interactions of each species with its environment. These include aspects like breadth of dietary preference and feeding envelope, food processing, energy requirements, home range size, social grouping, sexual selection, and locomotion. We collected information for these traits from the literature, direct observations, and the NOW database. The final dataset includes 2,130 occurrences for 185 proboscidean species, the greater proportion of which comes from the NOW database (1,427 records and 129 species). Based on these traits, and through nonmetric multidimensional scaling (NMDS) analysis, we condensed the proboscidean ecomorphological variation through a two-dimensional functional morphospace (Fig. 1A). We then reconstructed the global and continental diversification trajectories of proboscideans based on occurrence data (Silvestro et al., 2019) and used multidimensional phylogenetic models (Clavel, 2015) to assess the mode of evolution of lineages across the above-mentioned functional space.

The resulting functional space yielded eight proboscidean functional types (PFTs; Fig. 1B; Cantalapiedra et al., 2021), each representing a cluster of ecomorphologically similar species, and thus experiencing similar evolutionary pressures. During the first half of their history, until some 30 Ma, proboscideans were restricted to Afro-Arabia. Once proboscideans spread through Eurasia and the Americas, there was an increase in global diversity combined with niche partitioning in sympatric proboscidean species together with high speciation rates (Tassy, 1990). The first extinction episode took place at the Late Miocene (~7 Ma). Importantly, this and subsequent extinction peaks are intimately linked with specific ecomorphological configurations (Fig. 1C) and occurred simultaneously with specific paleoclimatic dynamics. Despite these extinction events, the initial demise of proboscidean diversity does not represent a case of lineage senescence: large branches of the proboscidean tree of life vanished long before proboscideans exhausted their evolutionary potential. The worldwide loss of proboscidean species began escalating from 3 Ma with further extinctions in Eurasia, and then a dramatic increase in Africa extinctions at 2.4 Ma. Overhunting by humans may have served as a final double jeopardy in the Late Pleistocene, following climate-triggered extinction trends that began long before hominins evolved suitable hunting capabilities (Faith et al., 2018; Fig. 1D).

KEYWORDS: Proboscidea; Functional groups; Diversification; Ecomorphology.

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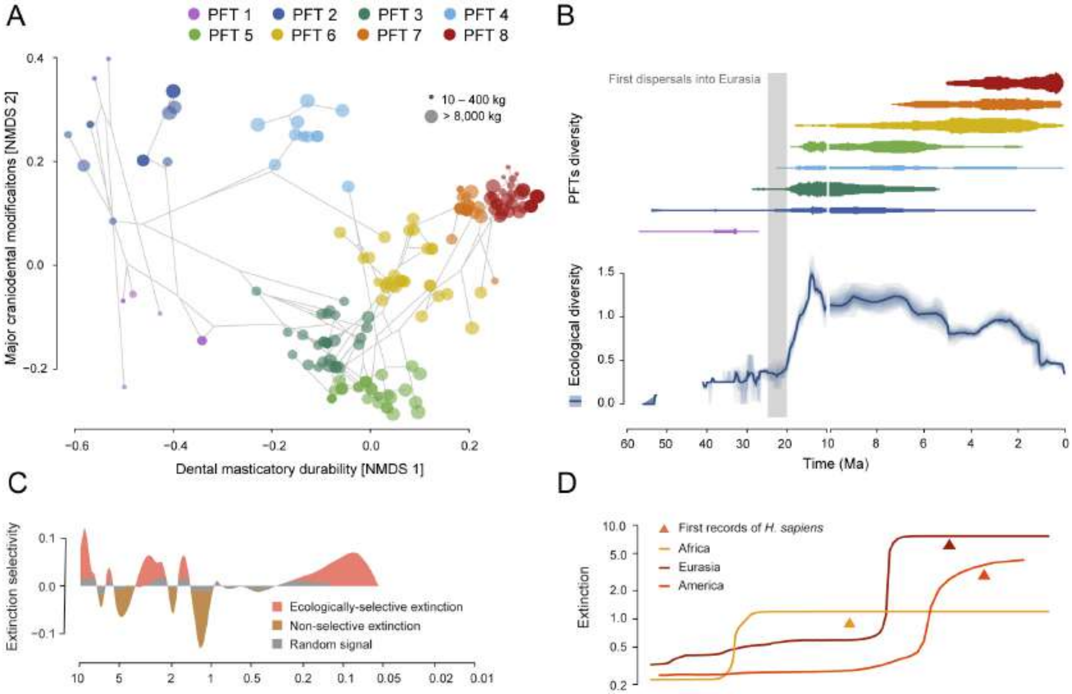

Figure 1. Ecological diversity and diversification in proboscideans. **A**, Two-dimensional functional space with color-coded assignation to the eight proboscidean functional types (PFTs). **B**, Species diversity of the PTFs through time (log-scaled), showing the timing of the proboscidean dispersal in Eurasia (gray bar), and ecological disparity, measured as the sum of variances. **C**, Extinction selectivity shows whether extinction is ecologically restricted (positive values) or hits on broad regions of the functional space (negative values). The gray band represents values consistent with a random signal (non-significant p-values). **D**, Continental extinction rates through time on log-scaled axes, where triangles mark the timings at which earlier presence of *Homo sapiens* s.l. became established on the respective landmasses.

Community composition scoring using a pre-human baseline: Applications for conservation, taphonomy, climate reconstruction

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ABSTRACT

Community structure analysis is a taxon-free approach which can quantify differences between faunas across space and time based on broad trait categories of the taxa within those faunas. Generally, community structure analyses use three ecological variables (diet, locomotion, and body mass) to describe member species, and apply multivariate statistical approaches to differentiate between communities (Kovarovic et al., 2018). These results can then be applied to paleocommunities for environmental reconstruction.

While other paleoclimate reconstruction approaches, like dental ecometrics, have undoubted merits, they cannot currently be considered taxon-free, as current models exclude herbivores other than those from four clades (Artiodactyla, Perissodactyla, Primates, Proboscidea). For continents with other dominant herbivores, especially South America and Australia, community structure approaches are more appropriate (Spradley et al., 2019). In addition, all paleoclimate reconstructions grounded using modern communities face the same challenge—the depletion of large mammals since the Late Pleistocene. We believe that all paleoclimate reconstruction approaches should take this fact into account (Wilson et al., 2022).

In an attempt to counter these two challenges, we have used generalized linear latent variable models (GLLVMs) to describe global mammal communities. Because distinguishing between different locomotion strategies can be challenging in the fossil record, particularly where only teeth are present, we used only two ecological variables: body mass and diet. Faunal lists were based on the 'Present-Natural' ranges of the PHYLACINE database (Faurby et al., 2018) and a hexagonal grid of the world's surface at a resolution of 50 km. Using these approaches, we have derived 14 linear models (based on potential taphonomic biases) that may be used to describe any community according to two latent variables. These in turn have a significant relationship with several environmental variables, such as mean and minimum annual temperature, seasonal temperature variation, mean annual precipitation and tree cover.

The use of these latent variables to describe both modern and fossil communities is straightforward and widely applicable. We here propose three ways that researchers might apply these scores. Firstly, we can compare the scores for the present-natural communities to both those of today and projected future communities to inform conservation priorities. Secondly, we believe that these approaches might have use for assessing taphonomic biases. By placing fossil communities within 'latent variable space', we can determine their similarity to modern communities, and therefore the likelihood that they approximate a completely preserved community. Finally, using latent variables as ecometric traits for a community will allow for paleoenvironmental reconstruction, with minimal trait coding required.

To test the applicability of this method for paleoenvironmental reconstruction, we have collated faunal lists, including body mass and diet, both from the NOW database and the published literature. For sites in Antarctica and South America, these represent the first estimates based on mammal communities. Our approach demonstrates the value of having a database that contains both faunal lists and trait data, but highlights the need to extend the NOW database into parts of the world that are currently underrepresented, and to continue to code traits for taxa already in the database.

KEYWORDS: Communities; Ecometrics; Taxon-free; Paleoenvironment.

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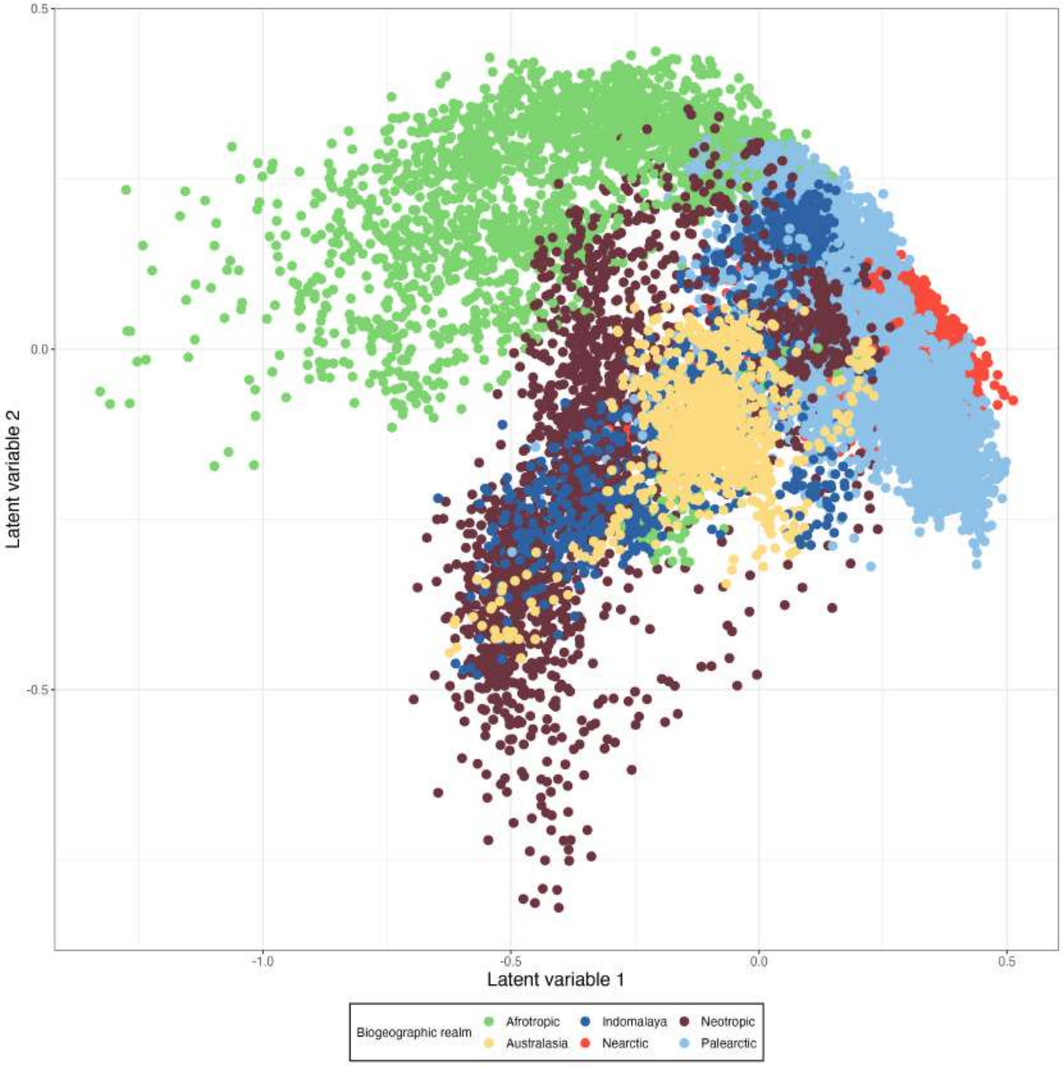

Figure 1. Ordination plot showing the latent variable space for the 50,083 modern mammal communities used to test the model, colored by biogeographic realm.

The Vallès-Penedès Miocene Vertebrates Paleobiodiversity Database

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ABSTRACT

The Vallès-Penedès Miocene Vertebrates Paleobiodiversity Database (VPDB) was devised in 2017 to manage paleontological information about continental vertebrates from the Miocene of the Vallès-Penedès Basin at the specimen level (Casanovas-Vilar et al., 2018). The database is run using an ad hoc software, the Paleobiodiversity Database management system, designed by D.M.A., I.C.V, and J.T. and programmed by Grisart Media with funds from R+D+I project "Paleobiodiversity dynamics of fossil vertebrate faunas from the Vallès-Penedès Basin and comparison with other Miocene basins" (CGL2016-76431-P, AEI/FEDER EU). The database is hosted by the Institut Català de Paleontologia Miquel Crusafont (ICP) and built on a MySQL database engine using web programming software—HTML5, PHP, Javascript (JQuery) and CSS3—in order to be accessible online using any web browser by multiple users simultaneously. Only the front-office webpage with information about the database is publicly accessible, whereas the private back-office requires authentication through login and password. Depending on their roles and privileges, users can perform multiple searches as well as consult and/or edit the data. The software allows bulk import from Excel as well as export in CSV format.

The copyright of the VPDB and its management system is owned by the ICP. The database is coordinated by D.M.A., but authorship must be attributed to all the researchers that have contributed as 'determiners' of the specimens. The database records specimen and locality information to generate data amenable to numerical analysis of paleobiodiversity dynamics at the species level while assessing sampling biases based on specimen counts. Thus, the VPDB is simultaneously a collection and a research database (sensu Uhen et al., 2013) that includes both published and unpublished information. Specimen records are identified by their catalog number, corresponding to fossils mostly housed in the ICP (>72,000 specimens recorded as for September 2022). The database enables multiple predetermined searches but emphasizes specimen counts per taxon and 0.5 or 0.1 Myr-duration stratigraphic bins (Fig. 1). A built-in algorithm assigns localities to a bin each time that their associated age data are modified. Such attribution may be univocal (when age uncertainty does not cross bin boundaries), equivocal (based on a pseudorandomized procedure), or uncertain (when age uncertainty is greater than thrice bin resolution).

The VPDB is currently of internal use by members of ongoing R+D+I project "Paleobiodiversity and paleoecology of Miocene vertebrate faunas during high-resolution intervals in the Vallès-Penedès Basin" (PID2020-117289GB-I00). In 2023, we will start implementing additional database functions by integrating scripts to automatically compute paleobiodiversity metrics as well as to display maps with locality or species occurrence data per bin. We will also continue compiling new data and refining taxonomic identifications and, before 2025, we expect to analyze paleobiodiversity dynamics in relation to paleoenvironmental change through time and upload species-locality data to the NOW database (The Now Community, 2022; Casanovas-Vilar et al., in press). Eventually, searches and locality records will be made publicly available to guest registered users, but specimen records will not be openly available until the most relevant results of the project have been published.

KEYWORDS: Fossil vertebrates; Vallès-Penedès Basin; Taxonomy; NOW database; Paleobiodiversity dynamics.

ACKNOWLEDGMENTS

This work is part of R+D+I project PID2020-117289GBI00 (MCIN/AEI/10.13039/501100011033/) and has also been funded by the Generalitat de Catalunya/CERCA Programme. The authors thank Marc Pi for programming the database, Marta Palmero for helping design the logo, and all the researchers that have thus far contributed with their taxonomic identifications.

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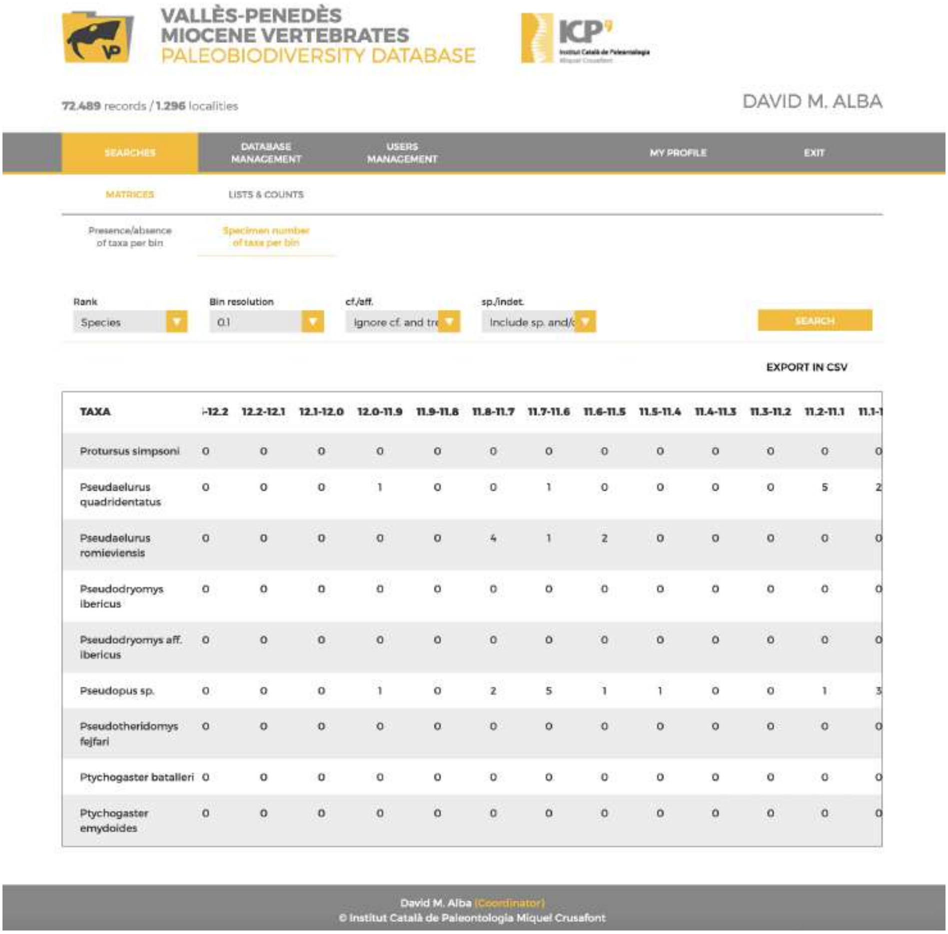

72.489 records / 1.296 localities

DAVID M. ALBA

Rank: Species

Bin resolution: 0.1

cf./aff.: Ignore cf. and tr

sp./indet.: Include sp. and/

TAXA	-12.2	12.2-12.1	12.1-12.0	12.0-11.9	11.9-11.8	11.8-11.7	11.7-11.6	11.6-11.5	11.5-11.4	11.4-11.3	11.3-11.2	11.2-11.1	11.1-
Protursus simpsoni	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudaelurus quadridentatus	0	0	0	1	0	0	1	0	0	0	0	5	2
Pseudaelurus romieviensis	0	0	0	0	0	4	1	2	0	0	0	0	0
Pseudodryomys ibericus	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudodryomys aff. ibericus	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudopus sp.	0	0	0	1	0	2	5	1	1	0	0	1	3
Pseudotheridomys fejfari	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptychogaster batalleri	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptychogaster emydoides	0	0	0	0	0	0	0	0	0	0	0	0	0

David M. Alba (Coordinator)
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Figure 1. Screenshot of the VPDB in the administrator's profile after performing a search of specimen number of taxa per 0.1 Myr-duration bin.

Paleoenvironmental inferences on the Late Miocene hominoid-bearing site of Can Llobateres (NE Iberian Peninsula): An ecometric approach based on functional dental traits

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ABSTRACT

Hispanopithecus laietanus from the Late Miocene (9.8 Ma) of Can Llobateres 1 (CLL1; Vallès-Penedès Basin, NE Iberian Peninsula; Alba et al., 2012) represents one of the latest occurrences of fossil apes in mainland Western Europe, where they are last recorded at ~9.5 Ma (Casanovas-Vilar et al., 2011). The reconstruction of the CLL1 paleoenvironment is thus relevant for understanding the factors that triggered the extinction of European hominoids.

To refine previous paleoenvironmental inferences for CLL1, this work applies an ecometric approach based on functional crown type (FCT) variables—a scoring scheme devised to capture the main functional traits of occlusal shape and wear surfaces of herbivorous large mammal molars. These variables have shown to be correlated with environmental parameters—such as precipitation and temperature—thus being suitable for making paleoenvironmental inferences based on fossil data (Žliobaitė et al., 2016). Paleotemperature and paleoprecipitation estimates for CLL1 are provided based on Žliobaitė et al. (2016) regressions between environmental and average FCT variables for extant Kenyan national parks. A Whittaker's biome classification is also attempted on the basis of these estimates and a canonical variate analysis based on FCT variables for an extensive dataset of extant localities from five relevant biomes.

The list of herbivorous large mammals from CLL1 was updated after revising the identification of some species. FCT variables were scored based on the M2s of the 19 recorded species and the average values for the former used to estimate environmental parameters. Estimates of mean annual temperature (23 °C) and mean annual precipitation (859 mm) classify CLL1 as a tropical seasonal forest/savanna (Fig. 1), as further supported by estimates of driest (196 mm) and wettest (2,283 mm) month of the year, indicating a clear rainfall seasonality. The CVA, with a moderately low classification accuracy of 49.5%, classifies CLL1 as a tropical rain forest (52%) or as a tropical seasonal forest/savanna (42%)—the latter option coinciding with the biome attribution based on paleoclimatic estimates. A tropical seasonal forest agrees better with previous inferences derived from fossil plants and mammals (Marmi et al., 2012), as well as preliminary isotopic data (Casanovas-Vilar et al., 2020). The misclassification of CLL1 as a tropical rain forest is attributed to the mixture of forest-adapted taxa with others adapted to more open environments, given that faunal and plant composition from CLL1 indicates the presence of a dense wetland/riparian forest with more open woodlands nearby (Marmi et al., 2012). According to this interpretation, the CLL1 local paleoenvironment would not be representative of the regional biome.

Although the FCT ecometric approach does not provide unambiguous biome classifications because the multivariate analyses do not adequately distinguish some particular biomes, our results are consistent with—and enable further refinement of—previous paleoenvironmental inferences for CLL1. Therefore, we consider that this approach is promising for investigating paleoenvironmental change through time in the Vallès-Penedès Basin by investigating additional well-sampled sites.

KEYWORDS: Fossil apes; *Hispanopithecus*; Functional crown types; Vallesian; Spain.

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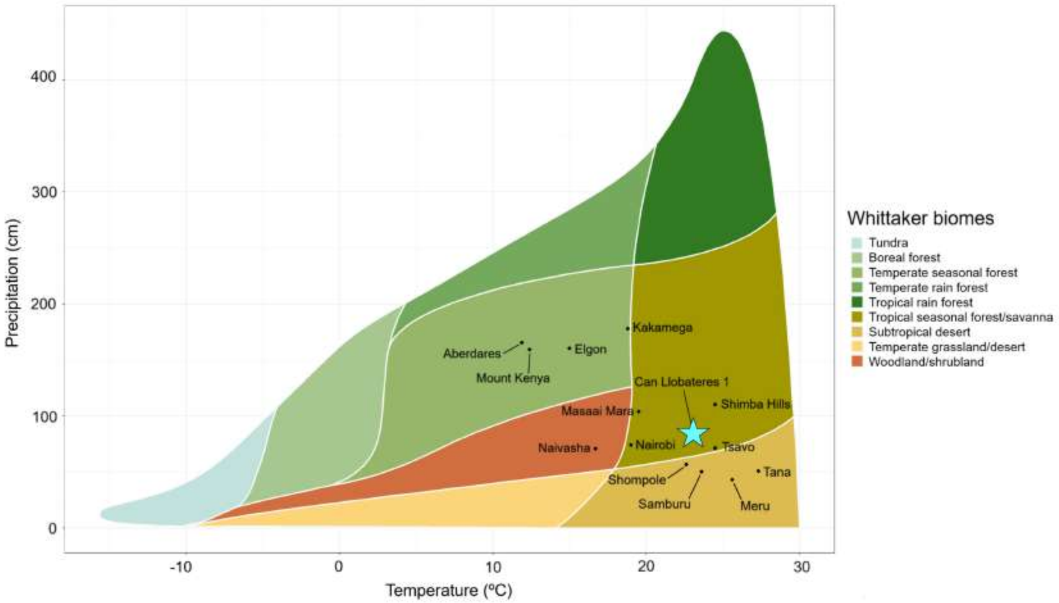

Figure 1. Whittaker's diagram with biome classification for Can Llobateres 1 based on estimated paleotemperature and paleoprecipitation, along with the nine extant localities from Kenyan national parks based on actual temperature and precipitation data.

Earliest Vallesian suid remains from Creu de Conill 20 (Vallès-Penedès Basin, NE Iberian Peninsula)

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ABSTRACT

Although the suid assemblages from the Miocene of the Vallès-Penedès Basin (NE Iberian Peninsula) are reasonably well known, taxonomic studies devoted to them have lagged behind during the last decades. We describe the unpublished suid dentognathic remains from the earliest Vallesian (MN9) of Creu de Conill 20 (CCN20; 11.18 Ma), which represents the First Appearance Datum of hipparionin equids in western Europe. The sample includes 118 specimens, mostly isolated teeth and a few maxillary and mandibular fragments. More than three-quarters of the specimens are assigned to the dicoryphochoerin suine *Propotamochoerus palaeochoerus*, which is characteristic of MN9. The rest of the sample is attributed to the large tetraconodontine *Parachleuastochoerus valentini*, recorded elsewhere from MN7+8 to MN9, except for two specimens that apparently belong to the small suid cf. *Albanohyus* sp.

The suine material from CCN20 lacks the lengthening of the third molar characteristic of *Hippopotamodon* spp. and fits well in shape and proportions with that of *P. palaeochoerus* from elsewhere (e.g., Van der Made et al., 1999; Iannucci & Begun, 2022). Although the *Propotamochoerus* remains from CCN20 are slightly larger than average for the species, based on currently available knowledge such a difference in size does not warrant a taxonomic distinction. An alternative attribution to either *Propotamochoerus hysudricus* or *Propotamochoerus provincialis* can be ruled out based on differences in dental proportions. The presence of *P. palaeochoerus* at CCN20, coupled with its absence from MN7+8 sites (Pickford, 2014), supports a roughly synchronous dispersal of this taxon and hipparionin horses into western Europe at ~11.2 Ma.

The tetraconodontine material from CCN20, based on its large size and several dental differences relative to *Versoporcus* spp., is assigned to *Pa. valentini*, which in the Vallès-Penedès Basin is also recorded from the MN7+8 site of Trinxera del Ferrocarril-Sant Quirze (Pickford, 2014). The validity of *Pa. valentini*, resurrected by Pickford (2014) on the basis of material from Saint Gaudens (France), is controversial, being alternatively considered a junior synonym of *Conohyus simorrensis* by Van der Made (2020). The remains from CCN20 refine our knowledge on the dental morphology of *Pa. valentini* and strengthen the view that this species is not a junior synonym of *C. simorrensis*. However, more complete remains would be required to settle its generic ascription more conclusively.

