



ABSTRACT BOOK



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CELLULAR-LEVEL PRESERVATION IN THE SOFT TISSUES OF THE THEROPOD DINOSAUR *SCIPIONYX SAMNITICUS*: AN OVERVIEW

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Keywords: *Dinosauria, Theropoda, vertebrate taphonomy, Lower Cretaceous, Italy.*

In 1998 the baby theropod *Scipionyx samniticus*, from the Lower Cretaceous of Pietraroia (Benevento Province, southern Italy), became famous worldwide thanks to its unique preservation of internal soft tissues. Subsequent detailed studies demonstrated that in this 110-million-year-old fossil the soft tissues are not simply imprints but are mineralized in three dimensions, and that their preservation is exceptional even at a cellular, and at some points subcellular, level.

Scanning electron microscopy (SEM) revealed astonishing micro-anatomical information, such as the sarcomere-related banded pattern within single muscular myofibers, a multi-layered epithelium in the duodenum, and capillary-size, branched blood vessels in the rectum; ultraviolet-induced fluorescence (UV) and SEM element microanalysis confirmed the haematic origin of the reddish macula formerly referred to the liver, demonstrating that even remains preserved as thin organic films retain authigenic chemical compounds derived from the decay of the dinosaur carcass. Internal tissues include axial ligaments, axial and appendicular articular cartilage, neck muscles and connective tissue, part of the trachea, oesophageal remains, traces of the liver and other blood-rich organs, the entire intestine, mesenteric blood vessels and pelvic and hindlimb muscles; external soft tissues are beautifully represented by the horny manual claws.

On the other hand, we demonstrated that the remains or imprints purported by some authors to be of the “diaphragmatic muscles” are, in fact, a calcite nodule of amorphous microstructure, inconsistent with the preservation of other muscle tissue in this fossil. This evidence denies the hypothesis of a hepatic-piston assisted breathing mechanism in *Scipionyx*.

Outstandingly, the degree of preservation of the soft tissues also permitted to map the relative position of the food remains in the digestive apparatus and thus to reconstruct a feeding chronology, an insight that is usually impossible to obtain from fossils. *Scipionyx*'s guts contain

bones from a lepidosaurian reptile in the stomach region, lizard-like polygonal squamae in the duodenum, fish scales in the rectum, and a variety of tiny remains in several points of the intestine. This is evidence that *Scipionyx* fed on both lizards and fish, and confirms that in theropod dinosaurs the partially undigested bones were guided through the entire intestine, eventually being incorporated within the faeces.

The exceptional preservation of labile soft tissue indicates that, after death, the carcass of this theropod hatchling was subjected to very little decay and rapid authigenic mineralisation. The highest taphonomic threshold is represented by substrate microfabrics, that occur where soft tissues have been phosphatised directly by very small apatite crystallites, replicating details at subcellular level. The amount and detail of information gained from this single specimen make the Pietraraja Plattenkalk a unique fossil Lagerstätte. In spite of the more frequent finds in China of dinosaurs with integumentary structures, the preservation of such a variety of internal soft tissues revealed by *Scipionyx samniticus* remains a unique in the fossil record.

THE BODY MASS OF *PALUDOTONA* (LAGOMORPHA, MAMMALIA), THE LAST STEM LAGOMORPH (TUSCO-SARDINIA PALAEOBIOPROVINCE, LATE MIOCENE)

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Keywords: *Insular endemism, refugium, gigantism, ghost lineage, Mediterranean islands, Turolian*

The genus *Paludotona* (Lagomorpha, Mammalia) is an insular taxon endemic of the Tusco-Sardinia palaeobioprovince (~8.3-6.7 Ma). *Paludotona* is the last representative of stem lagomorphs, a heterogeneous basal group of early lagomorphs, and its last record (6.7 Ma) postpones of 2.5 Ma the LAD of this stem group. Thus, during the late Miocene, *Paludotona* can be considered a living fossil. Since how long *Paludotona* was thriving in its insular refugium is unknown: fossils record less than 15% of its temporal distribution range, as there is evidence that the lineage developed in isolation *sensu lato* for at least 14 Ma (ghost lineage). *Paludotona* acquired a gigantic size with respect to continental ancestors, in accordance with the pattern followed by small mammals in insular environments. Its body mass (BM) is estimated in ~1100 g, which is three to five times the BM of MP28-MN1 stem lagomorphs of continental Europe, the group from which *Paludotona* likely stemmed. The reasons for such an enormous BM increase are multiple and interconnected. Some of them likely are synecological factors *s.l.*, lower extrinsic mortality, changes in size and degree/pattern of fragmentation of the area of the insular palaeobioprovince, and successive climate changes (which caused a rapid evolutionary pulse followed by a relative stasis following the pattern of Mein's biphasic model). Through BM estimation and morphological observation, we observed that *Paludotona* probably increased its

lifespan (though, at present, this datum is not quantitatively determined), and we suspect a change in posture and locomotion caused by the noticeable BM increase.