From a paleoenvironmental viewpoint, the suid assemblage from CCN20 strikingly differs from the more diverse assemblage from the roughly coeval site Castell de Barberà (Alba et al., 2019) within the same basin. Besides *P. palaeochoerus* and possibly *Pa. valentini* (authors' unpublished data), Castell de Barberà has further yielded abundant remains of *Listriodon*, *Albanohyus*, and *Versoporcus*. The absence of *Listriodon* and the scarcity of *Albanohyus* at CCN20 are indicative of a more open and arid environment, in agreement with other differences in small and large mammal composition that support the presence of a more closed and humid environment with a permanent water body nearby at Castell de Barberà (Alba et al., 2019).

KEYWORDS: Suidae; *Propotamochoerus*; *Parachleuastochoerus*; Late Miocene; Taxonomy; Spain.

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Diet and habitat of *Ampelomeryx ginsburgi* (Artiodactyla: Palaeomerycidae) of the Middle Miocene site of els Casots (Vallès-Penedès Basin, Catalonia)

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ABSTRACT

Paleomerycids are a group of strange-looking, three-horned giraffomorph ruminants that inhabited Eurasia from the late Early to the early Late Miocene. This group radiated approximately during the Early/Middle Miocene transition, when several different genera are known from Europe, particularly from the Iberian Peninsula (Sánchez et al., 2015). Among them, *Ampelomeryx ginsburgi* is abundantly represented at the earliest Middle Miocene (15.9 Ma) site of els Casots in the Vallès-Penedès Basin (Catalonia, Spain). Paleomerycids have generally been associated to dense humid or even boggy forested environments where they could have fed on soft vegetation. In the case of *A. ginsburgi*, sedimentological, palaeobotanical, and faunal data indicate that els Casots represents an ancient freshwater lacustrine/palustrine area (Casanovas-Vilar et al., 2022). Here we analyze carbon and oxygen isotope composition of dental enamel in *A. ginsburgi* from els Casots to infer its diet and ecology and discuss its congruence with available paleoenvironmental data from the site.

We analyzed 7 M3s and 3 m3s of *A. ginsburgi*. Third molars were selected to retrieve postweaning dietary and drinking stable isotope compositions. Carbon (^{13}C) and oxygen (^{18}O) isotopes are incorporated during the animal's lifetime and derive from dietary intake and (mostly) drinking water, respectively. Samples consisted of 10 mg of enamel powder and were analyzed using an isotope ratio mass spectrometer (IRMS) Thermo MAT253 with the attached dispositive Thermo GasBench II at the ICTA (Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona). We used the methods described in Kohn (2010) to infer $\delta^{13}C$ of consumed vegetation and corrected raw enamel data to consider metabolic isotopic fractionation and ancient atmospheric composition. On the other hand, raw $\delta^{18}O$ values were corrected and used to infer mean annual temperature (MAT) following the methods by Rozanski et al. (1993). Finally, we compared $\delta^{13}C$ and $\delta^{18}O$ values for *A. ginsburgi* with those of other contemporaneous ruminants compiled from the literature (Fig. 1), including other paleomerycids.

Corrected $\delta^{13}C$ values range from -27.9‰ to -25.8‰, thus indicating a diet consisting of exclusively C3 plants (Fig. 1), likely leaves of trees growing near the lake shore or in closed forest. $\delta^{18}O$ values are more difficult to interpret since they show a wide variation (–0.6 to 2.6‰) and are quite high, which would be consistent with a MAT range from ~6 to 19 °C (mean ~10 °C). Such low inferred temperatures are at odds with all other available evidence, since several megathermic taxa such as crocodiles or giant tortoises occur at els Casots (Casanovas-Vilar et al., 2022). Alternatively, *A. ginsburgi* would have ingested water from a ^{18}O-enriched source rather than meteoric water, most likely ^{18}O-enriched leaves defining the upper canopy. The same situation is observed in giraffids and other paleomerycids, such as *Ampelomeryx fahlbuschi* (see Tütken & Vennemann, 2009). Conversely, the paleomerycid *Triceromeryx pachecoi* from the Middle Miocene of the Madrid Basin apparently fed on C4 vegetation. This result correlates well with the more open environments inferred for the inner Iberian basins during the Middle Miocene and hints the plasticity of the brachyodont paleomerycid dentition.

KEYWORDS: Stable isotopes; Palaeomerycidae; Paleodiet; Paleoenvironment; Middle Miocene; Iberian Peninsula.

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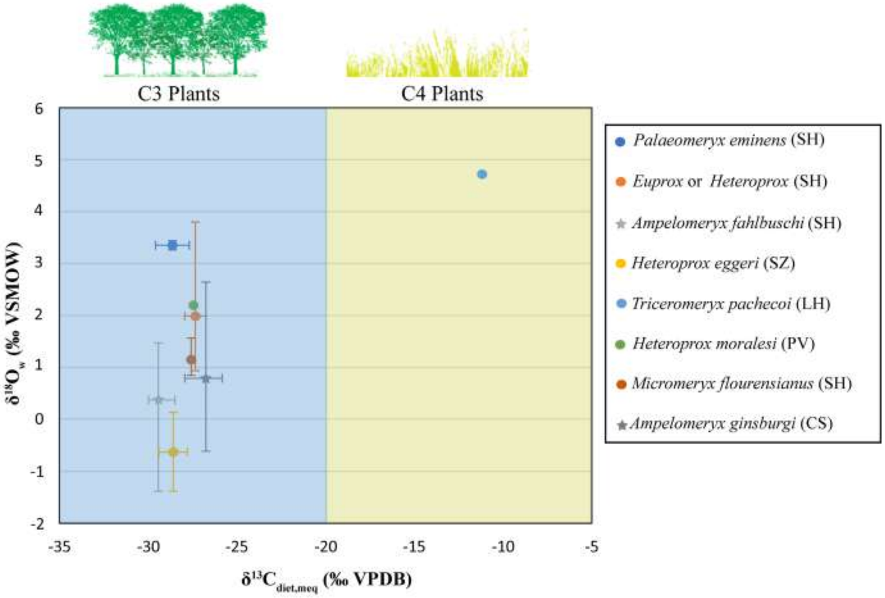

Figure 1. Corrected mean and standard deviation values for $\delta^{13}C$ and $\delta^{18}O$ for *Ampelomeryx ginsburgi* from els Casots as compared to approximately contemporaneous ruminants (Palaeomerycidae, Moschidae, and Cervidae). $\delta^{13}C$ for modern C3 and C4 vegetation is also indicated. $\delta^{13}C_{diet,meq}$ stands out for $\delta^{13}C$ values in the modern equivalent diet (considering ancient atmospheric composition) while $\delta^{18}O_w$ is the $\delta^{18}O$ value of ingested water. Locality acronyms: CS = els Casots; LH = La Hidroeléctrica (Madrid Basin, Spain); SH = Steinheim Basin (Germany); SZ = Sandelzhausen (Molasse Basin, Germany).

Going digital—The Elmar Heizmann Typenkatalog

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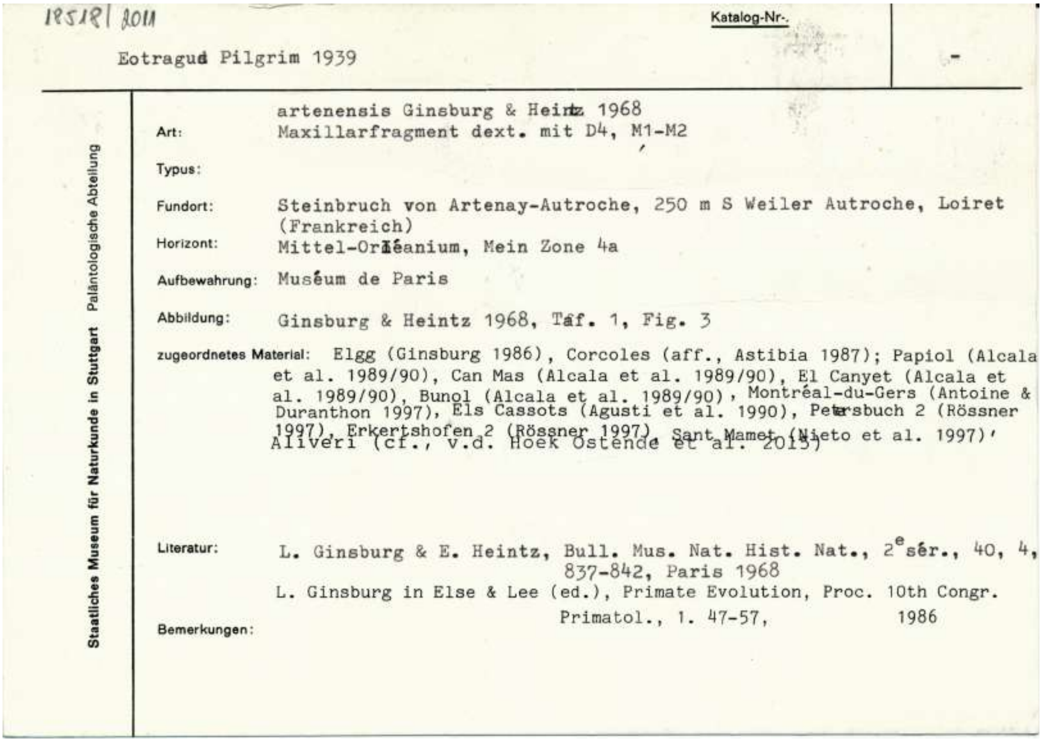
ABSTRACT

The analog, index card-based Elmar P. J. Heizmann's type catalog (EH-TyKa) of the Staatliches Museum für Naturkunde Stuttgart lists fossil mammal species from the Mesozoic to the Quaternary. It is the most complete documentation of fossil mammal taxa and related literature and was constantly updated over decades. Type, first description, type locality and age are recorded for each species included. In addition, the index cards contain literature and locality information for each taxon (see Fig. 1 for an example).

So far, no comparable data set is available digitally, neither in quality nor in quantity. The EH-Tyka includes approx. 24,000 species. By comparison, the New and Old Worlds database of fossil mammals (NOW database) is the most comprehensive digital database on fossil mammals and currently lists 'only' 16,083 species (The NOW Community, 2022).

Digitizing the EH-TyKa and providing its content as an online open access dataset would offer an open access



18518| 2011

Katalog-Nr.

Eotragud Pilgrim 1939

Staatliches Museum für Naturkunde in Stuttgart Paläontologische Abteilung

Art: artenensis Ginsburg & Heintz 1968
Maxillarfragment dext. mit D4, M1-M2

Typus:

Fundort: Steinbruch von Artenay-Autroche, 250 m S Weiler Autroche, Loiret (Frankreich)

Horizont: Mittel-Orléanium, Mein Zone 4a

Aufbewahrung: Muséum de Paris

Abbildung: Ginsburg & Heintz 1968, Taf. 1, Fig. 3

zugeordnetes Material: Elgg (Ginsburg 1986), Corcoles (aff., Astibia 1987); Papiol (Alcala et al. 1989/90), Can Mas (Alcala et al. 1989/90), El Canyet (Alcala et al. 1989/90), Bunol (Alcala et al. 1989/90), Montréal-du-Gers (Antoine & Duranthon 1997), Els Cassots (Agusti et al. 1990), Petersbuch 2 (Rössner 1997), Erkertshofen 2 (Rössner 1997), Sant Mamet (Nieto et al. 1997),
Aliveri (cf., v.d. Hoek Ostende et al. 2015)

Literatur: L. Ginsburg & E. Heintz, Bull. Mus. Nat. Hist. Nat., 2^{e} sér., 40, 4, 837-842, Paris 1968
L. Ginsburg in Else & Lee (ed.), Primate Evolution, Proc. 10th Congr. Primatol., 1. 47-57, 1986

Bemerkungen:

Figure 1. Front side of the species card for *Eotragus artenensis* from the Elmar P. J. Heizmann's type catalog.

data source on fossil mammals, unique in quantity and quality, available for all specialists. Furthermore, adding the primary data in the NOW database and thus complementing taxa information on this database, the standard tool when working with fossil mammals, would support the outstanding position of the NOW database by offering a much larger and more comprehensive dataset available to a wide community of scientists for their studies.

Including the NOW Community itself in an early stage of the project shall help to develop an efficient and practical project approach for reasonably digitize this huge amount of data and provide a useful tool accessible to many scientists. In addition, this will allow to include appropriate data information in NOW—thus also helping to make improve NOW and offer the best database on fossil mammals for numerous scientific works, far beyond paleontological research.

KEYWORDS: New and Old Worlds database; Catalogue of fossil mammals; Digitizing analogic data.

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The Harvard–Geological Survey of Pakistan Siwalik Database

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ABSTRACT

Paleontological research often involves abstracting information from a large collection of data to solve a specific problem. The unusually long sequence of Miocene–Pleistocene deposits forming the Siwalik Formations of the Indian Subcontinent contains abundant assemblages of vertebrates and invertebrates that provide an opportunity to study interacting biological and environmental processes over millions of years in a terrestrial setting. Such studies require detailed knowledge of the stratigraphy, geological age, and depositional context of the fossils, as well as knowledge of the species themselves. This in turn requires attention to documenting hundreds of fossil localities and integrating the resulting sedimentological, taphonomic, and geochronological data with data on hundreds of fossil species.

When datasets are small and not complicated, abstracting relevant information is straightforward, but for larger datasets only a digital database is practicable. Given the volume and complexity of data associated with the Harvard–Geological Survey of Pakistan (GSP) Siwalik Project collections, begun in 1973, developing a database focused on those collections was an important priority, and we began building one in 1977.

The structure and specific content of our database evolved over the years (45 years!), but the basics have remained the same. There are two primary files, one for specimens (with 54,806 records) and a second for localities (with 1,496 records), together with accessory files and programs to analyze and manage the data. The specimen file is relatively simple, with a record for individual fossils. Each record has, among other attributes, a unique specimen number (written on the fossils as well), its taxonomic identity, a description of the specimen, its locality, and who identified it. The locality file is more complex, leading with a locality number that corresponds to those in the specimen file, allowing fossils to be linked with the parent locality. In addition, there are fields for its stratigraphic position on a correlated section, geographic location, depositional setting, plus fields for comments and other details. Accessory files have information on the measured stratigraphic sections, carbon and oxygen isotope values (for both fossils and soil carbonates), measurements of the fossils, etc. These are linked to the specimen and locality files by the specimen number or the locality number.

Linked specimen- and locality-based data provide opportunities to examine patterns of variation in the Siwalik vertebrate record at environmental and temporal scales that reveal paleoecological attributes and taphonomic biases characteristic of the ancient sub-Himalayan alluvial deposystem. As an example, Morgan et al. (2009) showed that paleogeographic position along a 32 km transect across the Siwalik alluvial plain at ~9.4 to 9.2 Ma was correlated with diet based on $\delta^{13}C$ ratios in a wide variety of herbivores (equids, giraffids, anthracotheres, suids, and hominoids). Siwalik data also show how species richness at localities varies as a function of depositional setting and habitat, combined with different biological versus physical taphonomic processes that affected the skeletal assemblages prior to burial (Badgley, 1986; Behrensmeyer et al., 2005).

KEYWORDS: Siwalik; Vertebrate fossils; Database; Pakistan; Miocene.

ACKNOWLEDGMENTS

The research on the Siwalik sequence is part of a long collaboration with the Geological Survey of Pakistan and we appreciate the efforts of members of the Survey who have over the years supported the project. Financial support is from many sources, including the National Science Foundation, Smithsonian Foreign Currency Program, and the American School for Prehistoric Research. We also acknowledge the support of many colleagues and most importantly Dr. S. Mahmood Raza.

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The potential of intraspecies ecometrics in NOW: *Microtus guentheri* (Rodentia, Cricetidae) mesowear as an example

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ABSTRACT

The NOW database encompasses fossil data for the Cenozoic, allowing for long-ranging temporal and spatial analyses of mammalian evolution stemming from changes in species distribution. In contrast to much of the Cenozoic, the Pleistocene epoch (2.58–0.117 Ma) saw an increase in extensive climatic changes over short periods. In higher latitudes, species turnover was rapid, but in lower to mid latitudes, climate change was not as pronounced, resulting in species distribution stasis. Nonetheless, there is geological evidence for climate change. Can we track it in the fossil record?

Ecometrics are characteristics tied to function related to the local environment (Eronen et al., 2010). The measurement of these traits in fossil taxa can be used as a paleoecological proxy. Ecometric analyses focused on species averages, i.e., the variable's value averaged across several and compared across long temporal and spatial scales. The NOW includes a range of ecometrics, featuring diet, locomotion, size, and teeth under two tabs: (1) the ecometrics tab, which averages ecometric variables across all species in a site, and (2) the locality-species tab which includes individual species averages for each ecometric variable in each site. Nonetheless, different methods have rapidly developed to obtain intra-species ecometrics. For example, some mesowear studies may use upper or lower molars or different teeth. In addition, some ecometrics only consider one specific taxonomic group, e.g., mesowear which has been applied to ungulates.

As example for an intra-species mesowear analysis of non-ungulate species, we present a study on extant social voles (*Microtus guentheri*). The mesowear of the m1 was measured on 26 voles retrieved from localities across Israel. Mesowear angles were binned into quartiles. Logistic regression was used to correlate environmental parameters derived from Danin and Orshan's (1990) 26 phytogeographic regions. Two composite quotients were included in the analysis: Lang's (1920) rain factor where Lang = P/T; and Emberger's (1930) pluviothermic quotient where $EMB = P \times 100/(Tmx + Tmn) \times (Tmx - Tmn)$. Where P = mean annual precipitation (mm), T = mean annual temperature in ^{o}C, Tmx = mean monthly maximal temperature of the warmest month, and Tmn = mean monthly temperature of the coldest month. Higher EMB values and higher Lang's rain factor are associated with more humid and colder regions.

EMB correlated significantly with mesowear ($p = 0.02$) and Lang's rain factor was correlated with mesowear, albeit p is marginally insignificant ($p = 0.07$). More acute mesowear angles were associated with higher values in both cases. These results are consistent with laboratory experiments showing that a low-abrasive diet wears primarily due to tooth-to-tooth contact resulting in obtuse wear angle. In contrast, chewing hard food requires vertical occlusal pressure, such that the anterior enamel wall of prisms remains unworn (Kropacheva et al., 2017).

Thus, further developing the site-specific ecometrics for species in the NOW platform would expand the opportunities to study ecological changes through paleontological and ecological time scales and pick up some of the rapid climatic changes that occurred in the Pleistocene in lower to mid latitudes.

KEYWORDS: Pleistocene; Mid-latitudes; Rodentia; Ecometrics; Mesowear.

ACKNOWLEDGMENTS

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New contributions to the knowledge of the paleobiogeographical context of the Late Miocene–Early Pliocene rodent fauna from the Iberian Peninsula

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ABSTRACT

During the Late Miocene-Early Pliocene interval, encompassing MN13 and MN14 units (7.30–4.20 Ma) in the Iberian Peninsula, important paleobiogeographical changes of continental species took place, largely related to the Messinian Salinity Crisis. A direct consequence of this geological event was the establishment of land bridges that led to terrestrial faunal exchanges between Africa and the Iberian Peninsula (Gibert et al., 2013). Iberian rodent faunas of this time have an abundant and diverse fossil record that has allowed to establish an excellent chronological framework for fossil localities (Morales et al., 2013; García-Alix et al., 2016). Adequate spatial and temporal documentation allows us to analyze these faunas and manage the large amount of existing information. This work intends to support new fossil data to become part of the NOW database (The NOW Community, 2022). Our aim is compiling accurate information about species and localities, following the standards of the NOW database, and collaborate to the understanding of the paleobiogeographical context of the Iberian Peninsula during the Late Miocene–Early Pliocene.

The dataset presented consists of a georeferenced database of paleontological information managed by QGis software that contains the following data fields: locality, geographical distribution, chronology, taxon occurrence/absence, and associated publications. All the data included are referenced to a coordinate system (EPSG25830) that allows its management with GIS (Geographic Information Systems) tools. To build the database, we carried a review of available bibliography until April 2021, resulting in the compilation of more than 100 faunal lists that have been updated considering synonyms and the latest taxonomic opinions.

The resulting database includes rodent faunas from 186 Iberian sites (124 dating to MN13 and 62 to MN14). So far, about 73 different rodent species belonging to the following families have been recorded: Muridae, Cricetidae, Gliridae, Sciuridae, Zapodidae, Castoridae, Hystricidae and Gerbillidae. The database compiles information on the following basins and karstic sites: Alcoy, Alvalade, Almería-Níjar, Bajo Ebro, Cabriel, la Cerdanya, Duero, l'Empordà, Cenajo, Fortuna, Granada, Guadix-Baza, Málaga, Bajo Segura, Sorbas, Tajo, Teruel, Vallès-Penedès, Almenara-Casablanca-M and Mb, Caló d'en Rafelino, Na Burguesa-1, Salobreña, and Ses Fontanelles (Fig. 1). As compared to NOW (The NOW Community, 2022), our dataset includes a higher number of sites (186 vs. 114), with more precise spatial information for both deposits and taxa, and updated systematic and chronological data (e.g., Piñero & Verzi, 2020). However, NOW compiles other important data not recorded in our dataset, namely taphonomy, lithology, climate, size, and paleodiet fields. Thanks to its georeferenced character, the information contained in this database is interoperable with that of the NOW after converting the projected to geographic coordinate system.

Our database can contribute to complement and update the information of NOW. Additionally, it would allow to generate thematic cartographies (e.g., species distribution) and perform spatial analyses considering other thematic cartographies (e.g., paleotemperature). Future expansions of this database will involve the addition of rodent taxa from other periods (Middle and Late Pliocene and Pleistocene) and other localities from Europe.

KEYWORDS: Database; Iberian Peninsula; Mio-Pliocene; Paleobiogeography; Rodentia.

ACKNOWLEDGMENTS:

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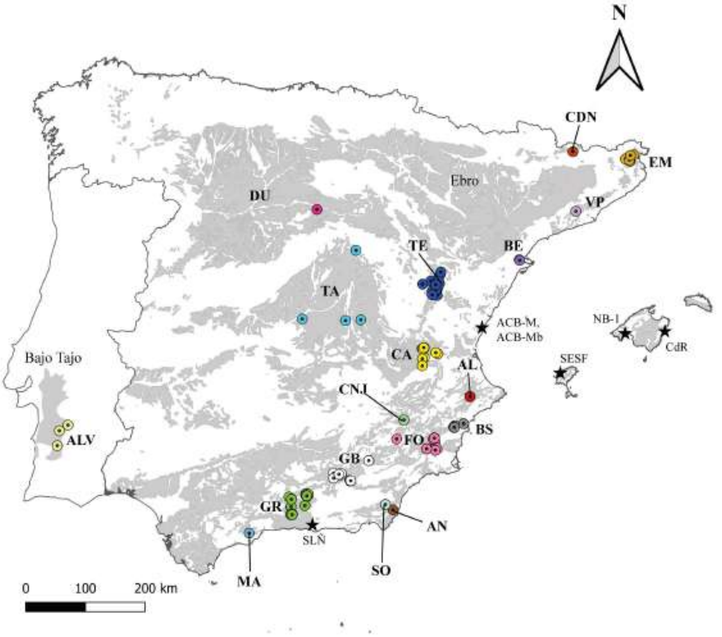

Basins/ localities	MN13 localities No.	MN14 localities No.	Total localities No.
● AL	4	15	19
⊙ ALV	3	0	3
● AN	1	0	1
● BE	0	2	2
● BS	5	0	5
● CA	5	4	9
● CDN	1	0	1
● DU	1	0	1
● EM	3	2	5
● CNJ	1	0	1
● FO	24	6	30
● GR	35	9	44
⊙ GB	10	12	22
● MA	0	1	1
⊙ SO	2	0	2
● TA	4	0	4
● TE	22	7	29
● VP	0	1	1
★ Karstic	3	3	6
Total No.	124	62	186

▨ Cenozoic

Figure 1. Localities included in the database. Basins: AL = Alcoy; ALV = Alvalade; AN = Almería-Níjar; BE = Bajo-Ebro; BS = Bajo-Segura; CA = Cabriel; CDN = La Cerdanya; DU = Duero; EM = Empordà; CNJ = Cenajo; FO = Fortuna; GR = Granada; GB = Guadix-Baza; MA = Málaga; SO = Sorbas; TA = Tajo; TE = Teruel; VP = Vallès-Penedès. Karstic localities: ACB-M = Almenara-Casablanca-M; ACB-Mb = Almenara-Casablanca-Mb; NB-1 = Na Burguesa-1; CdR = Caló d'en Rafelino; SESF = Ses Fontanelles; SLÑ = Salobreña.

Archaeology tab—A new feature in the NOW database

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ABSTRACT

Currently, more and more Pleistocene data are entered in the NOW database. This means that it is likely that the data are coming from a site or locality that bears evidence of human activity. If prehistoric humans were responsible, at least partly, for the accumulation of the mammal assemblage, one needs to consider how much the composition of the fossil data reflects human prey choices rather than the composition of the past mammal community. Thus, to better facilitate such source critical evaluations as well as studies of human-mammal interaction, it was decided to implement a new feature, Archaeology tab, in the database. Archaeology tab makes it possible to add basic information about evidence of human presence and activity in the locality. This includes evidence of presence of stone tools, stone tool-induced cut marks on animal bones, and hominin footprints. Furthermore, it is possible to be a bit more specific about the characteristics of human activity in terms of stone tool technologies and cultures by selecting technological modes (Modes 1–5), broad cultural stages (e.g., Early Stone Age, Middle Paleolithic) and by entering free text on regional cultures present in the material (e.g., Large Flake Acheulean, Mousterian, Aterian). It is hoped that this new feature will increase the usability of the Pleistocene data and attract even wider interest to the NOW database.

KEYWORDS: NOW database; Archaeology tab; Hominin activity; Human–mammal interactions.

The future and current NOW

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ABSTRACT

The NOW database of fossil mammals (The NOW Community, 2022) reached its 25th year in 2021 and celebrates this anniversary a year later in Sabadell, Spain. During its history, NOW has gone through many developmental phases, including many uplifts to the user interface and changes to the database engine (Fortelius et al., in press). Also, the application development has become more community based instead of depending on the ideas of a few NOW users.

As a good example of the community-based development of NOW, a two-day workshop was held in 2018 in Bratislava, bringing the users and developers of NOW together. During the workshop, several different subject areas were discussed, and new ideas and actions were proposed. After the workshop, many of these action points have been implemented while some are yet to be done.

In this presentation, we will briefly report the latest developments since the 2018 meeting, including the setting up of the NOW advisory board, user interface changes and major updates to the data contents. We also present our software development model and call for new members to our development team. We will also discuss the future requirements and opportunities for NOW.

KEYWORDS: NOW database; Fossil data; Rapid application development.

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FIELDTRIP GUIDE

The Miocene high-resolution record of the Vallès-Penedès Basin (Catalonia)

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KEYWORDS: Fieldtrip guide; Fossil vertebrates; Neogene; Iberian Peninsula; Miquel Crusafont-Pairó.

INTRODUCTION

This fieldtrip guide is an introduction to the Miocene terrestrial record of the Vallès-Penedès Basin (Catalonia, Spain). The Vallès-Penedès is one of the better-known Miocene continental records worldwide and comprises hundreds of different sites that have yielded tens of thousands of fossils belonging to all sorts of vertebrates. Furthermore, most of the sites have been accurately dated using a combination of bio- and magnetostratigraphic methods. Since the very beginning, the systematic study of the vertebrate faunas of the Vallès-Penedès has been led by the Institut Català de Paleontologia Miquel Crusafont (ICP) or its predecessors, beginning with its founder Miquel Crusafont-Pairó. Presently, the ICP coordinates excavation of the major sites and taxonomic research. Current studies focus on the evolutionary paleoecology and paleobiodiversity dynamics of the Miocene vertebrate faunas of the basin, as well as the paleobiology and phylogeny of many different groups.

The Vallès-Penedès record covers most of the Miocene, only missing the very beginning and the end of this epoch. However, fossil sites are not evenly distributed in space and time, so that certain areas and intervals are better represented. The record is particularly good for three intervals that further coincide with important climatic and/or faunal turnover events: the Miocene Climatic Optimum (MCO; ~17–15 Ma); the Aragonian/Vallesian transition (Middle/Late Miocene; ~12.5–11 Ma); and the Vallesian Crisis (early/late Vallesian, Late Miocene; ~10–8.5 Ma). These high-resolution intervals, particularly the Vallesian Crisis (see below), have deserved the greatest attention and sampling effort. The time interval represented by the Vallesian Crisis is covered by several sites near the towns of Sabadell and Terrassa and has been a central topic in previous congress fieldtrips, such as in the workshop held in the framework of an European Science Foundation network in 1996 (Agustí et al., 1996, 1998) or the annual meeting of the Sociedad Española de Paleontología in 2011 (Alba et al., 2011a). Until a few years ago, the Aragonian/Vallesian transition and particularly the MCO records were not that well represented. However, recent field campaigns and studies (see below) have vastly improved our knowledge of these key intervals, so we decided to make them central topics of this fieldtrip guide.

The guide is organized in four stops (Fig. 1), the first three at the town of Subirats (l'Alt Penedès, Barcelona) and the last one at els Hostalets de Pierola (l'Anoia, Barcelona). The first stop at the Subirats Castle provides a panoramic view of the basin and is ideal to observe its general structure. The second stop visits the site of els Casots next to it, which is an exceptional site dating back to 15.9 Ma—i.e., coinciding with the MCO. The third stop does not visit a vertebrate locality but a coral reef which formed when warm temperatures during the MCO caused a generalized marine transgression that flooded great part of the basin. The fourth and final stop visits the area of Can Mata, where the Abocador de Can Mata (ACM) macrosite (uncovered by the construction of the Can Mata landfill) and other sites from the area of els Hostalets are located, cover a great part of the late Aragonian as well as the earliest Vallesian. Paleontological surveillance of the construction works of such a huge landfill has allowed paleontologists to find a vast number of vertebrate fossils. For each fossil vertebrate site, a brief, updated, and fully referenced account of the geology, biota and paleoenvironment is provided. In addition, we give the geographical coordinates for each stop so that one may latter recreate the excursion using web mapping platforms.

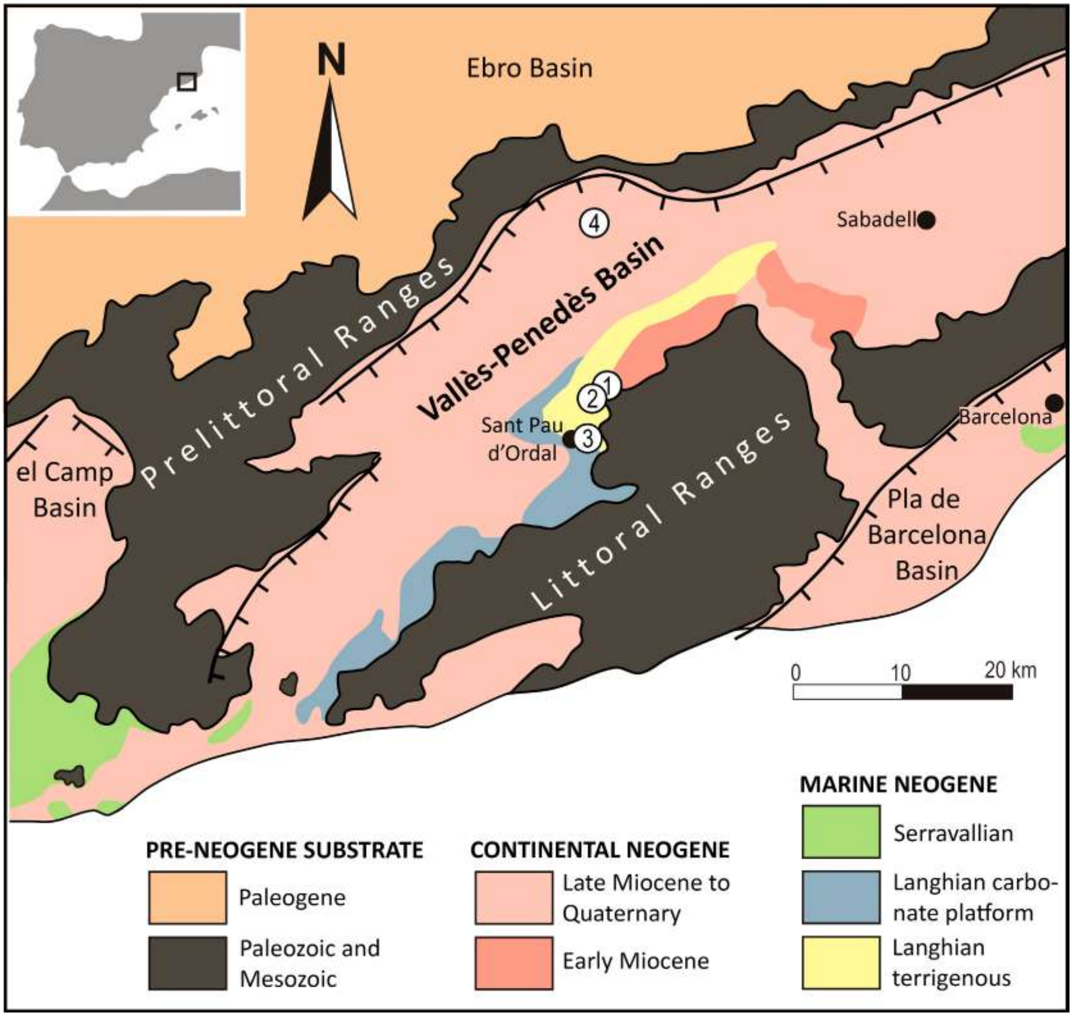


Figure 1. Simplified geological map of the Vallès-Penedès Basin showing locations of the stops: **1–2**, Castell de Subirats and els Casots; **3**, Can Sala coral reef; **4**, Can Mata. Modified from Cabrera et al. (1991).

HISTORICAL OVERVIEW

In the late 19th century, Reverend Jaume Almera, one of the earliest geologists and paleontologists from Catalonia, was the first one to report fossil vertebrates from the Vallès-Penedès Basin. These included mostly dental remains that had been recovered from the then-active coal mines of la Fontsanta, next to els Casots (CS; see Stop 2) and the Molí Calopa brickyard in Rubí (MC). Almera, who did not specialize in fossil vertebrates, left the identification of the remains in the hands of renowned foreign mammal paleontologists of his time, including Marcellin Boule, Charles Depéret, and Albert Gaudry (Almera, 1898). Those remains were kept at the Geology Museum of the Conciliar Seminary of Barcelona—which he had founded a couple decades before—and were lost or destroyed in 1936, at the beginning of Spanish Civil War, when the museum was sacked by anticlerical militias (Reguant i Serra, 2004).

In the following decades, the outcrops of the Vallès-Penedès were surveyed by paleontologists and amateur collectors linked to the Seminary Museum, led by Josep Ramon Bataller, who succeeded Almera in the direction of the Seminary Museum. Bataller's activity resulted in the discovery of new sites at Piera (PI; Bataller, 1918), Sant Quirze del Vallès (SQ; Bataller, 1924), Terrassa (Bataller, 1924), and els Hostalets de

Pierola (Bataller Calatayud, 1938). During the 1920s, Miquel Crusafont-Pairó started finding remarkable mammal fossils near his hometown, Sabadell, becoming interested in paleontology (Crusafont i Sabater, 2019). In the early 1930s, Crusafont graduated in pharmacy but, based at the Sabadell Museum, he started collaborating as an amateur paleontologist with Josep F. de Villalta-Comella, publishing their first joint papers (Villalta Comella & Crusafont Pairó, 1933; Villalta & Crusafont, 1934) shorty before the Spanish Civil War (1936–1939). After the war, Crusafont was determined to become a professional paleontologist and resumed, together with Villalta, Jaume Truyols, and various amateur collaborators a systematic surveying of the Miocene outcrops from the Vallès-Penedès Basin, resulting in the discovery of tens of new sites and the collection of thousands of specimens. Crusafont and Villalta focused on the study of mammals and occasionally other vertebrates (e.g., de Villalta Comella and Crusafont Pairó, 1941a, 1943a, 1943b; Crusafont Pairó & Villalta, 1948, 1951; Crusafont Pairó, 1950; Crusafont et al., 1955), whereas Truyols mostly studied the stratigraphical context and regional geology of the area (Truyols and Crusafont, 1951; Crusafont et al., 1955; Crusafont Pairó & Truyols Santonja, 1960).

Villalta and Crusafont's work progressively attained international recognition, in part thanks to a travel grant that soon after World War II allowed Crusafont to travel around Europe, visiting the museums of Lyon, Paris and Basel and establishing collaborative relationships with the most important paleontologists of his time (Crusafont i Sabater, 2019). This trip further prompted the publication by Villalta and Crusafont of a series of eight papers between 1946 and 1948 in the journal of the Société Géologique de France on Neogene mammals from the Iberian Peninsula, the first three of them focused on the Vallès-Penedès Basin (Villalta & Crusafont, 1946a, 1946b, 1946c). When Crusafont obtained his PhD with a dissertation on fossil giraffids from Spain supervised by Hernández-Pachecho in Madrid (Crusafont Pairó, 1952a), he and his coauthors had published dozens of contributions on the fossil vertebrates from the Vallès-Penedès and other Iberian basins. Thanks to their work, the Vallès-Penedès became a reference area for the study of European Miocene faunas, and eventually the Vallesian land mammal age was defined based on its record (Crusafont Pairó, 1950; see Stop 4), being readily accepted and applied to other regions of the Old World for the Late Miocene fossil faunas that postdate the entry of the first hipparionin horses. Crusafont also organized a series of short workshops with associated fieldtrips, named 'Cursillos Internacionales de Paleontología' (International Short Courses in Paleontology), which were held at Sabadell between 1952 and 1958. These served to present the Spanish mammal record to foreign researchers—leading to the publication of synthetic faunal catalogues from the Vallès-Penedès and other Iberian basin (Crusafont & Truyols, 1954, 1956)—as well as to foster international collaboration in scientific publications and fieldwork (Crusafont i Sabater, 2019).

In 1951, the paleontology section led by Bataller from the Seminary Museum and the Chair of Paleontology of the University of Barcelona, as well as the paleontology section of the Sabadell Museum led by Sabadell became ascribed to the Instituto "Lucas Mallada" of the Consejo Superior de Investigaciones Científicas (CSIC; Crusafont Pairó, 1969). Soon thereafter, in 1952, renamed it as Paleobiology Section to emphasize Crusafont's view of paleontology as part of life sciences. In the meantime, the collaboration between Crusafont and Villalta started to progressively fade, their last joint contributions being published in 1957. In 1961, Crusafont won the Chair of Paleontology at the University of Oviedo and moved there accompained by Truyols as associate professor (Crusafont Pairó, 1969; Truyols i Santonja, 1986). In 1963, however, Crusafont won the Chair of Paleontology at the University of Barcelona following Bataller's decease in 1962, and the CSIC paleontology sections from Barcelona and Sabadell were accordingly merged and the CSIC relationship with the Seminary Museum interrupted. During the early 1960s, Crusafont started collaborating with his student Juana María Golpe-Posse, who was hired at the university and eventually obtained her PhD on fossil suids from Spain in 1971. In 1965, the Barcelona-Sabadell paleontology section was linked to the Geological Institute of Barcelona recently established by the CSIC, ultimately leading to the loss of the link between the latter and the Sabadell Museum. However, since 1957 Crusafont had been trying to convince local and regional authorities to create a paleontological institute in Sabadell. Ultimately, the mayor of Sabadell of the time (Josep M. Marcet i Coll) decided to split the Sabadell Museum into three new museums (Crusafont Pairó, 1981).

The new paleontology museum, conceived by Crusafont as a research center and hence termed Instituto Provincial de Paleontología de Sabadell (IPS), was finally built under the auspices of the Diputación

Provincial de Barcelona, being formally inaugurated in 1969 (Crusafont Pairó, 1969; Crusafont i Sabater, 2019). Crusafont eventually retired from the university but remained as IPS director until his death in 1983, when the institute was renamed Institut de Paleontologia Miquel Crusafont (IPMC) in his honor. During the 1970s and early 1980s, several students performed their PhDs at the IPS, specializing in various groups of Miocene mammals: Josep Gibert (insectivorans), Josep Vicent Santafé (rhinocerotids), Jordi Agustí (rodents), and Salvador Moyà-Solà (bovids). These researchers further contributed to the discovery of new sites from the Vallès-Penedès Basin (see review in Agustí et al., 1985), whose chronology vastly improved thanks to rodent-based biostratigraphy (Agustí, 1981, 1982; Agustí et al., 1985) and the first paleoecological and paleobiodiversity analyses followed soon thereafter. The latter notably resulted in the discovery of an important extinction event in the European Miocene terrestrial record, the Vallesian Crisis (~9.7 Ma), which allegedly implied the disappearance of most of the taxa adapted to warm and humid forested environments and their replacement by taxa better adapted to more open and drier landscapes (Agustí and Moyà-Solà, 1990; Moyà-Solà and Agustí, 1990). This event has been studied in detail (Agustí et al., 1997, 2003, 2013; Casanovas-Vilar et al., 2014) and latest research has shown that, at least for micromammals, the purported crisis was likely a more protracted turnover event, which merely appears abrupt due to sampling biases (Casanovas-Vilar et al., 2014, 2016a; Madern et al., 2018). During the 1990s, the chronology of the Vallesian sites of the basin was further refined thanks to extensive magnetostratigraphic sampling (Garcés et al., 1996; Agustí et al., 1996b, 1997) and new excavations were conducted, particularly at els Casots and Can Llobateres (CL). The find of a partial skeleton of the hominoid Hispanopithecus laietanus at Can Llobateres 2 (Moyà-Solà & Köhler, 1993, 1996) confirmed the long known potential of the Vallès-Penedès Basin as a promising area for Miocene primate research (e.g., Golpe Posse, 1993).

The last two decades have been characterized by intensive surveying, sampling, and excavation, leading to the discovery of hundreds of new localities, mostly of latest Aragonian and Vallesian age. Many of these were found after the construction of major works such as highways or landfills, including the ACM at els Hostalets de Pierola (see Stop 4). The ACM has been excavated since 2002 and has yielded tens of thousands of vertebrate remains, most famously including the partial skeletons of the primates *Pierolapithecus catalaunicus* and *Pliobates cataloniae* (Moyà-Solà et al., 2004; Alba et al., 2015). All these sites are placed in long and continuous sections and their age has been accurately constrained using a combination of litho-, magneto-, and biostratigraphic methods (Moyà-Solà et al., 2009a; Casanovas-Vilar et al., 2011a, 2016b; Alba et al., 2017, 2022a), which allow for refined paleobiodiversity analyses (Casanovas-Vilar et al., 2014, 2016a). Although the paleontological surveillance performed at ACM had some precedents, such as during the construction of a wastewater treatment plant at EDAR (Checa Soler & Rius Font, 2003), near CL, the great international repercussion of the discovery of Pierolapithecus undoubtedly facilitated subsequent corrective measures in other large-scale construction works, such as the recycling plant of Ecoparc de Can Mata (ECM; Carmona et al., 2011; Alba et al., 2012a), near ACM, the B40 highway between Olesa de Montserrat and Viladecavalls (Alba et al., 2010a), or the road Ronda Oest de Sabadell (ROS; Alba et al., 2020a), among others. On the political side, the visibility granted by Pierolapithecus prompted the refoundation of the IPMC (linked to the Diputació de Barcelona) in 2006 as a CERCA research center with the Generalitat de Catalunya and the Universitat Autònoma de Barcelona as its patrons. This enabled the recruitment of a new generation of vertebrate paleontologists (such as I.C.V., D.M.A., Marc Furió, and Joan Madurell-Malapeira) focused on the study of Neogene vertebrate faunas, ultimately resulting in a huge impulse to research on the Vallès-Penedès vertebrate record. From the 2010s onward, fieldwork has also been directed to the Early and early Middle Miocene part of the record (Ramblian–early Aragonian), which had been largely neglected because it is poorer than younger intervals. These campaigns have resulted in the discovery of several new sites (Casanovas i Vilar et al., 2021) as well as the re-excavation of some major localities, including els Casots (Casanovas-Vilar et al., 2022). The age of many of these sites has been constrained using biostratigraphic data (Jovells-Vaqué & Casanovas-Vilar, 2021) and will further be refined thanks to ongoing magnetostratigraphical studies.

Currently, in the framework of a research project led by D.M.A. and I.C.V., the results of more than a century of research on the Vallès-Penedès terrestrial vertebrate record are being compiled in an online database with accurate information (Casanovas-Vilar et al, 2018a) about localities, taxa, and specimens with the aim of conducting high-resolution paleoecological and paleobiodiversity analyses for particular intervals of interest—namely, the Mid-Miocene Climatic Optimum, the Aragonian/Vallesian transition, and the purported Vallesian Crisis. This project thus aims to combine taxonomic and chronological data (by means of paleobiodiversity dynamics) with paleoecological and ecomorphological data (through isotopic, tooth wear, and ecometric analyses) from the Vallès-Penedès Basin in order to investigate the correlation between paleoenvironmental change and both faunal and functional turnover, with the ultimate goal of assessing to what extent ecosystem evolution is determined by environmental change or by its own intrinsic dynamics. The Vallès-Penedès Basin provides with the necessary chronologic and taxonomic resolution required to test these hypotheses. Thus, although the project is framed within a single basin, the hypotheses to be tested have a wider applicability, because they assess the integration of vertebrate communities as well as to what extent ecosystem dynamics is determined by (or resilient to) environmental change.

Figure 2. Panoramic view of the Vallès-Penedès Basin. The Subirats Castle (in the center-right of the image) is built over the reliefs of the Ordal mountains, which are part of the Littoral Ranges and define the southeastern margin of the basin. The iconic Montserrat mountains in the background are part of the Prelittoral mountain ranges that limit the basin in the northwest. The Miocene outcrop visible at center of the picture corresponds to Langhian marine deposits. Image by M.R. Ferré, courtesy of Ajuntament de Subirats.

STOP 1. SUBIRATS CASTLE: A VIEW OF THE VALLÈS-PENEDÈS BASIN

Geographic coordinates: 41.416725, 1.816327 (WGS84).

Introduction

The Subirats Castle (Subirats, Alt Penedès) was built during the 10th century on top of a small hill as part of a line of fortresses to watch over and guard the southern borders of the Catalan counties from the Muslim-ruled areas of the Iberian Peninsula (Esteve i Gràcia & Pérez Arriaga, 2017). Although it was almost completely destroyed during the Reaper's War in the 17th Century, the castle still offers an excellent panoramic view over the Vallès-Penedès Basin and the Prelittoral Range (Fig. 2).

The Vallès-Penedès is an elongated basin of 100 km length that attains its maximum width, about 14 km, in this area (Fig. 1). This basin formed in the context of the opening of the northwestern Mediterranean and its record is mostly continental, covering most of the Miocene. Hundreds of localities of different ages have yielded Miocene terrestrial vertebrates. Here we provide an updated overview of the geology of the Vallès-Penedès Basin. Further details on the structural geology and tectonics can be found in

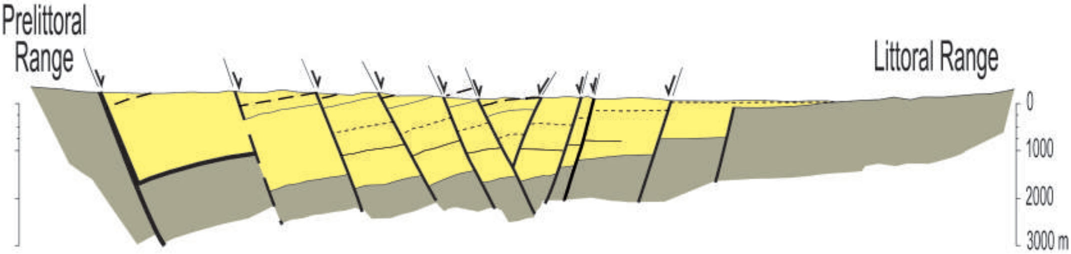


Figure 3. Structural cross-section of the Vallès-Penedès Basin in the Vallès Occidental area based on seismic data and surface geology. Note the half-graben morphology, with greater tectonic activity (allowing for more important sediment accumulation) at the northwestern major fault. Miocene sediments (in yellow) are also affected by normal faults. Modified from Garcés Crespo (1995).

Roca et al. (1999), while main features on Miocene stratigraphy are summarized in Cabrera & Calvet (1996) and Cabrera et al. (2004).

Structural geology of the Vallès-Penedès Basin

The formation of the Vallès-Penedès Basin started during the late Oligocene as the collision between the African and Eurasian plates affected the western Mediterranean. The subduction of the Tethys oceanic crust under the Eurasian plate resulted in the formation of a system of basins and reliefs (horsts and grabens) limited by normal faults of NE–SW and NNE–SSW orientation (Roca & Guimerà, 1992; Roca et al., 1999). These included the Valencia Trough and the Gulf of Lion, which separated Iberia from an uplifted block defined by Corsica, Sardinia, and the Balearic Islands during the late Oligocene (Roca & Guimerà, 1992; Roca et al., 1999). During the latest Oligocene and the Early Miocene, the Iberian margin of the Valencia Trough experienced a process of rifting resulting in the development of several basins parallel to the coastline, which include the Camp de Tarragona, Vallès-Penedès, Baix Llobregat, and Pla de Barcelona basins, among others (Roca & Guimerà, 1992; Roca et al., 1999; Cabrera et al., 2004).

The Vallès-Penedès Basin is a half-graben bounded by the horsts defined by two parallel mountain ranges (Fig. 3): the Prelittoral and Littoral Ranges (jointly known as the Catalan Coastal Ranges). The half-graben basement and surrounding reliefs consist of Paleozoic metasediments and intruded plutonic rocks, which extensively crop out at the Collserola, Montnegre, and Montseny reliefs (Fig. 4). These rocks are unconformably overlaid by terrigenous and carbonate Mesozoic rocks, which in turn are discordantly covered by Paleogene sediments (mostly terrigenous). These younger lithologies of the basement make up most of the Montserrat, Montmell, Garraf and Ordal mountains (Fig. 4). The half-graben is bounded at the northwest by the Vallès-Penedès master fault (Bartrina et al., 1992; Roca et al., 1999; Cabrera et al., 2004). Major features of the stratigraphic record in the Vallès-Penedès half-graben were controlled by tectonic activity of its main bounding faults and sea level changes in the western Mediterranean (Cabrera et al., 1991, 2004; Cabrera & Calvet, 1996). The Vallès-Penedès master fault was tectonically active throughout the Miocene, and even when the rifting phase concluded by the Middle Miocene (late Burdigalian-Langhian), thermal subsidence was concentrated on the northwestern margin, allowing for the accumulation of an important sediment thickness (up to 4000 m; Cabrera et al., 1991, 2004; Bartrina et al., 1992; Cabrera & Calvet, 1996; Roca et al., 1999). In the less tectonically active southeastern margin of the basin (limited by the Littoral Ranges) sediment thickness is notoriously lower (Fig. 3). Until the Middle Miocene the Vallès-Penedès presented the typical graben profile, with tectonic activity in all the bounding faults. However, from then on activity ceased in the southeastern faults and subsidence was concentrated into the northwestern margin effectively turning the basin into a half-graben (Fig. 3). Major and minor faults at the southeastern margin were overlapped by the sedimentary infill during the Burdigalian and Langhian, which, in turn was later affected by fault reactivations (Cabrera Pérez, 1981a; Cabrera & Calvet, 1996).

Main features of the Miocene record of the Vallès-Penedès Basin

The sedimentary infill of the Vallès-Penedès Basin spans from the Early Miocene (Ramblian) to the Late Miocene (Turolian; Fig. 5) and has been informally divided into three main lithostratigraphic units on

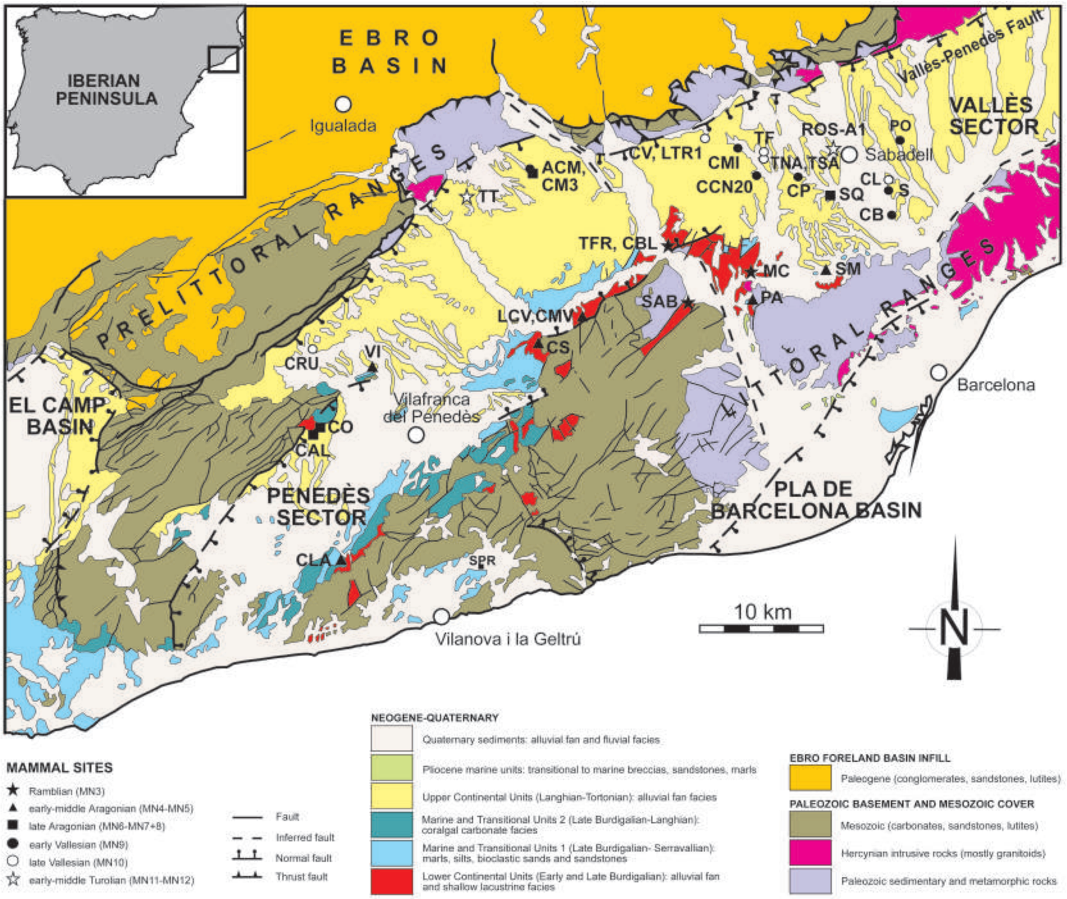


Figure 4. Simplified geological map of the Vallès-Penedès Basin showing major vertebrate sites and their age. Locality acronyms are as follows: ACM = Abocador de Can Mata (including Ecoparc de can Mata; although the symbol used stands for the late Aragonian the series ranges from the late Aragonian to the early Vallesian); CAL = Ca l'Almirall; CB = Castell de Barberà; CBL = la Costablanca; CCN20 = Creu de Conill 20; CL = Can Llobateres; CLA = Clariana paleokarst (also known as la Gornal); CM3 = Can Mata 3; CMI = Can Missert; CMV = Can Martí Vell; CO = les Conilleres; CP = Can Poncic; CRU = Can Cruset; CS = els Casots; CV = Ceràmiques Viladecavalls; LCV = les Cases de la Valenciana; LTR1 = La Tarumba 1; MC = Molí de Can Calopa; PA = les Escletexes del Papiol; PO = Polinyà; ROS-A1 = Ronda Oest de Sabadell A1; S = Santiga; SAB = Sant Andreu de la Barca; SM = Sant Mamet; SQ = Sant Quirze; TF = Torrent de les Febulines; TFR = el Turó de les Forques; TNA = Trinxera Nord Autopista; TSA = Trinxera Nord Autopista; TT = Torrentet dels Traginers; VI = Vilobí del Penedès. Modified from Casanovas-Vilar et al. (2016a)

the scale of a formation (Cabrera et al., 1991, 2004; Cabrera & Calvet, 1996; Casanovas-Vilar et al., 2016a): Lower Continental Units (LCU), Marine and Transitional Units (MTU), and Upper Continental Units (UCC).

The Lower Continental Units

The LCU are mostly defined by characteristically red-colored alluvial fan sediments intercalated with minor lacustrine units ranging from the Ramblian to the middle Aragonian (MN3–MN4, ~20–16 Ma). These units crop out in a narrow fringe close to the southern margin of the basin, attached to the Littoral Ranges, from the Garraf to Collserola mountains (Fig. 4). The age of the LCU and their fossil sites has been constrained by means of litho- and biostratigraphy (Agustí et al., 1985; Casanovas-Vilar et al., 2011b, 2016a; Casanovas i Vilar et al., 2021; Jovells-Vaqué & Casanovas-Vilar, 2021), although it will certainly be

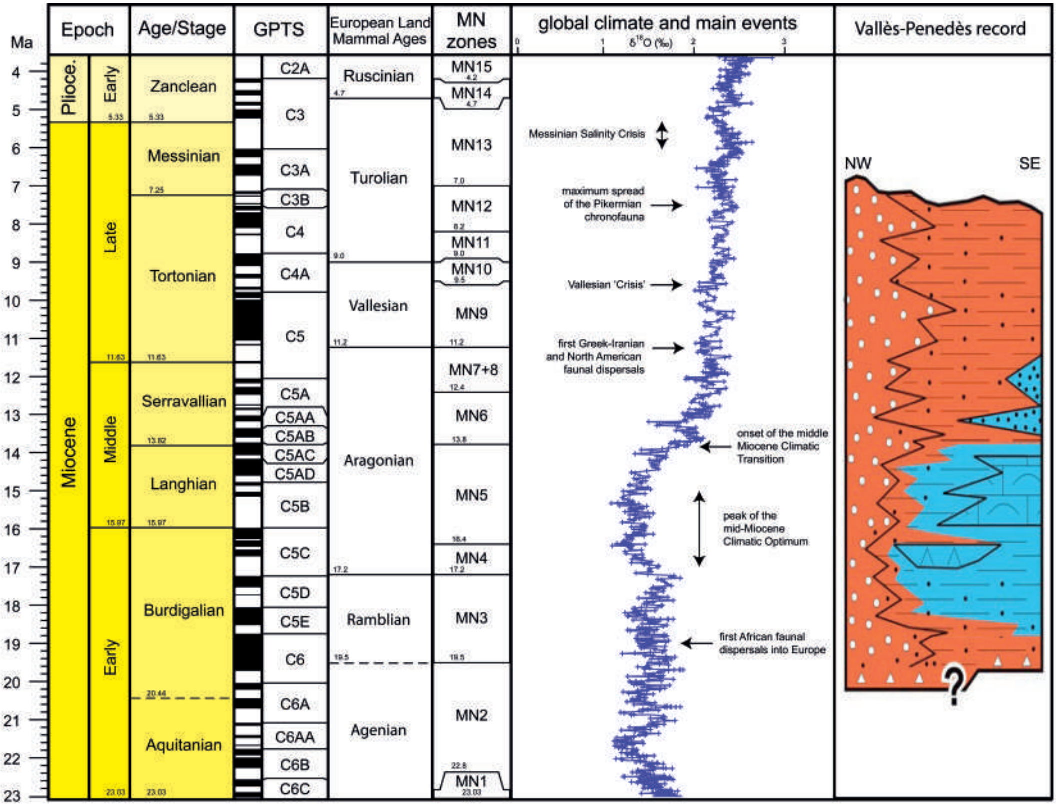


Figure 5. Miocene timescale and global $^{18}\delta$O curve with main climatic and biotic events indicated. The right panel shows a generalized lithostratigraphic framework for the Vallès-Penedès record indicating the relationships between alluvial fan facies (in red) and marine deposits (in blue). Note the important development of marine deposits (including bioconstructed carbonates) during the Langhian and the predominantly alluvial fan sedimentation afterwards. Also observe that the Vallès-Penedès record covers almost the entire Miocene. Timescale and global $^{18}\delta$O curve generated using the software TSCreator 8.0 (Ogg, 2022) and based on Raffi et al. (2020). Lithostratigraphic scheme for the Vallès-Penedès modified from Cabrera et al. (2004).

refined after ongoing magnetostratigraphical studies (Casanovas-Vilar et al., 2018b, 2019a). Their oldest sedimentary record corresponds to clast-supported and coarse-grained breccia deposits (5–10 m thick) that crop out in restricted areas of the basin such as Puig Pedrós (Rubí) or Turó de les Forques (Castellbisbal; TFR). These basal breccias directly erode materials of the basin basement and are interpreted as colluvial material deposited at the base of the hillslopes that defined the margins of the basin (Cabrera Pérez, 1979). They are followed by intensely red conglomerates, sandstones, and mudstones corresponding to alluvial fan facies (Cabrera Pérez, 1979; Cabrera et al., 1991, 2004). Alluvial fans were relatively small and sourced by local catchments from the southeastern reliefs (Fig. 6). This older detrital unit of the LCU includes very few fossil sites all of which indicate a Ramblian (zone A, MN3) age (Agustí et al., 1985; Casanovas-Vilar et al., 2011b, 2016a; Jovells-Vaqué & Casanovas-Vilar, 2018; Jovells Vaqué, 2020).

Shallow lacustrine deposits developed near the southeastern part of the basin and are generally associated with distal alluvial fan facies (Fig. 6). These include Sant Andreu de la Barca (SAB), Costablanca (Castellbisbal; CBL), MC (Rubí), and Subirats lacustrine units (Cabrera Pérez, 1979, 1981b; Cabrera et al., 1991, 2004; de Gibert & Casanovas-Vilar, 2011; Casanovas-Vilar et al., 2016a; Jovell Vaqué, 2020). They are of variable thickness, ranging from ~25 m at Subirats (CS; see also Stop 2; Casanovas-Vilar et al., 2022) to more than 150 m in CBL (Cabrera Pérez, 1979, 1981b; Parcerisa i Duocastella, 2002). Their lithology is also

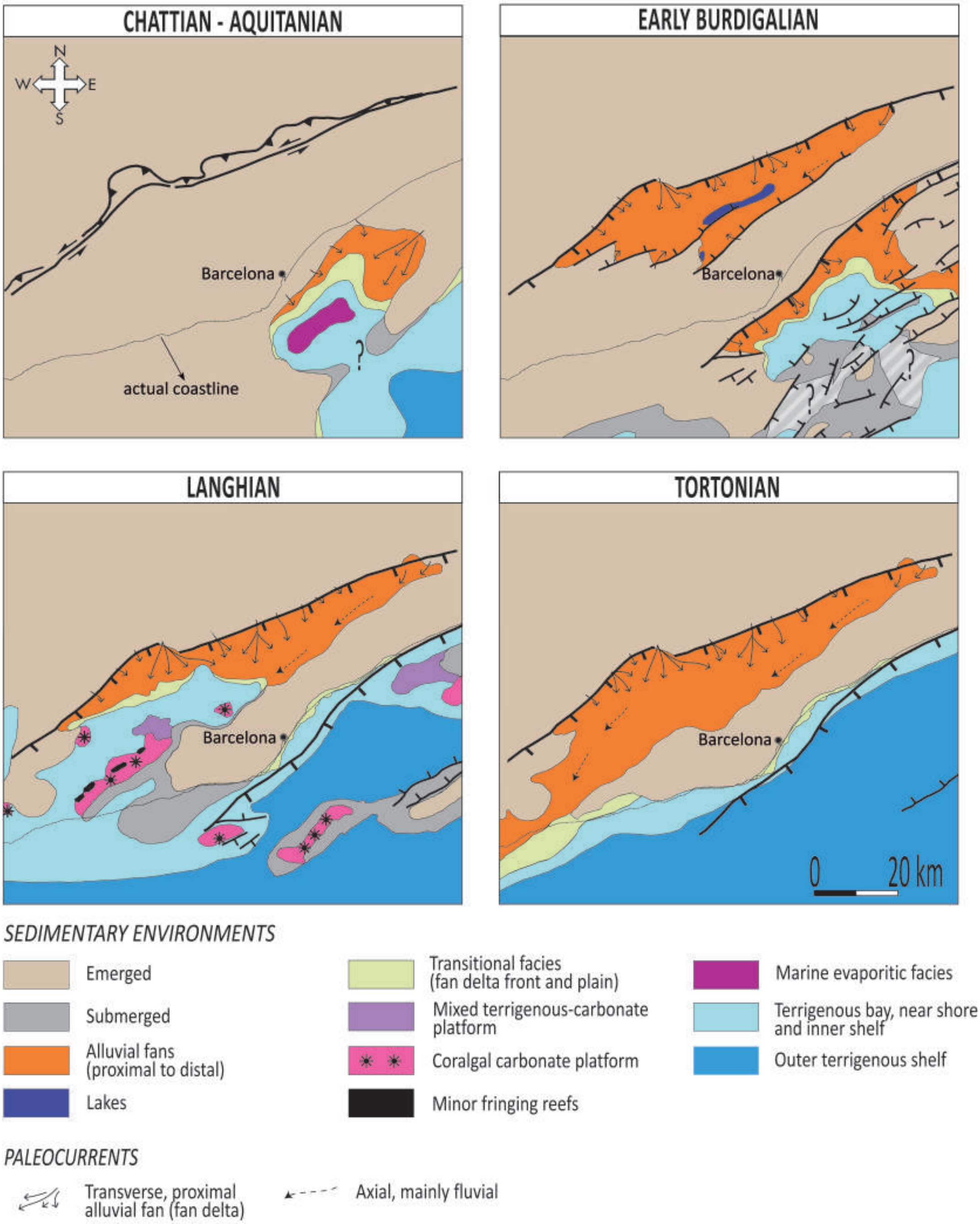


Figure 6. Paleogeographic schemes showing the evolution of the Vallès-Penedès Basin during the latest Oligocene and the Miocene: **a**, Chattian–Aquitanian; **b**, early Burdigalian; **c**, Langhian transgressive maximum; **d**, Tortonian. Modified from Cabrera et al. (2004) and Casanovas-Vilar et al. (2016a).

variable, in the Vallès Sector of the basin (CBL, MC) they show cyclical alternation of lutites, carbonates, and evaporites (gypsum), which indicates shallow ephemeral lakes that would periodically dry out (Cabrera Pérez, 1979, 1981b; Cabrera et al., 1991; Parcerisa i Duocastella, 2002). On the other hand, in the Penedès Sector, the Subirats unit predominantly consists of lutites interbedded with much thinner carbonate and lignite layers and contrasts by its total absence of evaporites (Cabrera Pérez, 1979, 1981b; Agustí Ballester & Cabrera Pérez, 1980; de Gibert & Casanovas-Vilar, 2011; Casanovas i Vilar et al., 2021; Casanovas-Vilar et al., 2022). These lake deposits comprise the richest Early and early Middle Miocene vertebrate sites in the basin (Agustí et al., 1985; Casanovas-Vilar et al., 2016a; Casanovas i Vilar et al., 2021; Jovells-Vaqué & Casanovas-Vilar, 2021) and in many cases have also yielded macroflora (Sanz de Siria Catalán, 1993). The various lacustrine units formed at different times; in the Vallès they date back to the Ramblian (zone A, MN3), while in the Penedès they are early Aragonian in age (subzones Ca and Cb, MN4–MN5; see Casanovas-Vilar et al., 2011b, 2016a; Jovells Vaqué, 2020; Casanovas i Vilar et al., 2021; Jovells-Vaqué & Casanovas-Vilar, 2021).

Finally, these lacustrine units are overlain by red-orange conglomerates, sandstones, and lutites, which again correspond to alluvial fan deposits. However, alluvial fans were sourced from the northwestern margin reliefs and covered wider areas than the older deposits sourced from the southeastern margins (Fig. 6; Cabrera Pérez, 1979, 1981b; Cabrera et al., 1991, 2004). This unit includes few fossil sites and is better represented in the Vallès Sector of the basin, where it may be as much as 580 m thick (Rubí; Parcerisa i Duocastella, 2002).

The Marine and Transitional Units

During the latest Early Miocene and the beginning of the Middle Miocene (Langhian), several sea-level changes took place in the context of the MCO (Zachos et al., 2001). The Littoral Ranges defined an important relief isolating the Vallès-Penedès from the Mediterranean, but the basin was still open to the sea on its southwestern extreme, so that part of the basin was flooded during sea-level highstands (Figs. 5–6). These resulted in the deposition of the MTU, which are better developed in the southwestern half of the basin (Penedès Sector) because it was more directly connected to the sea. At least three different episodes of marine transgression and regression affected the Vallès-Penedès (Fig. 5; Cabrera et al., 1991; Cabrera & Calvet, 1996; de Gibert & Casanovas-Vilar, 2011; Casanovas-Vilar et al., 2016a):

(1) Late Burdigalian?–early Langhian (latest Early Miocene–early Middle Miocene). Sediments belonging to this unit only crop out at Vilobí del Penedès (VI) and consist of notably thick (up to 60 m) gypsum that was deposited in coastal playa lakes (sabkha). These are followed by ocher to reddish lutite layers and gray marls, being ultimately capped by an oyster-rich biocalcarenite (Agustí et al., 1990). Planktonic foraminifera recovered from the gray marls indicate a late Burdigalian to Langhian age (Magné, 1978) while the oyster layers have also yielded small mammal remains (VI) that indicate an early MN5 age (early Aragonian, subzone Cb; Jovells Vaqué, 2020; Jovells-Vaqué & Casanovas-Vilar, 2021).

(2) Langhian (early Middle Miocene). Marine environments attained their maximum development during the Langhian (15.97–13.65 Ma; Fig. 6), when most of the Penedès Sector was persistently flooded. Marine deposits in that area are thick and rich in marine fauna (Domènech et al., 2011a; see Stop 3). During transgressive maxima the sea extended into the Vallès Sector, reaching Sant Cugat del Vallès and Cerdanyola del Vallès. Poorly developed shallow marine and transitional deposits can be found in these areas. Langhian deposits comprise sandstones and lutites deposited in transitional fan-delta systems that laterally grade to grayish-bluish marls rich in fauna, which correspond to shallow marine environments (see Stop 3). At the same time, carbonate platform deposits developed close to the southeastern margin of the basin. An important fringing reef system was formed bordering the Garraf mountains (Permanyer i Bastardas, 1990) while much smaller patch reefs also developed in small elevations, such as the Can Sala coral reef in Subirats (Fig. 6; see Stop 3; Bessedik & Cabrera, 1985; Permanyer i Bastardas, 1990; Cabrera et al., 1991). When sea level regressed, these reef systems were overlain by alluvial fan facies corresponding to the UCU. However, part of the fringing reef system at Castellet i la Gornal was exposed, and this implied the formation of karstic fissures that include abundant micromammal remains as well as some macromammals (Clariana paleokarst, CLA). Preliminary studies of the recovered fauna indicate a late MN5 (latest middle Aragonian) age

(Casanovas i Vilar et al., 2021).

(3) Serravallian (late Middle Miocene). These deposits correspond to mixed terrigenous-carbonate platform that only crop out at the southwestern margin of the basin, near el Vendrell, although they are much developed in the nearby el Camp de Tarragona Basin, located southwards. Recent fieldwork in the Alt Penedès (Sant Jaume dels Domenys) indicates that some marine and transitional deposits in this sector may be younger, dating back to the early Tortonian (early Late Miocene).

The Upper Continental Units

From the early Serravallian (late Aragonian) until the Tortonian (middle Turolian) sedimentation was again dominated by alluvial fans which define the UCU. The Vallès-Penedès master fault remained active until the Tortonian, and tectonic subsidence controlled the evolution of alluvial fan systems, which were sourced from the northwestern reliefs (Fig. 6; Agustí et al., 1985, 1997; Cabrera & Calvet, 1996; Garcés et al., 1996; de Gibert & Casanovas-Vilar, 2011). Alluvial fan sequences are thicker near the tectonically active northwestern margin of the basin, where they may attain as much as 1000 m (Bartrina et al., 1992; Cabrera & Calvet, 1996). Several alluvial fan systems can be identified; from southeast to northwest these are: Torrelles de Foix, els Hostalets de Pierola, Collbató, Olesa-Les Fonts, Terrassa-Viladecavalls, and Granollers (Garcés Crespo, 1995; Garcés et al., 1996; Casanovas-Vilar et al., 2008a; de Gibert & Casanovas-Vilar, 2011). The Olesa-Les Fonts alluvial fan system was by far the most important, expanding over a radius of 10 to 15 km, its distal facies reaching the southern margin of the basin and perhaps even prograding over the margin reliefs (Garcés Crespo, 1995; de Gibert & Casanovas-Vilar, 2011; Casanovas-Vilar et al., 2016a). The proximal coarse-grained facies were deposited near the northwestern margin of the basin, whereas the mudstone-dominated medial to distal facies spread towards the south and southeast. The middle and distal areas of these fan systems interfered and coalesced with each other during their evolution. The lithology of the UCU resembles that of the older LCU, though their deposits are not predominantly red, ocher, yellowish, and grayish tones being more common, particularly in the distal alluvial fan facies.

Most of the vertebrate-bearing sites of the Vallès-Penedès occur in the distal to terminal, mudstone-dominated facies (Fig. 4). These formations have been systematically sampled since the 1940s and even represent the type area for an European Land Mammal Age, the Vallesian (Crusafont Pairó, 1950; Crusafont Pairó & Truyols Santonja, 1960), currently known to range from 11.2 to 8.9 Ma (Van Dam et al., 2001, 2006; Casanovas-Vilar et al., 2016b). To date, hundreds of fossil localities from the Vallès-Penedès Basin, ranging in age from the late Aragonian to the middle Turolian, have yielded tens of thousands of remains (Casanovas-Vilar et al., 2016a, 2016b; Alba et al., 2022a). Most of the sites are located in the Can Mata area, including ACM and various historical localities in the fossiliferous area of els Hostalets de Pierola (Penedès Sector; see Stop 4), as well as around the cities of Sabadell, Terrassa, and Sant Quirze del Vallès (Vallès Sector). Detailed bio- and magnetostratigraphic analyses allow for a high dating accuracy for this part of the record (Garcés et al., 1996; Agustí et al., 1997; Moyà-Solà et al., 2009a; Casanovas-Vilar et al., 2011a, 2016a, 2016b; Alba et al., 2017, 2019, 2022a; see Stop 4).

During the latest Miocene, sedimentation was truncated by the end of the tectonic subsidence at the northwestern margin of the basin and the Messinian Salinity Crisis (5.96–5.33 Ma; Fig. 5). Sea-level lowering during the Messinian resulted in the development of deeply entrenched erosive surfaces affecting both the basement and earlier Miocene sequences (Cabrera & Calvet, 1996).

Pliocene and Quaternary deposits

The continental Early Pliocene (Zanclean) is scarcely represented at the Vallès-Penedès Basin by alluvial-fluvial deposits near Piera (Gallart, 1981). During the Zanclean, an important marine transgression flooded many coastal basins (Martinell, 1988). These Early Pliocene deposits are rich in marine invertebrates and well developed in the nearby Llobregat River valley, where they lay discordantly over Miocene and basement deposits. However, in the Vallès-Penedès Basin they are restricted to just a small area near Castellbisbal. Finally, Pleistocene and Holocene alluvial and colluvial sediments were deposited unconformably over the Neogene series. Some of them have yielded abundant vertebrate remains from the late Early and early Middle Pleistocene, such as those of Cal Guardiola and Vallparadís Estació sites in the Vallparadís section (Madurell-Malapeira et al., 2010).

Figure 7. Reconstruction of the fauna and paleoenvironment of els Casots. In the foreground the felid "*Pseudaelurus*" *lorteti* stares at a large amphycionid that has hunted an individual of the suid E*urolistriodon adelli*. Behind them, three individuals of the palaeomerycid *Ampelomeryx ginsburgi* walk away. To their left and in the background, partly hidden behind a palm, there is the cervid *Procervulus* cf. *dichotomus*. The crocodylian *Diplocynodon ratelii* can be seen resting in the lake. In the background, a herd of *Gomphotherium* cf. *subtapiroideum* approaches the lake shore. Plant remains at els Casots are too fragmentary, so the reconstructed vegetation is based on that from contemporaneous nearby sites (see Sanz de Síria Catalán, 2001). Large plants include the palm *Sabal* and leguminous trees *Acacia* and *Mimosa*. Bushes in the foreground are *Caesalpinia* and *Cassia*, whereas reeds (*Typha*) grow abundantly on the lake shore. Paleoart by Ó. Sanisidro, courtesy of Ajuntament de Subirats.

STOP 2. ELS CASOTS: AN EXCEPTIONAL SITE FROM THE MIOCENE CLIMATIC OPTIMUM

Geographic coordinates: 41.415998, 1.812035 (WGS84).

Introduction

The MCO is the most recent and prolonged global

Geographic coordinates: 41.415998, 1.812035 (WGS84).

Introduction

The MCO is the most recent and prolonged global warming episode. This event marked the Early to Middle Miocene transition (peaking between ~17–15 Ma; Fig. 5; Zachos et al., 2001) and interrupted the long-term Cenozoic cooling trend and Antarctic glaciation, which had started by the late Eocene. With estimated mid-latitude atmospheric temperatures 5–7 °C warmer than today and only moderately higher *p*CO2 levels (~400–600 ppm; Shevenell et al., 2008; Foster et al., 2012; Steinthorsdottir et al., 2021a), the MCO has been proposed as a particularly good analog for future global warning scenarios (Steinthorsdottir et al., 2021b). On the other hand, the MCO coincided with the dispersal of several new groups into Western Europe which, contrary to earlier Miocene dispersals, were not facilitated by new continental connections. These newcomers include, for example, modern cricetid rodents and bovids, which turned into major components of the Middle and Late Miocene faunas.

This time interval is very well represented in the Vallès-Penedès Basin by several sites that have yielded both large and small vertebrates (Casanovas-Vilar et al., 2016a; Casanovas i Vilar et al., 2021). However, the site of CS in Subirats (l'Alt Penedès, Barcelona) stands out as one of the richest sites in the whole basin (Fig. 7). Even though in the late 19th Century some vertebrate fossils had been found in the now abandoned coal mines near CS (Almera, 1898; see also Introduction), this particular site was discovered by an amateur fossil hunter in 1989. Salvador Moyà-Solà from the IPS led several systematic excavation campaigns between 1989 and 1993, resulting in the recovery of more than 3,000 macrovertebrate remains (Moyà-Solà & Rius Font, 1993). In 1995, the site was acquired by City Council of Subirats and eventually protected as cultural heritage by the Generalitat de Catalunya. However, excavations were interrupted because of the limited funding and personnel available. Nevertheless, the study of the fauna sporadically continued during the 1990s and 2010s, mostly focusing on artiodactyls (Pickford and Moyà-Solà, 1994, 1995; Duranthon et al., 1995; Alba et al., 2014) and, to a lesser extent, rodents (Agustí & Llenas, 1993; Jovells-Vaqué et al., 2017) and reptiles (Díaz Aráez et al., 2017). The ICP finally resumed fieldwork in 2018, and currently yearly campaigns are conducted at the site. New studies on the CS fauna have been recently published, including a synthetic paper on the geology, age, biota, and paleoenvironment of the site (Casanovas-Vilar et al., 2022). Simultaneously the Subirats municipality has undertaken different actions to protect the site and promote its paleontological heritage.

Geological setting, stratigraphy, and age

Els Casots site is located at the southern margin of the Vallès-Penedès Basin, just over the pre-Miocene basement defined by the Catalan Coastal Ranges (Figs. 4, 8). The morphology of the basement at the CS area has been studied by means of geoelectrical prospection methods (Casanovas-Vilar et al., 2022), which revealed that it consists of Mesozoic (mainly Early Cretaceous) marine carbonates which also define the surrounding reliefs. During the Early and Middle Miocene these rocks defined a weathered, eroded and karstified paleorelief that was soon covered by Miocene sediments. Later on, the basement and Miocene sediments were affected by faults related to extensional processes in the area (Casanovas-Vilar et al., 2022).

In the Vallès-Penedès Basin, the Early to early Middle Miocene (Ramblian–early Aragonian) is recorded by the sequences of the LCU (Fig. 4), an extensive lithostratigraphic unit that mostly crops out near the southern margin of the basin (see Stop 1; Cabrera et al., 1991; Casanovas-Vilar et al., 2016a; Casanovas i Vilar et al., 2021). This unit consists of intensely red alluvial fan facies sourced from the surrounding reliefs and minor cyclically-arranged alluvial-shallow lacustrine facies of various ages (Agustí Ballester & Cabrera Pérez, 1980; Cabrera Pérez, 1981a, 1981b). These correspond to small lacustrine areas that developed in the lowlands and include the major paleontological sites of this age, such as CS, which is part of the Subirats alluvial-lacustrine unit (Casanovas-Vilar et al., 2016a; Jovells-Vaqué et al., 2018; Casanovas i Vilar et al., 2021). The Miocene stratigraphy at the site area has been studied by means of geological core sampling (Fig. 9; Casanovas-Vilar et al., 2022). The cores reached the pre-Miocene basement and revealed that it is overlain

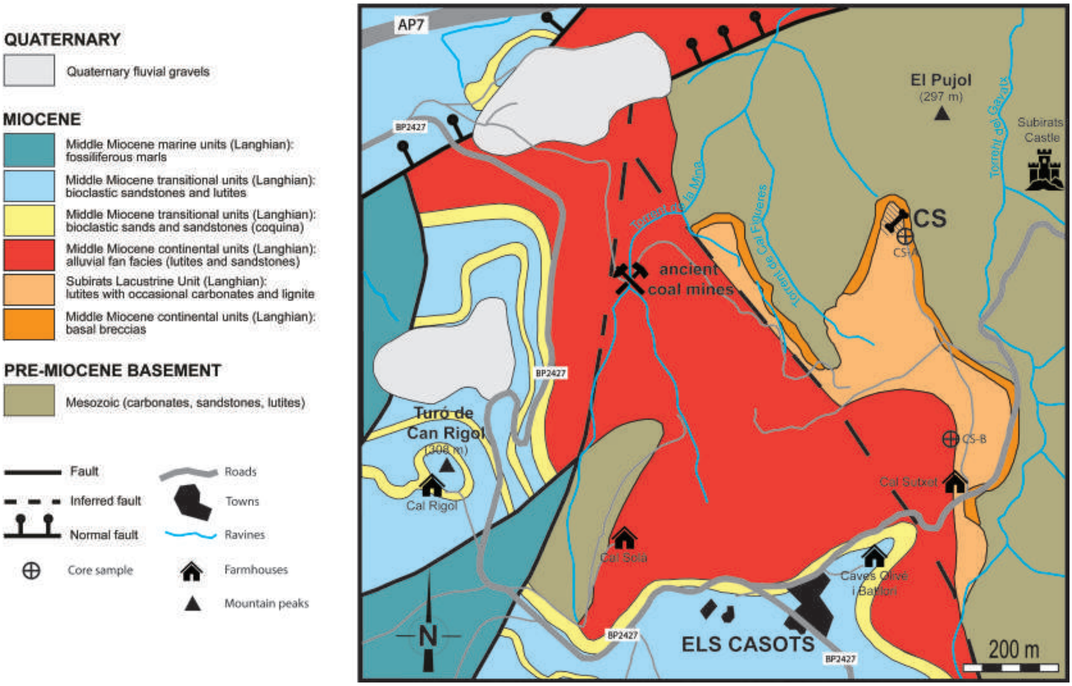


Figure 8. Detailed geological map of the area around els Casots, showing the location of the fossil site and core samples (see Fig. 10). Observe the proximity of els Casots to the ancient coal mines as well as its situation directly overlying the Mesozoic basement. Also notice the close proximity of the site to the first Middle Miocene (Langhian) transitional and marine deposits. Modified from Casanovas-Vilar et al. (2022).

by matrix-supported scree breccias that include some macrovertebrate remains. Such breccias also crop out near the excavation area (e.g., east of Cal Sutxet farmhouse and in the road leading to the site; Fig. 8). They are followed by a 25 m-thick, cyclically arranged mudstone/limestone succession that also includes thin (mm to dm-thick) coal deposits at the bottom. The carbonate layers, which can be up to a couple of meters thick, include bioclastic laminae made up of accumulations of ostracods, charophytes and micrite-coated algal filaments. This lacustrine/marshy lacustrine succession has yielded abundant vertebrate fossils in the excavated area. The lacustrine succession ends rather abruptly and is topped by mottled silts and sandstones, and finally carbonate-rich pedogenic to palustrine facies devoid of vertebrate fossils (Fig. 8). They are overlain by red mudstones and green/gray sandstones that record subaerial distal channelized alluvial fan facies which crop out west of the Cal Sutxet farmhouse (Fig. 8). Finally, following the road in direction to the cellar Caves Olivé i Batllori (Fig. 9) the continental deposits are in turn overlain by an oyster coquina and a bioclastic sandstone, which marks the early Langhian transgressive surface in this sector.

Els Casots has been usually correlated to unit MN4, which corresponds to the early Aragonian, i.e., the latest Early Miocene (e.g., Agustí et al., 1990; Agustí & Llenas, 1993; Casanovas-Vilar et al., 2016a; Jovells-Vaqué et al., 2017). Such correlation was mostly based on the rodent fauna, which includes the modern cricetids *Democricetodon hispanicus* and *Megacricetodon primitivus* together with the eomyid *Ligerimys ellipticus*. The MN4/MN5 boundary was previously defined by the extinction of the genus *Ligerimys*, but the persistence in the Iberian Peninsula of the endemic species *L. ellipticus* implied a diachronous boundary when compared to Central Europe, so that the extinction of *Ligerimys florancei* (common to both areas) was proposed as diagnostic criterion instead (Hilgen et al., 2012; Van der Meulen et al., 2012). Therefore, CS must be correlated to MN5, more precisely to the Aragonian local biozone Cb (see Van der Meulen et al., 2012), which corresponds to the earliest Middle Miocene. The geological cores

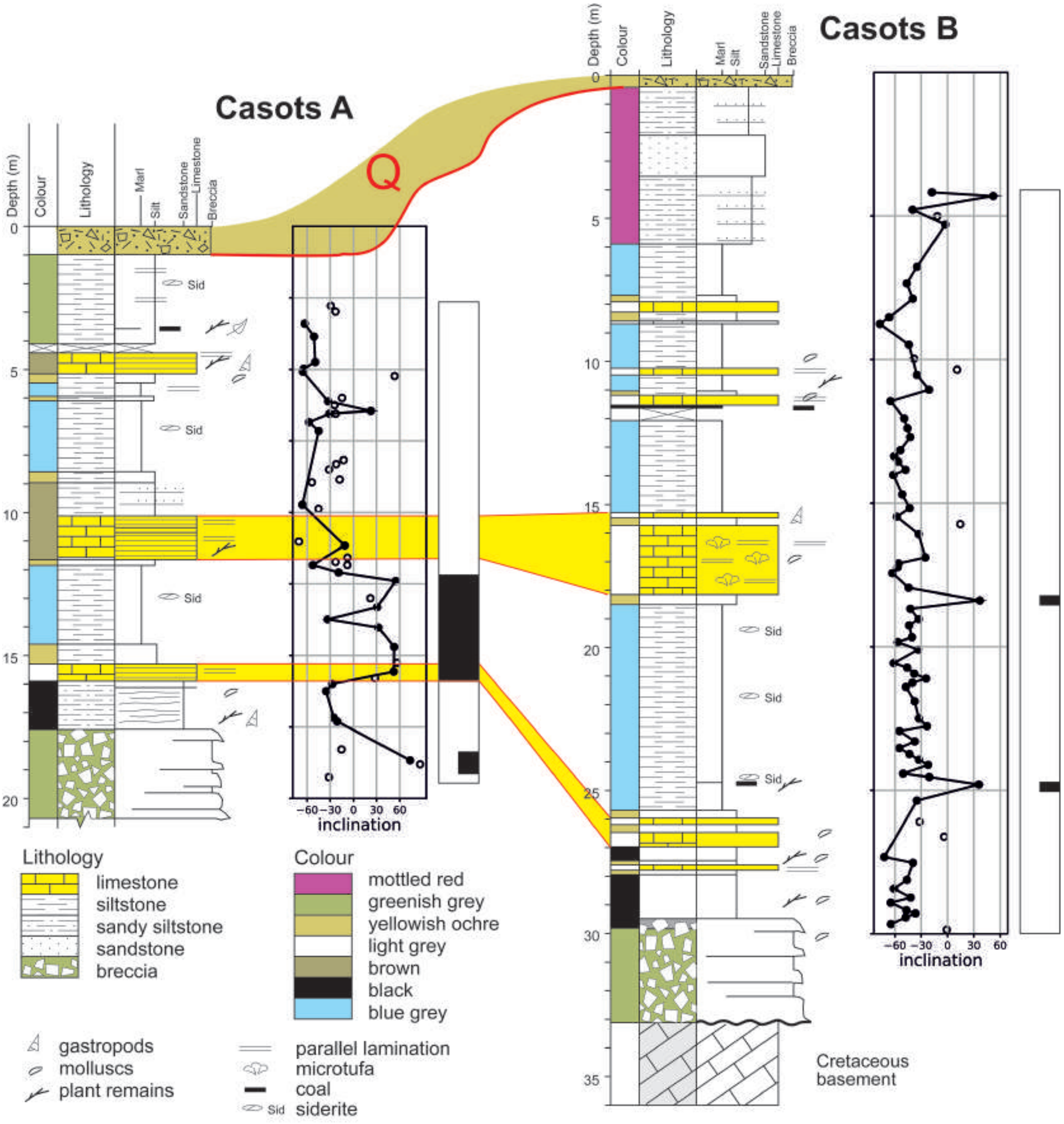


Figure 9. Stratigraphic logs of cores Casots A and B (see Fig. 9) and palaeomagnetic inclination from studied samples. Positive inclinations represent normal polarity (in black) and negative inclinations represent reverse polarity (white). Black circles indicate directions of best quality (Quality 1), while white circles indicate directions of lower quality (Quality 2). Note the long reverse polarity interval in CS-B core. modified from Casanovas-Vilar et al. (2022).

taken at CS were sampled for magnetostratigraphy and the whole series yielded reverse polarity, except for brief normal polarity signals which are attributed to secondary magnetization (Fig. 9). Biostratigraphical constraints favor a correlation with chron C5Br (15.974–15.160 Ma; boundaries after Ogg, 2020) and result in an estimated age of ~15.9 Ma for the site of els Casots (Casanovas-Vilar et al., 2022).

Biota

A complete, updated overview of the Casots biota can be found in Casanovas-Vilar et al. (2022); here we

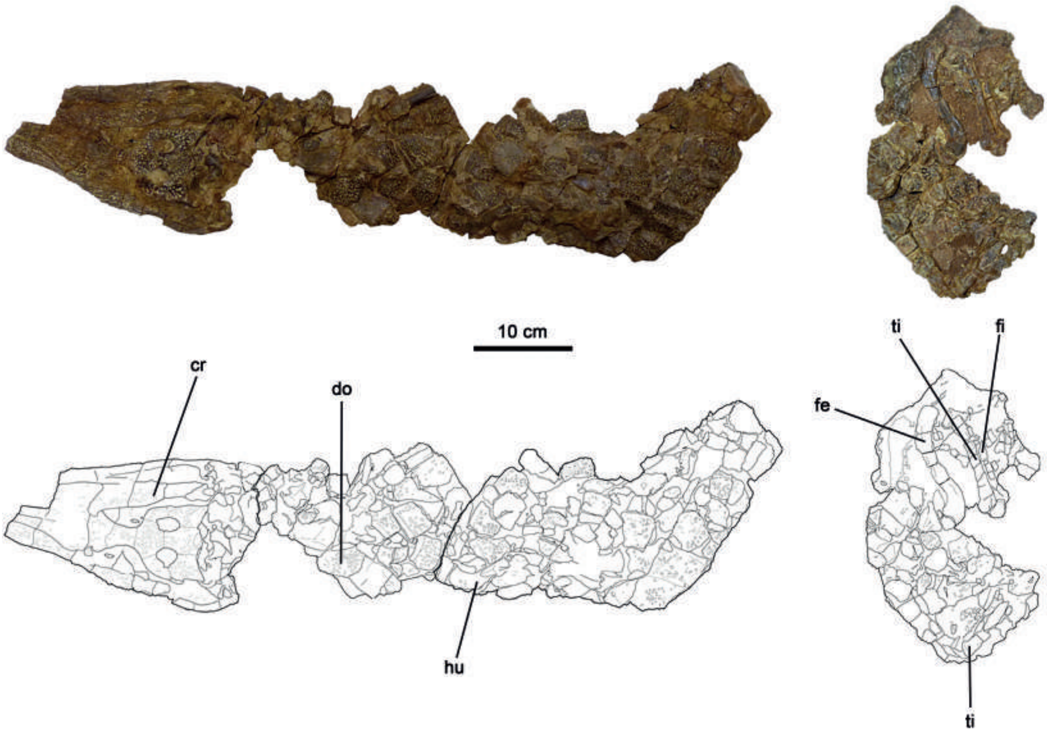


Figure 10. Partial skeleton of the crocodilian *Diplocynodon ratelii* (field number CS-558) recovered in the 2021 field campaign at els Casots. Most of the bones and osteoderms are in anatomical connection. The schematic drawing below indicates some of the recovered elements. Anatomical abbreviations: cr = cranium; do= dorsal osteoderms; fe = femur; fi = fibula; hu = humerus; ti = tibia. Photograph and drawing by P. Logrosan Soriano, © Institut Català de Paleontologia Miquel Crusafont.

summarize the results of that paper. Poorly preserved plant remains have been recovered from many of the excavated layers and include leaf fragments of plants growing at the edges of the lake (reeds and sedges) as well as some wood fragments. Charophyte algae and other microfossils have been recovered after screen-washing (Sanjuan et al., 2022). Other taxa inhabiting freshwater environments include ostracods, gastropods, fishes, amphibians (three species of anurans and one urodele), pond turtles (*Ptychogaster* sp.) and abundant remains of small-sized crocodylians (*Diplocynodon ratelii*). The latter include complete skulls (Díaz Aráez et al., 2017) and even an articulated skeleton found during the 2021 campaign (Fig. 10). The herpetofauna also features terrestrial tortoises, including the giant *Titanochelon* sp.; a diverse lizard fauna (at least 8 different species) that comprises gekkotans, lacertids, anguids, varanids, and amphisbaenians; and various snakes (4–5 different species), including a pythonid (*Phyton* sp.). Bird remains are rare and include a few bones attributed to diurnal and nocturnal raptors as well as to the peafowl *Miophaisanus altus*.

Figure 11. Almost complete mandible of the gulonine mustelid *Iberictis buloti* (field No. CS-150) recovered in the 2019 campaign at els Casots. Photograph by I. Casanovas-Vilar © Institut Català de Paleontologia Miquel Crusafont.

Small mammals are abundant in all fossil-bearing horizons and include one of the latest occurrences in the Iberian Peninsula of the marsupial *Amphiperatherium frequens*. Chiropterans are rare, contrary to insectivorans (Eulipotyphla) which include erinaceids (*Galerix symeonidisi*), heterosoricids (*Heterosorex neumayrianus*), soricids (*Paenelimnoecus* cf. *truyolsi*) and dimylids (cf. *Plesiodimylus*). The insectivoran assemblage is somewhat poorer than that of MN3–MN4 sites of the same basin (Van den Hoek Ostende et al., 2020) and is overwhelmingly dominated by *G. symeonidisi*. Lagomorph remains are abundant and are attributed to the genus *Lagopsis*. Rodents are incredibly diverse (19 species), with glirids and cricetids being the most common elements. Cricetids are represented by a few teeth belonging to the archaic form *Melissiodon*, which has here one of its latest records, and abundant material belonging to the modern cricetids *Democricetodon* (*De. hispanicus* and *Democricetodon gracilis*, plus a larger indeterminate species) and *M. primitivus* (Jovells-Vaqué et al., 2017; Jovells-Vaqué & Casanovas-Vilar, 2021). Glirids comprise 9 different species, the most abundant being *Simplomys simplicidens*, a form with simple dental pattern typically associated with open and arid environments. Presumably arboreal/scansorial glirids, characterized by their more complex dental patterns (Van Dam, 2006), are generally scarce. Sciurids in turn, solely include terrestrial forms (xerines), such as Heteroxerus rubricati and *Atlantoxerus idubeidensis*. Finally, eomyids are represented by a few teeth of *Ligerimys ellipticus*, the last surviving species of the genus, which disappeared from central Spain at 15.93 Ma (Van der Meulen et al., 2012).

Carnivorans are well represented and include small-sized forms such as mustelids (*Iberictis buloti*, Fig. 11; *Paralutra* sp.; and two species of '*Martes*'), herpestids (*Leptoplesictis aurelianesis*), and hyaenids (cf. *Protictitherium* sp.). Larger carnivorans comprise two undescribed amphycionid species of different size, one being represented by a partial skeleton; hemicyonids (*Hemicyon stehlini*); and abundant remains, including complete crania, of the lynx-sized felid '*Pseudaelurus*' *lorteti*. Carnivoran coprolites have been found during the latest campaigns and are currently under study.

Among ungulates, rhinocerotids stand out as one of the most abundant elements and include the poorly-known, long-legged *Dromoceratherium mirallesi*, present at somewhat older sites of the Vallès-Penedès Basin (Crusafont et al., 1955), and a second indeterminate species. In contrast, the equid *Anchitherium* is only represented by a lower molar fragment at els Casots (Rotgers & Alba, 2011). Artiodactyls are one of the most diverse and better-studied groups. Non-ruminant artiodactyls consist of the small-sized *Cainotherium miocaenicum* (Cainotheriidae) and two suoids for which els Casots is the type locality: the small 'peccary-like' *Choeromorus ibericus*, best represented by a crushed skull (Pickford & Moyà-Solà, 1994; Pickford, 2017), and the larger listriodontine *Eurolistriodon adelli*, represented by a skull with associated partial skeleton (Pickford and Moyà-Solà, 1995). Ruminants include several dentognathic fragments of the tragulid '*Dorcatherium*' *crassum* (see Alba et al., 2014) as well as abundant material, such as complete crania and articulated skeletons of various individuals, belonging to the paleomerycid *Ampelomeryx ginsburgi* (Fig. 12), a species erected based on the CS material (Duranthon et al., 1995). Other ruminants include the cervid *Procervulus* cf. *dichotomus*, which is quite common, and rare remains of the lagomerycid *Lagomeryx rutimeyeri*. Finally, the bovid *Eotragus noyei*, is profusely represented by dentognathic remains and even a partial skeleton. The faunal list is completed with two species of proboscideans: the gomphothere *Gomphotherium* cf. subtapiroideum and the deinothere *Prodeinotherium* cf. *bavaricum*. The former is more common and is represented by cranial material and even a partial skeleton, whereas only a few cheek teeth of *Prodeinotherium* have been found to date (Gasamans et al., 2021).

The CS fauna shows some biogeographical affinities with Central Europe. Among small mammals, these refer to the presence of dimylids (Van den Hoek Ostende et al., 2020) and the cricetid *Melissiodon* sp. (Jovells-Vaqué & Casanovas-Vilar, 2018), which are absent from contemporaneous sites of inner Spain. On the other hand, the cricetid *De. hispanicus* is restricted to Iberia but there are also a few remains of *De. gracilis*, a common component of central European faunas that had only been previously recorded from the Ebro Basin in Spain (Jovells-Vaqué & Casanovas-Vilar, 2021). Concerning the larger mammals, the suoid *Choeromorus* is common in France and Central Europe, but unknown from inner Spain, its presence being restricted to Catalonia and Valencia (Bunyol). The rarity of *Anchitherium* at els Casots and other Vallès-Penedès sites as compared to its abundance in the inner Iberian basins is also remarkable and further indicates biogeographic differences. Throughout the Miocene, Catalonia (and the Vallès-Penedès Basin in particular) has been recognized as a transitional area between the more humid and forested environments

Figure 12. Cast of the holotype of the palaeomerycid *Ampelomeryx ginsburgi* (IPS10610) from els Casots. The cranium corresponds to an adult male and is only slightly deformed. Photograph by P. Figuerola © Institut Català de Paleontologia Miquel Crusafont.

of central Europe and the drier landscapes of inner Iberia (Casanovas-Vilar et al., 2005, 2008a). Els Casots and other sites show that this situation already existed during the Early and early Middle Miocene, and is more evident in the case of small mammals (Van den Hoek Ostende et al., 2020; Jovells-Vaqué & Casanovas-Vilar, 2021). Yet, affinities with inner Iberian basins were higher than in younger intervals (late Aragonian, Vallesian).

Taphonomy and paleoenvironment

Vertebrate fossils have been recovered from all excavated levels at CS. Macrovertebrate remains often occur in high concentrations, often belonging to partially articulated individuals (e.g., Fig. 10), and do not show signs of transport. Although detailed taphonomic analyses have yet to be conducted, we interpret that the biota from CS represents an autochthonous to parautochthonous assemblage (Casanovas-Vilar et al., 2022). Lithostatic pressure has resulted in extensive crushing and deformation of many remains.

Sedimentological evidence, as well as the presence of charophytes, helophytic plants, freshwater gastropods, fishes, crocodylians and pond turtles, all indicate that els Casots represents a shallow freshwater lacustrine-palustrine environment (Fig. 7; Casanovas-Vilar et al., 2022). Carophyte assemblages provide further details, as they solely comprise *Chara* cf. *vulgaris* and *Chara molassica* var. *notata*, which indicate very shallow, eutrophic freshwater lakes (Sanjuan et al., 2022). In addition, rare and abraded tests of the Miocene rotaliid foraminifer *Ammonia* sp. have been found. These suggest that the coastline was probably just a few meters away from the site and were washed into the lake during storm events. The mammal assemblage also includes semiaquatic (the otter *Paralutra*) and aquophilous elements (the chevrotain '*Dorcatherium*'). *Ampelomeryx*, which is abundantly represented at the site, as well as many other paleomerycids are thought to be linked to very humid environments, presumably boggy forests, where they would have fed on soft vegetation (Köhler, 1993; DeMiguel et al., 2014). Stratigraphic data show cyclical fluctuations in the water level, probably related to climatic cycles and evidencing rainfall seasonality. The presence of some megathermic taxa, such as the crocodylians, monitor lizards, or pythonid and boid snakes, are consistent with the high temperatures associated with the MCO. The herbivores include only browsing species, many of them of relatively small size (e.g., *Choeromorus*, *Lagomeryx*, *Procervulus*), which likely inhabited forested environments. However, small mammals include relatively few arboreal (only some dormice but no tree or gliding squirrels) and insectivorous species (four insectivorans plus the marsupial *Amphiperatherium* and, probably, the cricetid *Melissiodon*). Since the number of arboreal and insectivorous species is positively correlated to precipitation and environmental humidity (Van Dam, 2006), this may indicate that more open environments were also present.

We interpret that dense forest environments were restricted to the lake surroundings, whereas not far from the wetlands more open and arid woodlands occurred (Fig. 7; Casanovas-Vilar et al., 2022). This is consistent with macrofloral (Sanz de Siria Catalán, 2001) and palynological (Bessedik & Cabrera, 1985; Jiménez-Moreno & Suc, 2007; see also Stop 3) data from slightly younger Langhian deposits of the same area, which indicate subtropical environments with seasonal rainfall. Scattered forests rich in tropical elements would have developed near the humid areas and in the mountains at low altitudes.

Figure 13. Detail of a massive coral colony corresponding to the reef core of the Can Sala Langhian coral reef. Coral colonies can be several decimeters in diameter and are affected by diagenesis (dissolution, recristalization). Photograph by I.C.V., © Institut Català de Paleontologia Miquel Crusafont

STOP 3. CAN SALA REEF: THE LANGHIAN COASTAL ENVIRONMENTS

Geographic coordinates: 41.389053, 1.811793 (WGS84).

Introduction

The presence of Miocene coral reefs in the Vallès-Penedès Basin is known since the late 19th Century (de Angelis d'Ossat, 1898). Later on, Chevalier (1957) recognized two kinds of reefs in the basin, fringing and patch reefs, and assigned them to the Vindobonian (obsolete division equivalent to the Middle Miocene and part of the Late Miocene). Subsequent studies correlated these reefs to the late Burdigalian (latest Early Miocene; Permanyer i Bastardas, 1990) and the Langhian (early Middle Miocene; Agustí et al., 1990; Cabrera et al., 1991). Current synthetic studies recognize at least three different episodes of marine transgression and regression in the Vallès-Penedès Basin (Cabrera et al., 1991; Cabrera & Calvet, 1996; Domènech et al., 2011a; de Gibert & Casanovas-Vilar, 2011; Casanovas-Vilar et al., 2016a; see also Stop 1): early Burdigalian, Langhian, and Serravallian. However, it is generally agreed that the Vallès-Penedès reef complex developed during Langhian highstands associated with the MCO (Figs. 5–6).

Reefs developed when the southeastern half of the basin was flooded and always occur near the borders of the basin. Flooded inner areas were dominated by terrigenous platform deposits, whereas alluvial sedimentation persisted in the northwestern half of the basin (Fig. 6; Cabrera et al., 1991; Cabrera & Calvet, 1996; Domènech et al., 2011a). As said above, there are two different types of reef systems in the Vallès-Penedès Basin. The most important one is a 20 km-long fringing reef system bordering the Garraf mountains, with excellent outcrops at Castellet i la Gornal and Olèrdola (Fig. 6; Permanyer i Bastardas,

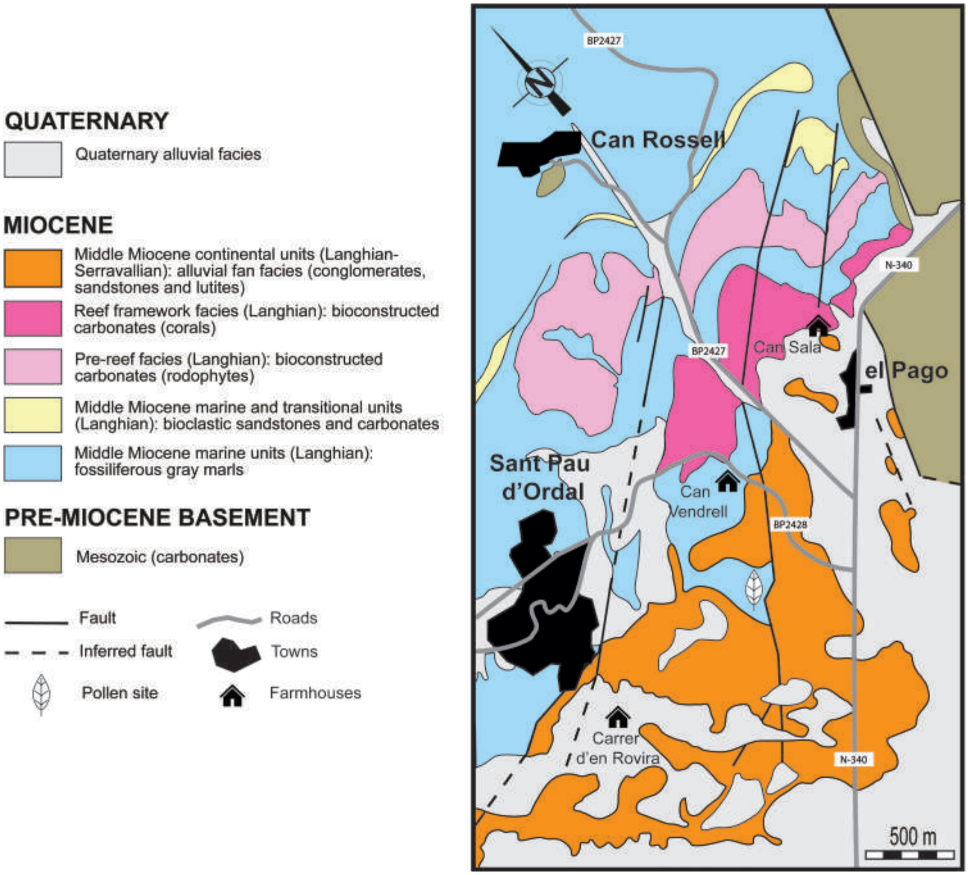


Figure 14. Detailed geological map of the area around Can Rosell, el Pago, and Sant Pau d'Ordal, showing the extension of the Langhian coral reef facies. The location of the pollen samples is also indicated. Note the extension of the bluish lutites that correspond to restricted bay environments and the younger alluvial deposits. Modified from Bessedik & Cabrera (1985).

1990). It may measure as much as 2 km wide and reef deposits may be up to 60 m thick. The second type are the much smaller patch reefs, which are located in more inner areas of the basin and developed in small elevations, such as in Sant Sadurní d'Anoia (Domènech et al., 2011b), el Papiol, or Sant Pau d'Ordal (Fig. 6; Bessedik & Cabrera, 1985; Permanyer i Bastardas, 1990; Cabrera et al., 1991). These are usually less than 1 km long and a few hundred meters wide. Patch reef series are generally just around 10 m thick. The Can Sala patch reef at Sant Pau d'Ordal (Fig. 13) is one of the best-known examples of such structures in the basin (Permanyer & Esteban, 1973; Permanyer i Bastardas, 1990; Cabrera et al., 1991) and is further associated with other marine sediments which have yielded both macro- and microfossils, including a rich pollen assemblage (Bessedik & Cabrera, 1985; Agustí et al., 1990).

Geological setting, stratigraphy, and age

A very continuous succession of the Langhian marine units is exposed along the road BP2427 from Sant Sadurní to Sant Pau d'Ordal (Fig. 14). At els Casots, next to the Caves Olivé i Batllori, an oyster coquina and a bioclastic calcarenite mark the Langhian transgressive surface in this sector of the basin (Fig. 8). Along the road, the marine succession consists of yellowish and gray lutites with minor intercalations of conglomeratic sandstones and bioclastic sandstones predominantly containing oyster fragments. These deposits are interpreted as restricted bay and are rich in marine invertebrates and microfossils (Agustí et al., 1990; Cabrera et al., 1991). Planktonic foraminifera recovered at the old quarry of Can Rossell (Fig. 14) indicate a correlation to the early Langhian (zone N8; Magné, 1978; Bessedik & Cabrera, 1985; Agustí et al., 1990). The marine clay deposits are of variable thickness, being thicker (up to several hundred meters) toward the central part of the basin. At Can Rossell. they are about 100 m thick. From this point on, the marine succession includes meter-thick biocalcarenitic packstones mostly consisting of rodolithes. Finally, a small coral patch reef can be observed at the old Can Sala quarry near el Pago (Subirats; Fig. 13).

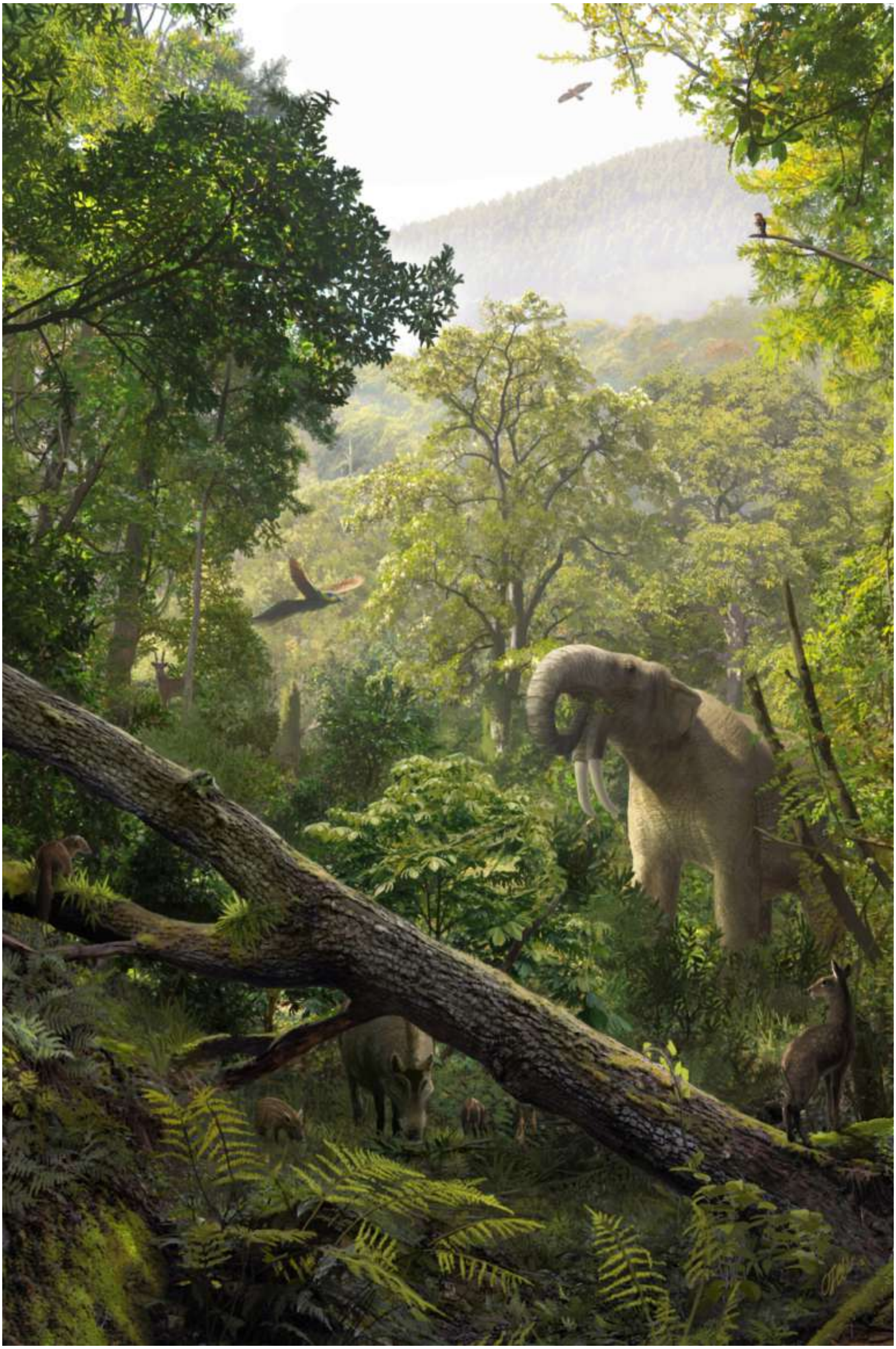
The Can Sala patch reef is 1 km long by 200–300 m wide (Fig. 14) and reef facies have a maximum thickness of just 10 m (Cabrera et al., 1991). The best outcrops are in and next to the old quarry, near Can Vendrell (Caves Albet i Noya). The structure and stratigraphy of the Can Sala reef has been described in detail by Permanyer & Esteban (1973), Permanyer i Bastardas (1990), and Cabrera et al. (1991). Pre-reef facies consist of marls with coralline algae (rhodolithes), large mollusks (mostly oysters), and some isolated coral colonies. These are followed by reef framework facies in which the size of the coral colonies progressively increases from bottom to top. In the reef core, corresponding to the time of main reef activity, coral colonies are rounded and massive, measuring up 0.5–1 m in diameter (Fig. 13). *Mussismilia*, *Montastrea*, *Tarbellastrea*, and *Porites* are the main coral genera present at the reef. However, the reef as a whole is highly affected by diagenesis, which implies dissolution and recristalization that hinders the identification of corals. Corals also show significant perforation activity by drilling mollusks. Bivalve, gastropod, and sponge fossils are common in these facies. The reef framework facies attain a maximum thickness of up to 6 m and are covered by a cap of broken branching *Porites* that would indicate very shallow water.

The reef is covered by sandy clays and sandstones with oyster fragments that are affected by a ferruginous hardground that is well exposed at the road leading to Sant Pau d'Ordal (BV2428) near Can Vendrell (Fig. 14). These indicate the transition toward more continental environments. At Can Vendrell, post-reef clay facies have yielded a rich pollen assemblage (Bessedik & Cabrera, 1985) that includes mangrove pollen (*Avicennia*), thus suggesting that these layers were deposited in littoral environments. Planktonic foraminifera have been also recovered from these layers and still indicate an early Langhian age (zone N8; Magné, 1978; Bessedik & Cabrera, 1985; Agustí et al., 1990). Finally, continental alluvial fan facies cover these deposits and crop out towards the south and southwest, next to the Garraf reliefs (Fig. 14).

Paleoenvironment

The development of the reef system coincided with a Langhian marine transgression highstand and therefore represents a warm peak during the MCO. The Can Sala coral reef, in particular, was a small patch reef parallel to the coast, just 200–300 m away from it (Cabrera et al., 1991). The Can Vendrell pollen assemblage is slightly younger but still framed within this warming episode (Bessedik & Cabrera, 1985). The presence of *Avicennia* pollen (3%) indicates the existence of an impoverished mangrove swamp. Today mangroves solely defined by *Avicennia* represent the high latitude limit for mangroves (e.g., Persian Gulf, Red Sea), yet their presence indicates temperatures above 20 °C (Sanz de Siria Catalán, 2001; Jiménez-Moreno & Suc, 2007). These impoverished mangroves with halophytes (2% of Aramanthaceae–Chenopodiaceae) would define Langhian coastal environments in the area (Bessedik & Cabrera, 1985; Jiménez-Moreno & Suc, 2007). The pollen assemblage includes many thermophilous taxa such as *Engelhardia* (11%), *Platycarya* (5%), Sapotaceae (4%), or Meliaceae (0.3%). Overall, mega- and mesothermic taxa account for ~60% of the assemblage, thus indicating warm temperatures (Bessedik & Cabrera, 1985). Thermophilous elements requiring high humidity, such as *Engelhardia*, *Platycaria*, or *Myrica*, are relatively common. In contrast, herb and shrub pollen is rare, not exceeding 15% (Bessedik & Cabrera, 1985; Jiménez-Moreno & Suc, 2007). This may indicate that the lowlands and up to elevations of about 700 m were dominated by a broad-leaf evergreen forests coexisting with few relatively more open areas occupied by herbs and leguminous trees such as Acacia (Jiménez-Moreno & Suc, 2007). The Can Vendrell samples also include deciduous tree (*Alnus*, *Betula*) and coniferous pollen which would derive from higher-altitude forests (Bessedik & Cabrera, 1985; Sanz de Siria Catalán, 2001; Jiménez-Moreno & Suc, 2007).

The Can Vendrell pollen data indicate a tropical to subtropical and relatively humid climate. Interestingly, this shows some differences with approximately contemporaneous pollen (La Rierussa, Sant Llorenç d'Hortons; Jiménez-Moreno & Suc, 2007) and macrofloral data (Sant Sadurní d'Anoia; Sanz de Siria Catalán, 2001) from the same area, where herbaceous plants and leguminous trees are the most important components. These sites are located in more inner areas of the basin and may indicate that more open woodlands occurred there whereas more humid environments may have characterized areas near the bounding reliefs.



STOP 4. CAN MATA: A HIGH-RESOLUTION RECORD OF THE ARAGONIAN/VALLESIAN TRANSITION

Geographic coordinates: 41.52981, 1.80451 (WGS84) [Can Mata de la Garriga farmhouse].

Introduction

The late Aragonian and early Vallesian (late Middle Miocene to early Late Miocene) vertebrate faunas from the fossiliferous area of Hostalets (Fig. 15)—including the municipalities of els Hostalets de Pierola, Piera, and Masquefa, in the Penedès Sector of the Vallès-Penedès Basin—are currently among the most profusely documented of the whole basin in terms of recovered fossil remains. The Miocene vertebrate remains from this area were first reported by Bataller Calatayud (1938), based on material recovered by amateur collector Màrius Guerín during previous years from the surroundings of Can Mata de la Garriga farmhouse and nearby areas (Fig. 16a–b). Additional surveying and excavations in this area were performed by Miquel Crusafont Pairó and collaborators from the 1940s onward, leading to the discovery of abundant fossil remains (e.g., Villalta Comella & Crusafont Pairó, 1941b, 1941c, 1943b, 1944a, 1944b, 1945; Villalta & Crusafont, 1946b; Schaub, 1947; Crusafont Pairó, 1952a, 1952b; Crusafont-Pairó & Golpe-Posse, 1973). It took a couple of decades to realize that the sediments from els Hostalets represented a considerable time span covering two different land mammal ages, being exclusively assigned to the 'Vindobonian' (e.g., Villalta & Crusafont, 1946b). However, following Crusafont Pairó's (1950) definition of the Vallesian—based on the entry of hipparionins and giraffids—Crusafont & Truyols (1954) distinguished two sets of more or less loosely defined sites and localities from the area, which they grouped based on their presumed age: Vindobonian (currently, late Aragonian), such as Can Mata 1 (or Bretxa de Can Mata; Fig. 17) and Can Vila; and Vallesian, including Can Mata 2 and Can Flequer, among others.

The Can Mata landfill, corresponding to the ACM macrosite (Figs. 4, 17c–18) progressively developed between the farmhouses of Can Vila and Can Mata de la Garriga throughout the 1980s–1990s without any type of paleontological surveillance. When an enlargement was planned in the early 2000s (Figs. 18–19), thanks to the new laws protecting fossils as cultural heritage, a rescue paleontological intervention was organized. Fieldwork, including the surveillance of the removal of thousands of tons of Miocene sediments with digger machines and associated samplings and excavations (Fig. 20), was performed almost uninterruptedly between late 2002 and early 2014 (up to 126 months of fieldwork in total), leading to the recovery of tens of thousands of fossil vertebrate remains from the late Aragonian (Alba et al., 2006, 2007, 2009, 2011b, 2017, 2022a). This huge sampling effort led to the recovery of rare vertebrate taxa, such as primates (Moyà-Solà et al., 2004, 2009a, 2009b; Alba, 2012; Alba et al., 2010b, 2015). Additional fossils were recovered in 2007–2010 thanks to paleontological surveillance during the construction of a nearby recycling plant known as Ecoparc de Can Mata (ECM; Fig. 16c), which mostly affected Vallesian sediments (Carmona et al., 2011; Alba et al., 2012a). Finally, additional intermittent fieldwork associated with another expansion of the dump in 2017–2022 enabled the recovery of further fossils and extended the ACM composite sequence up to the Vallesian (Alba et al., 2022a).

Further research is required to discern to what extent the faunal turnover that characterizes the Aragonian/Vallesian transition (~11.5–11.0 Ma) was a protracted or punctuated event (Alba et al., 2022a). Given the high chronostratigraphic resolution available from the ACM sequence, the recovery of abundant fossil vertebrate remains during the last couple decades, and future fieldwork prospects associated with the landfill enlargement, Can Mata represents a privileged window into late Aragonian and early Vallesian terrestrial ecosystems and emerges as one the most promising fossiliferous areas in western Europe to investigate the Aragonian/Vallesian transition.

Figure 15 (previous page). Reconstruction of the fauna and paleoenvironment of Abocador de Can Mata at ~12 Ma. A *Deinotherium levius* feeds from the lush vegetation growing in a forest clearing. In the foreground, the musk deer *Micromeryx* sp. and the mustelid *Trocharion albanense* stand on a fallen tree. Below them, a female of the suid *Listriodon splendens* and her piglets patrol the undergrowth in search of fallen fruits. Hidden between the background trees, a male of the cervid *Euprox furcatus* contemplates the scene while a peafowl of the genus *Miophasianus* flies away. No plant fossils have been recovered at Abocador de Can Mata, so the vegetation is based on the evidence from nearby sites that indicate the presence of warm-temperate forests with some more open woodland in the lowlands. Artwork by Ó. Sanisidro, © Institut Català de Paleontologia Miquel Crusafont.

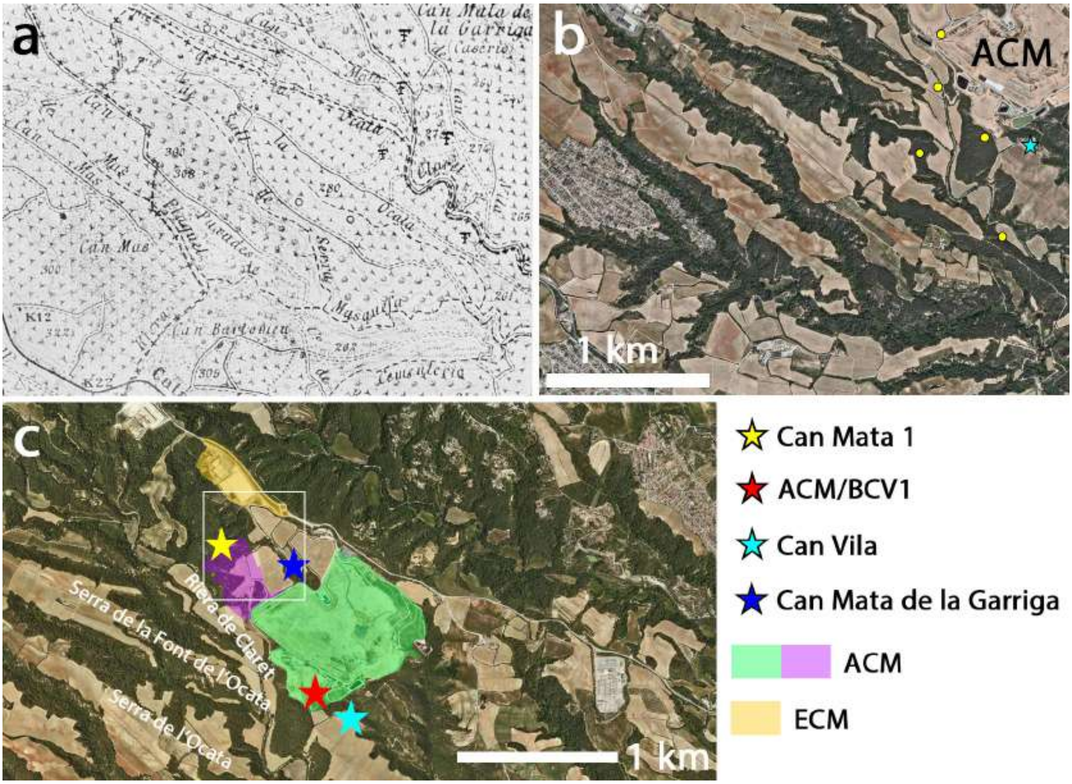


Figure 16. a–b, Map of the fossiliferous localities (F) near els Hostalets de Pierola sampled by Bataller (**a**) and orthophotomap of the same of the area in 2022 with the localities indicated by yellow dots (**b**). **c**, Orthophoto from 2019 showing the extension of Abocador de Can Mata (ACM; green up to 2017, pink from 2017 to 2021) and Ecoparc de Can Mata (ECM; orange), relative to the nearby farmhouses of Can Mata de la Garriga and Can Vila, as well as Can Mata 1 and ACM/Barranc de Can Vila 1 (ACM/BCV1). Panel (**a**) reproduced from Bataller Calatayud (1938) and panel (**c**) modified from Alba et al. (2022a). Base orthophotomaps for panels (**b**) and (**c**): © Institut Cartogràfic i Geològic de Catalunya, downloaded from VISSIR and reproduced with permission by means of a Creative Commons license CC BY 4.0.

Geological setting, stratigraphy, and age

The area of els Hostalets de Pierola is characterized by thick alluvial fan sequences from the Middle and Late Miocene that mostly consist of reddish to brown mudstones, coupled with sandstones, breccias, and conglomerates. These sediments were deposited in the distal-to-marginal inter-fan zones of the coalescing alluvial fan system of els Hostalets de Pierola and the more extensive system of Olesa de Montserrat-Les Fonts (Fig. 6; Alba et al., 2006, 2009, 2011b, 2017; Casanovas-Vilar et al., 2008a; Moyà-Solà et al., 2009a). Mudstones show evidence of soil formation to varying intensities, being characterized by the widespread presence of early diagenetic carbonates and the alternation of different colorations due to changing reducing/oxidizing conditions (Alba et al., 2009, 2017). Lithostratigraphic correlation mostly relies on intensely red-colored horizons interpreted as paleosols (Alba et al., 2017, 2022a). Detailed bio- and magnetostratigraphic correlation has enabled an accurate dating of most of the fossil remains recovered from ACM, where >250 localities have formally been defined (Alba et al., 2017, 2022a).

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The current composite lithostratigraphic sequence of ACM (i.e., excluding ECM) includes 51 largely overlapping local sections of varying thickness, of which six have been sampled for paleomagnetism (>400 stations; Moyà-Solà et al., 2009a; Alba et al., 2017, 2022a). Estimated ages for given localities or isolated remains are interpolated based on the resulting composite magnetostratigraphic sequence by considering the sedimentation rate computed for each subchron (Alba et al., 2017, 2022a). Overall, the ACM composite sequence (Fig. 21) currently has a thickness of 300 m and includes up to 12 magnetozones (correlated to subchrons C5Ar.1r to C5n.2n), ranging in time from ~12.6 to ~11.1 Ma (Alba et al., 2022a). This time span corresponds to four different local biozones of the Vallès-Penedès Basin (Casanovas-Vilar et al., 2016b): the *Megacricetodon crusafonti* + *Democricetodon larteti* concurrent range subzone (up to 12.39 Ma, latest MN6); the *M. crusafonti* – *Democricetodon crusafonti* interval subzone (12.39–11.88 Ma, early MN7+8); the *D. crusafonti* – *Hippotherium* interval subzone (11.88–11.18 Ma, late MN7+8); and the *Hippotherium* – *Cricetulodon hartenbergeri* interval subzone (11.18–10.3 Ma, MN9).

The nearby composite sequence of ECM was previously interpreted to be exclusively Vallesian in age (Alba et al., 2012a; Casanovas-Vilar et al., 2016b), with the whole uppermost part of the sequence being correlated to subchron C5n.2n. However, currently available data (Alba et al., 2022a) indicate that the base of the ECM sequence is roughly coeval with ACM/CCV1 (~11.5 Ma), with the lowermost ECM localities being older than previously considered (e.g., ECM/VCE-A1 ~11.2 Ma; ECM/VCE-Bb ~10.9 Ma). Historical localities from Hostalets Inferior and Superior cannot be accurately dated, except for Can Vila (minimally older than ACM/BCV1, ~12.0 Ma; Alba et al., 2013, 2020b, 2022a), and Can Mata 1 and 3 (correlated to subchron C5r.1r, with an estimated age of ~11.1 Ma; Alba et al., 2022a). Therefore, both Can Mata localities postdate the short normal magnetic polarity subchron C5r.1n where hipparionins are first recorded in the Vallès Sector of the basin—Creu de Conill 20 (CCN20) and Castell de Barberà (CB; see Fig. 4)—with an estimated age of ~11.2 Ma (Garcés et al., 1996, 1997; Agustí et al., 1997; Casanovas-Vilar et al., 2016a, 2016b; Alba et al., 2019). The historical locality of Can Mata 2, corresponding to some of the oldest giraffid remains from the area (Crusafont Pairó, 1952a), cannot be accurately dated but is most likely penecontemporaneous with Can Mata 3.

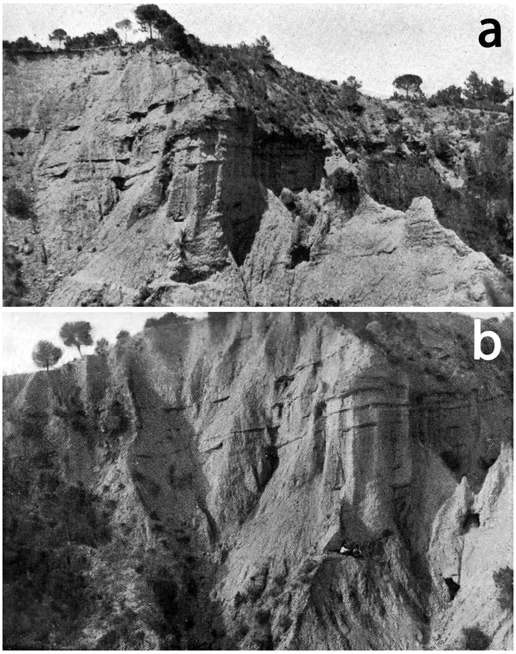


Figure 17. The locality of Can Mata 1 in the early 1940s. The location of the fossiliferous level is indicated by the paleontologists excavating in panel (**b**). Photograph in panel (**a**) by Crusafont, reproduced from Villalta Comella & Crusafont Pairó (1943: Pl. XV); photograph in panel (**b**) by Bataller, reproduced from Villalta Comella & Crusafont Pairó (1941b: Pl. XVI Fig. 2).

It has been customarily assumed that the latest Aragonian and earliest Vallesian rodent assemblages from the Vallès-Penedès Basin were virtually indistinguishable (Agustí et al., 1985, 1997; Alba et al., 2006; Casanovas-Vilar et al., 2011a, 2016a, 2016b). Nevertheless, such a contention largely relies on the grouping of purportedly late Aragonian localities from Hostalets (those without hipparionins) into Hostalets

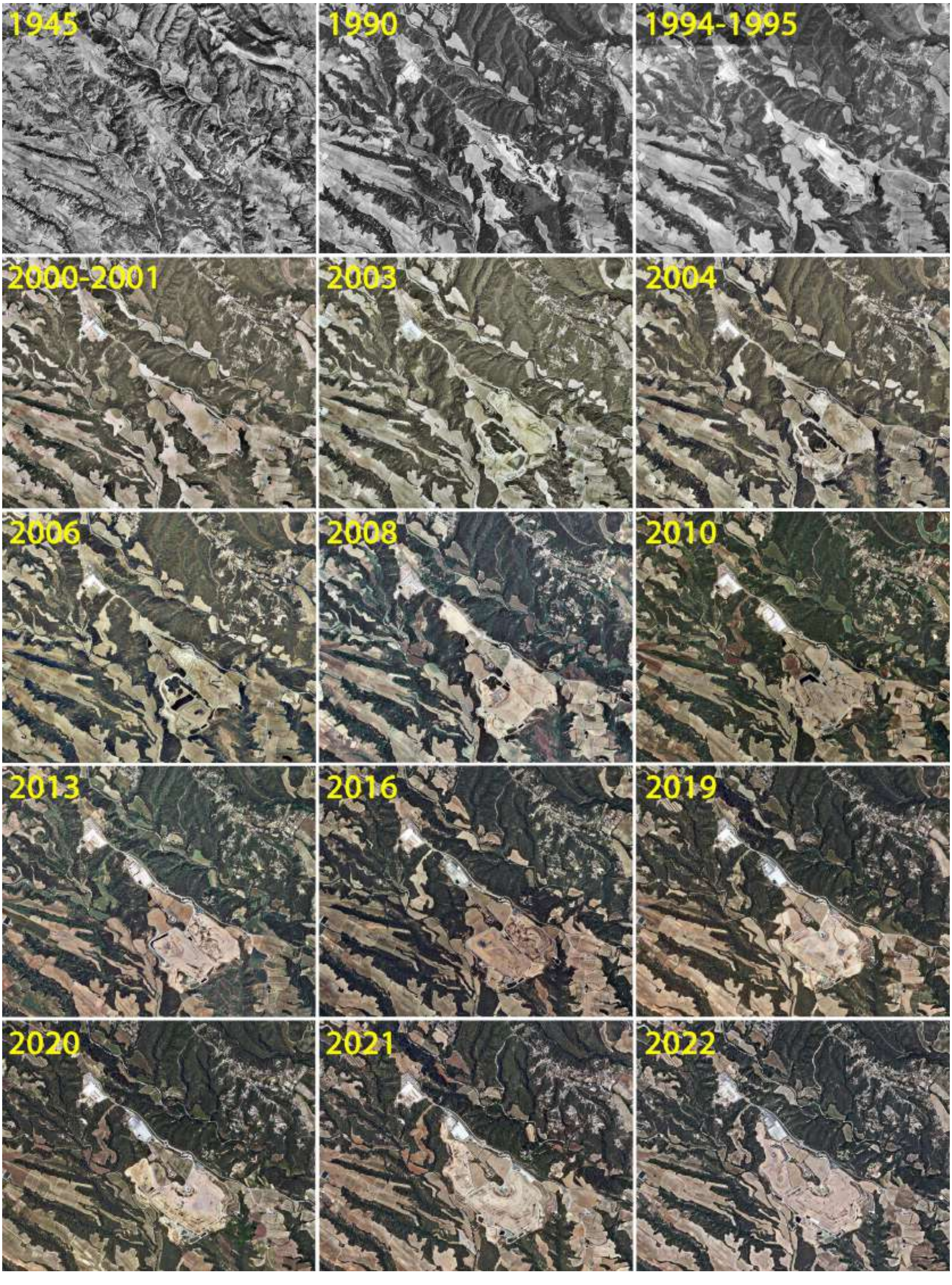


Figure 18. Orthophotos of the area of Can Mata showing the progressive development of the landfill over the years. Base orthophotomaps: © Institut Cartogràfic i Geològic de Catalunya, downloaded from VISSIR and reproduced with permission by means of a Creative Commons license CC BY 4.0.

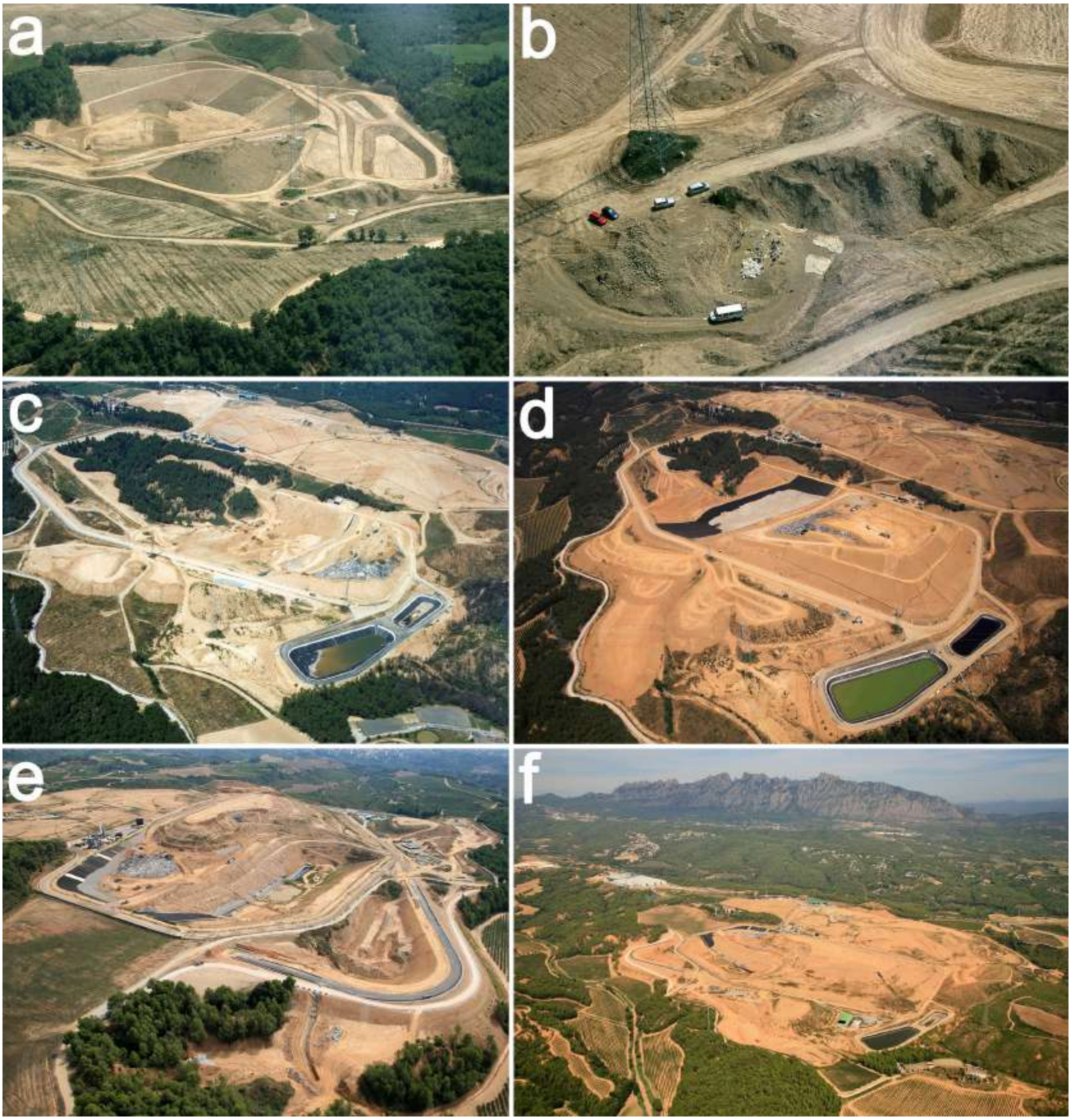
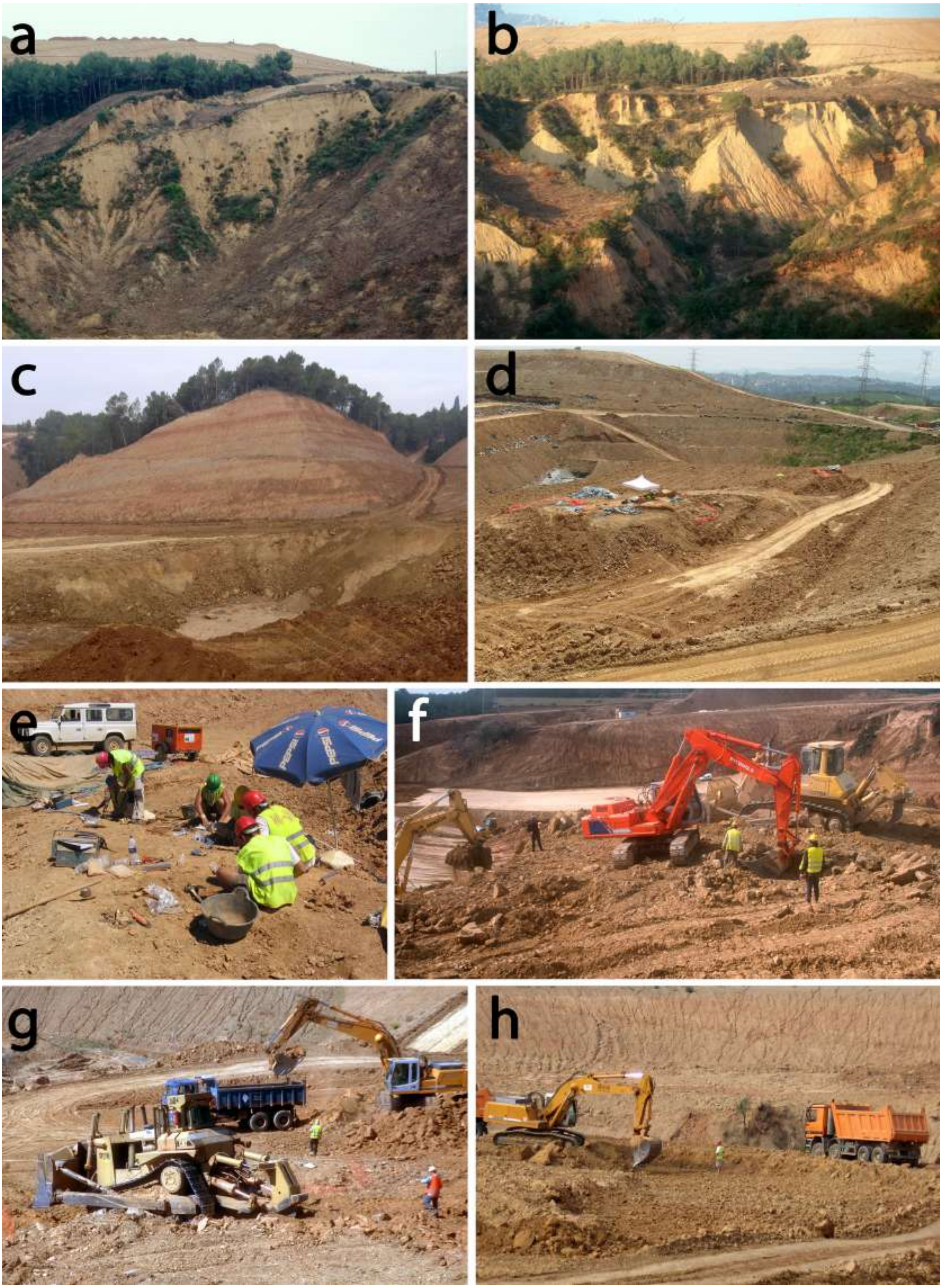


Figure 19. Aerial photographs of ACM throughout the years: **a**, Cell 1 and accessory structures in 2003; **b**, detail of excavations at ACM/BCV1 in 2003; **c–f**, panoramic views in 2004 (**c**), 2006 (**d**) and 2010 (**e–f**). Photographs courtesy of Magí Miret (**a–b**) and CESPA Gestión de Residuos, S.A.U. (**c–f**).

Inferior. The lack of *Hippotherium* from Vallesian levels of ECM (Alba et al., 2012a) and its scarcity from the earliest Vallesian site of CB (Alba et al., 2019) indicate that hipparionin absence is not a reliable criterion to exclude a Vallesian age (Alba et al., 2019, 2022a). This is further confirmed by the dating of Can Mata 1 to ~11.1 Ma, indicating that Hostalets Inferior is a mixture of latest Aragonian and earliest Vallesian remains (Alba et al., 2022a). The accurately dated localities from ACM and ECM show that the latest Aragonian is characterized by the appearance *Hispanomys lavocati* (since ~11.6 Ma), whereas *Hispanomys dispectus* (and *Hispanomys daamsi* elsewhere in the same basin) are apparently restricted to the earliest Vallesian (~11.2–11.0 Ma), thus preceding the earliest record of *Hispanomys aragonensis* ~10.8 Ma (Alba et al., 2022a).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This suggests that, contrary to previous expectations, it might be possible to refine the local biozonation of the Vallès-Pendès Basin around the Aragonian/Vallesian transition based on cricetids of genus *Hispanomys*.

As for large mammals, the more or less simultaneous record (~11.1 Ma) of both hipparionins and giraffids at ACM and Can Mata 3 (Alba et al., 2022a), only slightly postdating the Aragonian/Vallesian elsewhere in the basin (CCN20 and CB; Garcés et al., 1996; Agustí et al., 1997; Casanovas-Vilar et al., 2016a, 2016b; Alba et al., 2019), vindicate Crusafont Pairó's (1950) original conceptualization of the Vallesian as characterized by the dispersal of both hipparionins and giraffids. Subsequently, biochronological emphasis shifted toward hipparionins only (Crusafont Pairó & Truyols Santonja, 1960), and eventually a pre-Vallesian biozone characterized by giraffids and the lack of hipparionins was defined (Crusafont Pairó & Golpe Posse, 1971) for localities such as Can Mata 2 and CB (e.g., Golpe-Posse, 1974; Agustí et al., 1985, 1997, 2001; Agustí & Moyà-Solà, 1990). Current evidence from ACM and elsewhere in the Vallès-Penedès Basin (Casanovas-Vilar et al., 2016a, 2016b; Alba et al., 2019, 2022a) supports instead the more or less simultaneous dispersal of hipparionins and giraffids, together with other eastern immigrants (*Propotamochoerus* and *Machairodus*), coupled with the replacement of multiple genera (e.g., *Gomphotherium* by *Tetralophodon* and *Anisodon* by *Chalicotherium*) and species of the same genus (e.g., *Hispanomys*, *Prolagus*, *Euprox*, and *Deinotherium*).

Biota

The fossil localities from Hostalets/ACM have yielded a rich collection of continental vertebrates (>73,000 macroremains collected at the field plus >14,000 microremains recovered by means of screen-washing), including amphibians, reptiles, birds, and both small and large mammals. Many of the remains recovered from ACM have yet to be prepared, and others have not been studied in detail yet. Therefore, much work remains to be done to clarify how faunal composition changed through time, as not all the recorded species coexisted in time.

According to available sources (Crusafont Pairó & Villalta, 1952; Delfino et al., 2015), amphibians are represented by both caudates (the salamandrid *Pleurodeles*) and anurans (the alytid *Latonia*, the pelobatid *Pelobates*, and the ranid *Pelophylax*), while reptiles are more diverse, including both chelonians (Bergounioux, 1957a, 1957b, 1957c, 1958; Luján et al., 2014a, 2014b, 2016; Delfino et al., 2015) and squamates (Crusafont Pairó & Villalta, 1952; Carmona et al., 2010; Bolet et al., 2013, 2014; Delfino et al., 2015; Villa et al., 2018). Chelonians are represented by freshwater geoemydid turtles (*Ptychogaster*) and much more abundant remains of terrestrial tortoises (testudinids), both giant (*Titanochelon*) and of 'normal' size (*Testudo*). In turn, squamates are represented by indeterminate gekkotans and lacertids, abundant anguids (*Ophisaurus* and *Pseudopus*), varanids (*Varanus*), blanids (*Blanus*), and abundant snakes (colubrids, the elapid *Naja*, and viperids of the 'oriental group'). Birds from ACM have yet to be studied, but historical finds from Hostalets (Villalta Comella & Crusafont Pairó, 1950; Villalta, 1963; Sánchez Marco, 1995, 1999, 2006, 2021) have been attributed to an indeterminate accipitrid, several phasianids (*Miophasianus*, *Palaeoperdix*, and *Palaeortyx*), a fringillid (*Fringilla*), and a tytonid (*Tyto*).

Mammals are more diverse than other vertebrates. Small mammals include a diverse assemblage of rodents and, to a lesser extent, insectivorans, coupled with a few lagomorph and very rare indeterminate chiropterans. Lagomorphs are represented by two prolagids (*Prolagus* and *Eurolagus*; Alba et al., 2006, 2011b; Casanovas-Vilar et al., 2010a), while insectivorans are represented by about ten species (Villalta Comella & Crusafont Pairó, 1943b; Gibert, 1975; Agustí & Gibert, 1982; van den Hoek Ostende & Furió, 2005; Alba et al., 2006, 2011b; Furió et al., 2011a, 2015), including soricids (*Miosorex* and other indeterminate species), talpids (*Talpa* and cf. *Proscapanus*), erinaceids (*Parasorex*, *Galerix*, and '*Amphechinus*'), heterosoricids (*Dinosorex*), and dimylids (*Plesiodimylus*). Rodents are by far much more diverse (>30 species; Schaub, 1947; Agustí, 1980, 1981; Agustí & Gibert, 1982; Agustí et al., 1985, 1997; Aldana Carrasco, 1992a, 1992b; Alba et al., 2006, 2011b, 2022a; Casanovas-Vilar et al., 2008b, 2010a, 2018c), including the diverse and abundant cricetids (*Eumyarion*, *Hispanomys*, *Democricetodon*, and *Megacricetodon*), the rarer anomalomyids (*Anomalomys*) and eomyids (*Keramidomys* and *Eomyops*), the diverse but not particularly abundant glirids (*Glirudinus*, *Muscardinus*,

Figure 20 (previous page). Fieldwork at ACM: **a–b**, Miocene outcrops in November 2002, just before excavations began; **c–d**, extensive outcrops generated by the digging activity in 2005 (**c**) and 2008 (**d**); **e**, rescue excavation in 2005; **f–h**, paleontological surveillance of heavy machinery in 2003 (**f**), 2004 (**g**), and 2005 (**h**). Photographs © Institut Català de Paleontologia Miquel Crusafont.

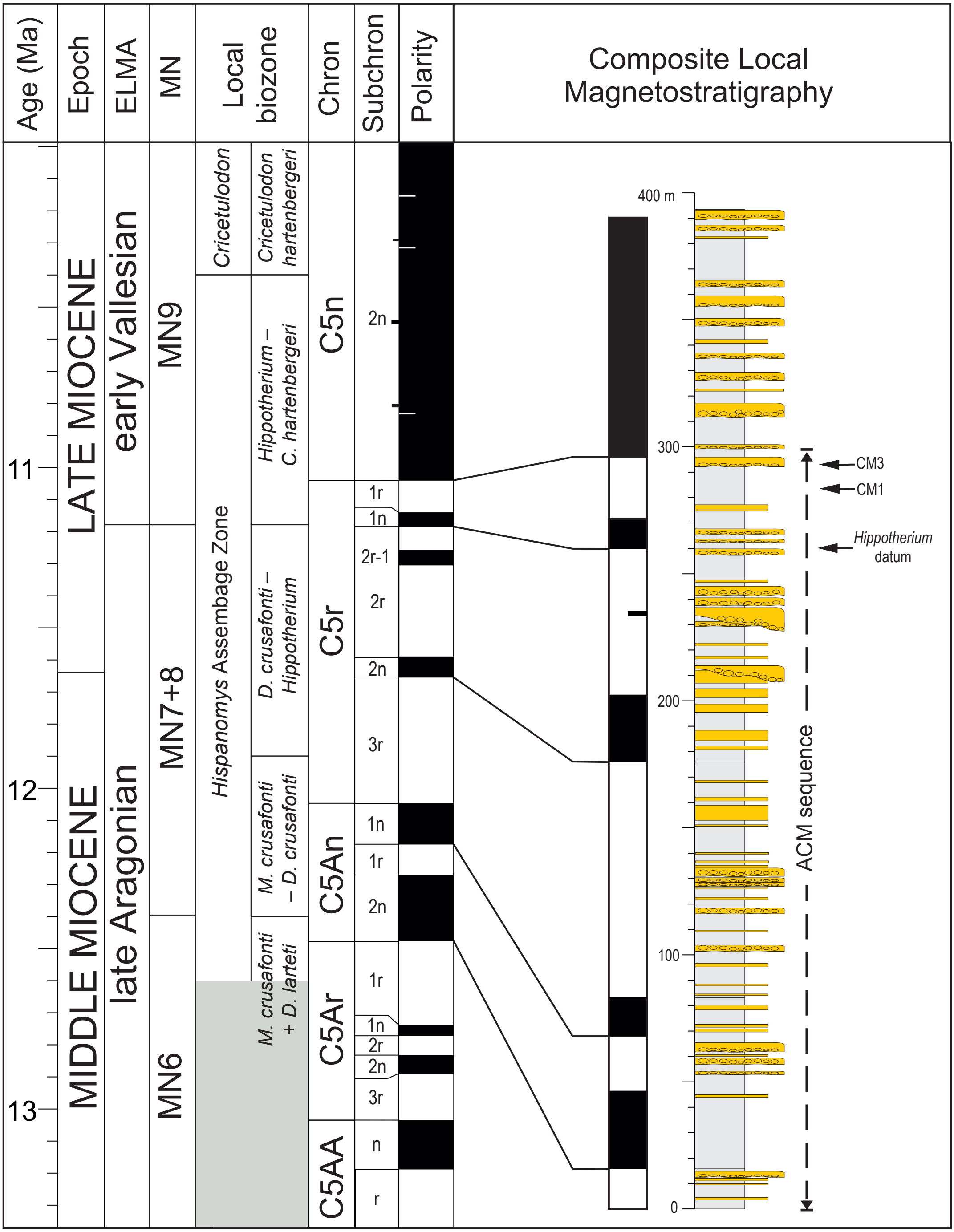

Figure 21. Synthetic correlation of the composite local magnetostratigraphy of ACM and nearby areas with the Geomagnetic Polarity Time Scale (GPTS; after Ogg, 2020), as well as European land mammal ages (ELMA), Mammal Neogene units (MN), and local biozones of the Vallès-Penedès Basin after Casanovas-Vilar et al. (2016b). The current depth of the ACM sequence is indicated, coupled with the stratigraphic position of Can Mata 1 (CM1), Can Mata 3 (CM3), and the *Hippotherium* datum (as recorded elsewhere in the Vallès-Penedès Basin). Modified from Alba et al. (2022a).

Myoglis, *Microdyromys*, and *Paraglirulus*), terrestrial (*Csakvaromys* and *Heteroxerus*) and flying (*Albanensia*, *Miopetaurista*, *Neopetes*) sciurids, and scarce castorids with natatory adaptations (*Chalicomys*).

Large mammals are represented by proboscideans, perissodactyls, artiodactyls, carnivorans, and primates. The latter are rare but have been extensively studied, including both small-bodied catarrhines (*Pliobates* and pliopithecoids such as *Pliopithecus*; Alba et al., 2010b, 2012b, 2015) as well as three great ape genera (*Pierolapithecus*, *Anoiapithecus*, and *Dryopithecus*; Villalta Comella & Crusafont Pairó, 1941b, 1944a; Golpe-Posse, 1993; Van der Made & Ribot, 1999 zzz; Moyà-Solà et al., 2004, 2009a, 2009b; Alba, 2012; Alba & Moyà-Solà, 2012; Alba et al., 2013, 2020b). *Pierolapithecus* stands outs because the holotype partial skeleton (Fig. 22) combines a great ape-like facial morphology with the first unambiguous evidence of an orthograde body plan (Moyà-Solà et al., 2004; Alba, 2012; Pugh et al., 2022). This taxon is customarily interpreted as a stem hominid (Pugh, 2022), thereby being key for understanding the ancestral morphotype from which crown hominids evolved.

The carnivorans from the area, in turn, have also been subject to considerable research (Villalta Comella & Crusafont Pairó, 1941c, 1943b, 1944b; Crusafont Pairó, 1952b; Petter, 1963, 1967, 1976; Crusafont Pairó & Petter, 1969; Golpe-Posse, 1981, 1984; Robles et al., 2010, 2013a, 2013b, 2014; Abella et al., 2012; Madurell-Malapeira et al., 2014; Alba et al., 2022b). They include almost 20 species: among the caniforms, hemicyonids (*Hemicyon*), ursids (*Kretzoiarctos*), mephitids (*Mesomephitis*), and mustelids (*Martes*, *Ischyrictis*, *Palaeomeles*, *Trocharion*, and *Eomellivora*); and, among the feliforms, viverrids (*Semigenetta*), barbourofelids (*Albanosmilus*), felids (*Styriofelis*, *Pseudaelurus*, and *Machairodus*), hyaenids (*Thalassictis*, *Plioviverrops*, and *Protictitherium*), and herpestids (*Leptoplesictis*).

Proboscideans are represented by two families (Bergounioux & Crouzel, 1957, 1962; Alba et al., 2006, 2011b; Mazo & Van der Made, 2012): deinotheriids (*Deinotherium*) and gomphotheriids (*Gomphotherium* and *Tetralophodon*). In turn, ungulates are represented by some perissodactyls and the more diverse artiodactyls. The former include three families (chalicotheriids, equids, and rhinocerotids), whereas artiodactyls include suids, tragulids, moschids, cervids, and bovids. Chalicotheriids are moderately abundant, being mostly represented by *Anisodon* but also, in Vallesian levels, by *Chalicotherium* (Villalta Comella & Crusafont Pairó, 1945; Alba et al., 2006, 2011a). Equids are very rare in the Aragonian levels, being only represented by rare finds of *Anchitherium* (Rotgers et al., 2011; Rotgers & Alba, 2011), whereas in Vallesian levels the endemic hipparionin *Hippotherium catalaunicum* occurs (Pirlot, 1956; Bernor et al., 1996, 2021). Nevertheless, in earliest Vallesian levels (such as Can Mata 3), a seemingly more plesimorphic indeterminate species of *Hippotherium* is recorded (Alba et al., 2022a), which more closely resembles the earliest Vallesian hipparionins from the Vienna Basin (Bernor et al., 2017). Rhinocerotids are recorded by three species of the genera *Alicornops*, *Hoploaceratherium*, and *Lartetotherium* (Santafé Llopis, 1978a, 1978b; Alba et al., 2006, 2011b; Sanisidro & Cantalapiedra, 2022).

As for artiodactyls, suids are quite diverse (Golpe-Posse, 1971, 1972; Van der Made, 1996, 1997; Alba et al., 2006, 2011b; Tomàs et al., 2011), including four or five genera (D.M.A., unpublished data). Listriodonts (*Listriodon*) are the most abundant, followed by the small suid *Albanohyus* and tetraconodonts. Following the revision of the latter group during the preceding decade (Pickford, 2014, 2016), most tetraconodont remains from ACM seem attributable to *Versoporcus* species (formerly *Parachleuastochoerus steinheimensis*), although a larger species attributable to *Parachleuastochoerus valentini* (a junior synonym of *Conohyus simorrensis* according to Van der Made, 2020) might also be present. In contrast, *Propotamochoerus* appears to be restricted to Vallesian levels. Tragulids (*Dorcatherium*) are quite rare (Alba et al., 2011c), contrasting with moschids, which are extraordinarily abundant and diverse. All remains had been formerly attributed to *Micromeryx florensianus* (Sánchez & Morales, 2006; Alba et al., 2006) but indeed are represented by multiple indeterminate species of *Micromeryx* at ACM (DeMiguel et al., 2021) and an *Hispanomeryx* species from ECM (Sánchez et al., 2019). Cervids are only recorded by *Euprox* (Azanza & Menéndez, 1990; Alba et al., 2006, 2011b), while bovids are somewhat more diverse (Moyà-Solà, 1983; Alba et al., 2006, 2011b; DeMiguel et al., 2012), being represented at least by *Miotragocerus*, *Tethytragus*, and *Austroportax*. Giraffids are only represented by a poorly-known, indeterminate species that is not recorded until the earliest Vallesian, both at ACM and ECM (Crusafont Pairó, 1952a; Alba et al., 2012a, 2022a). Originally identified as *Palaeotragus* sp. based on remains from Can Mata 2 (Crusafont Pairó, 1952a), it differs from *Decennatherium pachechoi* from the

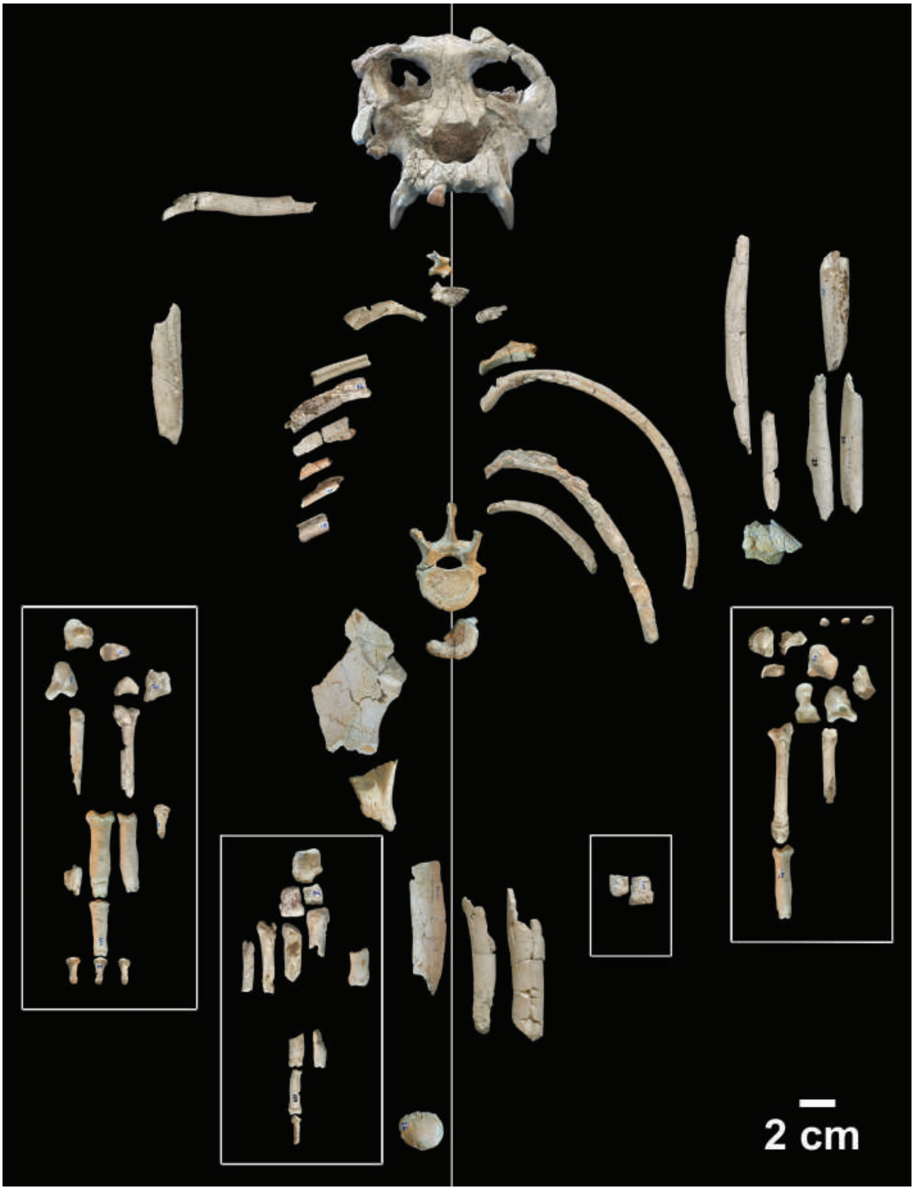

Figure 22. IPS23500, holotype skeleton of *Pierolapithecus catalaunicus* from ACM/BCV1. Reproduced from Moyà-Solà et al. (2004).

inner Iberian basins (Crusafont Pairó, 1952a; Ríos et al., 2016) but might belong to a more basal member of the same lineage (Alba et al., 2022a).

Taphonomy and paleoenvironment

There are not many records about how specimens were collected from historical Hostalets localities but many of them were loosely defined fossiliferous areas where most of the specimens were probably surface-collected, only with few exceptions, such as the bone bed from Can Mata 1, which was systematically excavated. Work at ACM indicates that isolated fossil macroremains are frequent throughout the area, with scattered bone accumulations restricted to a single stratigraphic horizon (usually between 0.2 and 1 m in thickness)—mostly, but not exclusively, composed of mudstones. Such accumulations are quite heterogeneous in type of remains (normally consisting of mixed assemblages of micro- and/or macrovertebrates, or more infrequently partial skeletons of a single individual), lateral extension (from 1–2 to >100 m2), and number of recovered fossil remains (from a few tens to >5,000 specimens; Alba et al., 2017). Although spatial information has been recovered for most important localities, thus far taphonomic analyses have focused on ACM/BCV1 (Casanovas-Vilar et al., 2008a), the type locality of *P. catalaunicus*. These indicate that the accumulation involved different taphonomic agents. The partial skeleton of *P. catalaunicus* shows bite marks produced by predators/scavengers, but the rest of the large vertebrate bones do not and probably accumulated after the burial of scattered remains across the flood plain. Concerning small mammals from this locality, part of the assemblage clearly derived from the activity of predators, particularly nocturnal raptors (Casanovas-Vilar et al., 2008a). Although taphonomic analyses have yet to be conducted for the whole ACM series, the sedimentary environment is essentially the same, so it may be assumed that similar taphonomical processes were involved throughout. The combination of high rates of subsidence and sediment supply in the area would have enabled the rapid burial of vertebrate remains in a mudstone-dominated environment, thereby favoring their preservation (Alba et al., 2009).

With regard to paleoenvironmental conditions, the late Aragonian and early Vallesian sites of the Vallès-Penedès Basin appear to have been more similar to those of France and central Europe than to those of the inner Iberian Peninsula (Casanovas-Vilar et al., 2005, 2008a, 2010b; Casanovas-Vilar & Agustí, 2007; Furió et al., 2011b) by displaying taxa indicative of more forested (some glirids, flying squirrels, arboreal primates) and humid (many insectivorans) environments, and even some associated to permanent water bodies (castorids). This is supported by multivariate analyses based on small mammals from ACM/BCV1 (Casanovas-Vilar et al., 2008a) and would explain why hominoid primates have only been found in the Vallès-Penedès and Seu d'Urgell basins during the Iberian Miocene (Alba, 2012). Multivariate analyses of the large mammal composition classified ACM as a tropical deciduous forest (Casanovas-Vilar et al., 2008a), suggesting that the presence of some degree of rainfall seasonality, which agrees with ongoing analyses of muroid enamel stable isotopes (Casanovas-Vilar et al., 2019b, 2020). The presence of pond turtles (Luján et al., 2014a), castorids (Casanovas-Vilar et al., 2008b), and tragulids (Alba et al., 2011c) is indicative of permanent water masses in the area, but the fact that these taxa are only sporadically present, and that primates are neither uniformly distributed throughout the series (Alba et al., 2017, 2022a; DeMiguel et al., 2021), suggest that such water bodies were only intermittently present in the depositional area.

Several sources of evidence hint at changes in local paleoenvironmental conditions through time. For example, cervids appear to be more common than bovids at the lower portion of the sequence, and the same applies to small vs. giant tortoises, overall suggesting the progressive development of less humid and more open environments toward the Late Miocene. This is confirmed by mesowear and stable isotope analyses of the ubiquitous moschid *Micromeryx* (DeMiguel et al., 2021). These indicate that the lowermost portion of the series (~12.4–11.9 Ma), where great apes are more common, was characterized by humid and densely-forested environments that were subsequently replaced by less humid and patchy ecosystems with reduced tree cover inhabited by pliopithecoids (~11.9–11.8 Ma), followed by mosaic environments combining more open habitats with gallery forests (~11.7–11.6 Ma). This kind of mosaic environment recalls that inferred for later Vallesian localities from elsewhere in the basin, such as Can Llobateres 1 (Marmi et al., 2012). Further analyses are required to characterize paleoenvironmental changes through the ACM sequence, with emphasis on the time span comprising the earliest Late Miocene (~11.6 Ma) up to the Aragonian/Vallesian boundary (~11.2 Ma). However, the abundance of giant tortoises suggests that both the latest Aragonian and the earliest Vallesian were characterized by quite open and arid conditions, maybe punctuated by humid episodes and/or locally humid habitats, as suggested by the the presence of hominoids primates at Can Mata 1 (Crusafont-Pairó & Golpe-Posse, 1973). At the moment, is uncertain whether the Aragonian/Vallesian faunal turnover was accompanied by concomitant changes in the local paleoenvironmental conditions. However, the apparently simultaneous dispersal of several eastern immigrants into Europe (hipparionins, giraffids, the suid *Propotamochoerus*, and the felid *Machairodus*; Alba et al., 2022a) suggests that environmental changes took place at a continental scale.

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ADDENDUM

EDITORS' NOTE:

Owing to technical problems with the submission system, four abstracts could not be processed in time and had to be included in this addendum at the proof stage. We sincerely apologize for the inconvenience.

Book of Abstracts

THE TIMES THEY ARE A-CHANGIN': SYSTEMATICS & BIOCHRONOLOGY:

NEW AVENUES FOR INCREDIBLY OLD TRAVELERS: MODERN-DAY PALEOBIOGEOGRAPHY & PALEOBIODIVERSITY RESEARCH AND FUTURE DIRECTIONS:

ECOMETRIC AND PALEOECOLOGICAL RESEARCH BASED ON THE NOW DATABASE: NOVEL RESEARCH QUESTIONS, DATA, AND METHODS TO UNRAVEL LARGE-SCALE CLIMATE, PALEOENVIRONMENTS, AND BIOTIC PATTERNS:

Biochronology of the Pleistocene localities in Northern Eurasia with the emphasis on large mammals of the former USSR territories

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ABSTRACT

Data on the Pleistocene localities of Northern Eurasia were collected since 2000 for a large-scale Pleistocene study of warm-adapted large mammals, represented on the former USSR territory. The interest in warm-adapted species was sparked due to apparently unchanging nature of large mammal presence in Eastern Europe and Siberia during interglacial and glacial periods—unlike in Central Europe, where interglacial and glacial communities exchanged accordingly. The former USSR territories were extensively explored and Russian publications still contain a lot of untranslated information; the study incorporated these literature sources of the last century.

Stratigraphic correlations introduced certain difficulties due to different temporal resolution as well as vastness and heterogeneity of landscapes, especially when comparing localities from the former USSR, which resulted in lumping together longer time periods. Stratigraphic resolution has since been improved, enabling a better adjustment and more detailed separation of the time periods for the 1,000 paleontological and archaeological localities containing mostly large mammals of the Pleistocene.

Current work is aimed at bringing together and better understanding of the data on the evolution and paleoecology of faunal communities across Northern Eurasia, facilitating future research. The data will soon be opened for public use in the NOW database of fossil mammals (The Now Community, 2022).

KEYWORDS: Biochronology; Northern Eurasia; NOW; Megafauna.

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The NOW Community (2022). New and Old Worlds Database of Fossil Mammals. Licensed under CC BY 4.0. Retrieved from https://nowdatabase.org/now/database/. http://doi.org/10.5281/zenodo.4268068.

Where's dinner? Variation in carnivoran distributional responses to Vallesian faunal turnover

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ABSTRACT

Carnivorans, such as lions, wolves, and leopards, have some of the widest distributions among mammals. The distribution of carnivorans in the Late Pleistocene is even more impressive in both glacial and interglacial periods. This wide distribution in the past might indicate that carnivorans are able to cope with varying climatic circumstances and prey species. We could therefore assume that carnivorans are less susceptible to environmental changes and stand a better chance of surviving major faunal turnovers.

In order to test this hypothesis, we investigate the response of carnivorans during the mid-Vallesian faunal turnover, also dubbed the 'Vallesian Crisis'. We compare the remarkably rich carnivoran assemblage of Can Llobateres (late Vallesian, MN10), which is one of the richest Vallesian localities in the Vallès-Penedès Basin (Catalonia, Spain; Alba et al., 2011a, 2011b), with the European assemblages of the Middle and Late Miocene. We aim to assess to what extent the Vallesian carnivoran assemblage was part of the southward diversity trend noted by Madern & Van den Hoek Ostende (2015) or was a unique assemblage in itself.

The area under investigation ranges from Europe to Anatolia—longitude between 10° W and 50° E, latitude between 15° to 55° N, excluding North Africa. We applied several thresholds to filter out most singletons, finding that a 10% filter provided the most consistent results. Out of 367 localities and 130 genera, a total of 332 localities and 51 genera were retained, covering European Neogene mammal units MN4 to MN13 (~17 to 5.3 Ma).

Similarity maps using the Raup-Crick index show that the origin of this Vallesian carnivore assemblage lies to the north of the Iberian Peninsula, gradually making its way south. Migrations in the late Aragonian and early Vallesian lead to the biodiversity hotspot. Shortly after the beginning of MN10, the mid-Vallesian turnover, the carnivoran assemblage collapses. This is mainly because of the extinction of part of the fauna, and a retread of some species to the north, disappearing from Spain. Among the latter there are several genera that had dispersed at the beginning of the Vallesian. As such, clearly the Vallesian fauna of the Vallès-Penedès partly consisted of transients that only occur in the Iberian Peninsula when conditions were optimal.

The Vallesian is recognized as a period in which older faunal elements survived while new taxa already appeared. This rich ecosystem was sustained by the exceptionally favorable conditions in the region. The carnivoran fauna fits this scenario, with mainly older elements disappearing at the mid-Vallesian turnover. However, this picture is enhanced by transient taxa that survive at higher latitudes. The turnover in response to a changing climate with more open landscapes is certainly real. But its original classification as a 'Vallesian Crisis' appears to be governed by the exceptional circumstances in the area where this turnover was first recognized.

KEYWORDS: Late Miocene; Paleobiogeography; Carnivora; Vallesian Crisis; Mammals.

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The effects of Cenozoic ecosystem change on small mammal community ecology over three continents

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ABSTRACT

Dramatic changes in terrestrial ecosystems through the Neogene have had a significant effect on the evolution of mammals. The increasing dominance of open habitats and cool, seasonal climates have driven greater hypsodonty in ungulate herbivores (Janis et al., 2000; Jernvall & Fortelius, 2002) with an increasingly grassy diet, as well as larger body mass and more frequent cursoriality (Janis et al., 2002). Large carnivorans likewise see increases in cursoriality and body size to keep pace with their prey (Van Valkenburgh, 2007). Recent studies of North American small mammals have revealed that the ecological adaptations to open habitats appear much earlier in smaller species, with increases in both hypsodonty and open-habitat locomotor adaptations such as digging and hopping appearing in the Oligocene, before grassy habitats were dominant on the landscape (Samuels & Hopkins, 2018). I have added to this dataset to ask how small mammals in Asia and Europe responded to similar changes, given that the timing of the spread of open habitats was similar throughout the Holarctic.

While the types of changes in diet and locomotor habits are similar between the Holarctic continents, the timing and extent of ecological changes is distinct between Eurasia and North America. The change in dental morphology and diet is less dramatic in Europe than it is in North America, as well as occurring more than 10 Myr later. In Asia, hypsodont morphologies indicative of abrasive diets become common in the Oligocene, as they do in North America, but the extent to which high-crowned taxa dominate the diversity of small mammals is much less than it is in North American ecosystems, with hypsodont and hypselodont taxa never more than half the diversity of Asian fossil small mammals. In locomotor habits, the European and Asian records have a much smaller increase in open-adapted habits such as fossoriality and saltation than North America, although the timing of their appearance is similar across all three continents.

It is difficult to determine how much of the difference between the Holarctic continents represents real ecological and evolutionary differences and how much is a reflection of the preservational differences between habitats. Europe and Asia both have extensive fossil records of forested habitats through the Oligocene and the Neogene, while the more forested eastern half of North America has few fossil sites through the Cenozoic. Future studies will determine the role of preservational environment in dictating these patterns. In spite of these potential preservational differences, my finding shows the importance of small mammals, which respond more rapidly to environmental change than their larger cousins, in detecting the timing of ecosystem changes. The distinct responses in Europe and Asia also highlight global differences in patterns of ecological change, making it all the more important to add data from South America, Australia, and Africa to these databases in order to get a clear sense of the relationship between mammals and ecosystem change.

KEYWORDS: Rodentia; Open habitats; Hypsodonty; Locomotion; Community ecology.

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A recommender systems approach to reconstructing mammal faunas across Pleistocene Eurasia

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ABSTRACT

We present a novel approach to estimating more complete community composition across a subset of sites in the NOW database with uneven sampling or preservation of mammalian taxa. The unknown extent to which collected fossils represent the full animal community that was present at a point in the past presents a major stumbling block for analyses aiming to compare fossil community structures across sites, as their levels of preservation vary drastically. We apply recommender systems modeling, a method widely used in computer science for the recommendation of products or items to users based on those users' previous interactions with other items, to output estimates of complete fossil mammal communities based on co-occurrences of taxa across a range of training sites (these sites are treated as the 'users'; Žliobaitė 2022). The recommender systems produce a ranking of the suitability of each site for each taxon in the training dataset. Using different model parameters and suitability cutoffs, we can produce an approximation of the total community of taxa present at each site. This approach holds great promise for future studies aiming to compare community structures between fossil sites with varying levels of collection effort or preservation.

We applied the recommender systems methodology to the Pleistocene mammal fossil record of Eurasia in the NOW database, which currently encompasses 1,095 sites with at least one terrestrial mammal fossil present. We carried out these analyses at the genus level, assigning higher certainty of occurrence to genera for which more than one species were present at a site. We evaluated model performance using tests of whether each model produced low suitability scores for genera at sites dating to outside of their known age ranges (true negative occurrences) and high suitability for genera for which fossils of multiple species have been reported at a site (true positive occurrences).

We then interrogated how these recommender systems capture ecological reality by comparing the body size distributions from the mammal communities outputted by the recommenders with the characteristics of body size distributions in modern communities. Body size distributions for each site based on only recorded fossils differ significantly from the size distributions of modern communities in the same area (Faurby et al., 2018). Figure 1 shows body mass distributions for two Pleistocene sites in the Nihewan Basin of China, plotting the size distributions for their input fossil communities alongside those of reconstructed communities from a recommender model and local modern mammal communities. The model output communities exhibit body size distributions similar to those typical of modern mammal communities. However, the mean and maximum body sizes of the reconstructed communities are significantly higher than modern ones due to the presence of extinct megafaunal genera. With further methodological developments, recommender systems can enable future ecometric analyses requiring comparable community trait distributions across fossil sites.

KEYWORDS: Communities; Body size; Recommender systems; Sampling.

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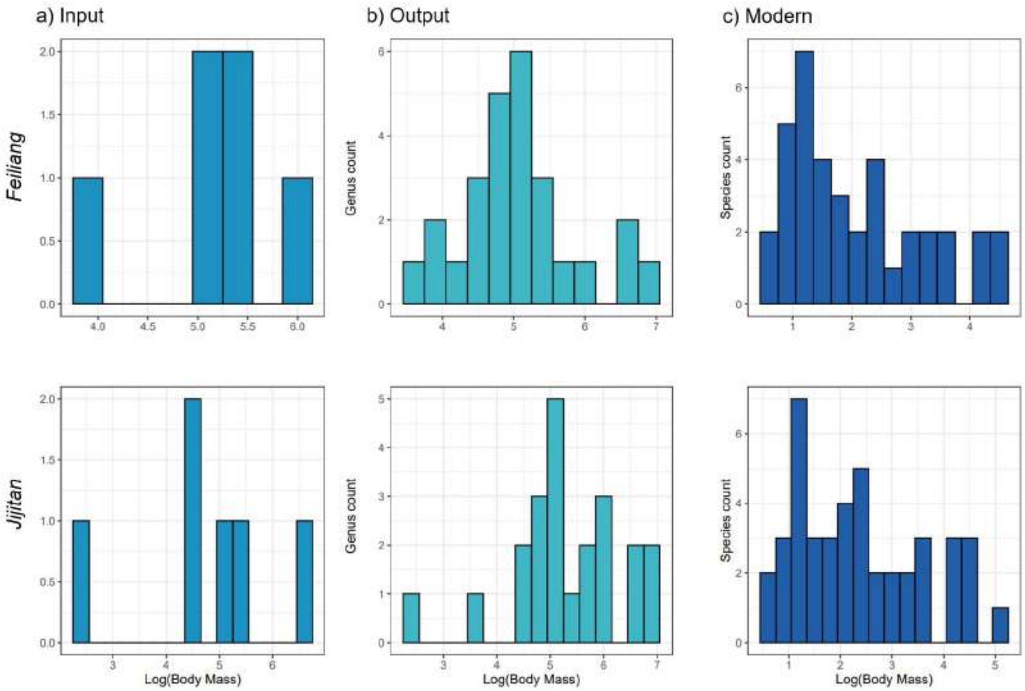

Figure 1. a, Distribution of body masses for the fossil mammal genera recorded at the Nihewan Basin fossil sites Feiliang (1.38–1.18 Ma) and Jijitan (14–13.800 ya). **b**, Reconstructed community size distribution from a recommender system model. **c**, Example body size distributions of modern mammals in the region (data: Faurby et al., 2018).

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