INTEREST OF ACCURATE SPECIES IDENTIFICATION IN FOSSIL RECORD, THE STORY OF LEMMINGS

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Keywords: *geometric morphometrics, lemmings, taxonomy, Pleistocene*

Taxonomic identification is the cornerstone of all investigations regarding past faunal communities or ecosystem and, more generally, fossil biodiversity. For ancient time period, systematics is only based on morphology, due to the absence of preserved DNA in fossil specimens. However, similarity between closely related species and intra-specific morphological variability make identification a difficult task, and can lead to spurious classification of fossils. Accurate identification is crucial in periods of major environmental changes implying important faunal turnovers and rapid species evolution, such as the climatic cycles during the Pleistocene. This study proposes a global revision of the status of an emblematic species complex of European glacial environments, the Lemmings (*Lemmus* sp., *Myopus* sp.). Their dental morphological similarity makes them difficult to identify in the fossil record, and it was considered that the only genus present in Europe during Pleistocene was the True Lemming (*Lemmus* sp.). The reinvestigation of Late Pleistocene fossil specimens using geometric morphometrics demonstrated that *Myopus* sp. was also a member of the Pleistocene European faunas. These results question the identification of other Lemming specimens in Europe, as well as the relevance of the taxonomic status of previously identified fossil species, such as *Lemmus kowalski*. To avoid a typological description and in order to characterize the variability of morphological characters with statistical confidence, we emphasize the need of using geometric morphometrics, in taxonomic identification. The re-investigation of fossil specimens using such methods is undoubtedly necessary to have a more accurate understanding of past faunal communities and thus environmental reconstructions.

PRELIMINARY STUDY OF THE RODENTS ASSEMBLAGES FROM THE LATE MIOCENE OF MOȘNA 1 (MOLDAVIAN PLATFORM – ROMANIA)

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Keywords: *micromammals, rodents, Late Vallesian, Late Miocene, Moldavian Platform, Romania.*

The micromammals assemblage from one Late Miocene locality (Moșna 1) of the Moldavian Platform present the occurrences of new specimens of rodents. This locality is located south of Iași county, in the northeast part of Romania. Fossils were collected from at least 2.5 tons of sediment that was wet sieved on a set of stable sieves. Important fossil fragments have been identified in these sediments, including micromammals teeth. The rodents assemblage contains 25 identifiable teeth belonging to eight taxa: *Spermophilinus bredai*, *Progonomys hispanicus*, *Byzantinia* sp., *Neocricetodon moldavicum*, *Pliospalax* sp., *Lophocricetus* sp., *Glirulus lissiensis*, *Muscardinus* sp. The age of the assemblage is interpreted as Late Vallesian, Late Miocene. Moreover, *Byzantinia*, *Neocricetodon*, *Lophocricetus*, and *Pliospalax* are for the first time described in the Late Miocene of Romania. This rodents assemblage represent an important contribution to the study of micromammals from the Late Miocene of Moldavian Platform and also for interpreting paleoenvironment.

CHALLENGES AND OPPORTUNITIES FOR INTEGRATING TRAIT DATA ACROSS THE TEMPORAL DIVIDE

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Keywords: *functional traits, climate change, evolution, ontology, linked open data*

Functional traits are the measurable features of organisms that directly interact with the environment. Quantifying changes in these traits is key to understanding how climate and anthropogenic change affects species. An historical perspective can illuminate changes in intensity of change for animal populations. Zooarchaeological data, representing early to modern human occupation periods, provide a bridge from paleontological and prehuman data, to modern data. However, paleontological and zooarchaeological trait data are based on skeletal metrics rather than soft tissues, include additional long-tail data such as contextual and temporal data, and are often curated in discipline specific data repositories, hindering discoverability of datasets across the temporal divide. Further, gathering trait data that cuts across time requires much onus on the researcher to standardize disparate datasets. However, modern, paleontological and zooarchaeological datasets can be linked based on locality, and zooarchaeological and paleontological datasets can be temporally linked as well. Preserving the necessary metadata and aligning discipline-specific standards to make these linkages is a challenge. We present the Functional Trait Resource for Environmental Studies (FuTRES), a data store that aggregates and standardizes trait data from paleo, archaeo, and modern specimens, making such data findable and searchable. We show the utility and potential of FuTRES in accelerating science across time, and present a tool to help multidisciplinary researchers standardize their datasets for trait based research.

3D CRANIAL RECONSTRUCTIONS OF THE ENIGMATIC THALATTOSAURIFORMES

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Keywords: *Scanning, retrodeformation, 3D-modeling, Thalattosauriformes, Triassic*

The Thalattosauriformes are an ecomorphologically diverse, but enigmatic group of Triassic marine reptiles known predominantly from fragmented material. Their relative rarity in the fossil record means that their evolutionary origins and biology have remained poorly understood. (Re)Description of historic and new material from North America, Europe and China provide insights into intraspecific and intrageneric variability, detailed cranial anatomy and mode of tooth implantation.

Here we use digitization, 3D-restoration and retrodeformation to study the morphology of Thalattosauriformes skulls of 5 genera in unprecedented detail. The wide variety of preservational artefacts makes their remains an excellent subject to push the boundaries of current reconstruction methods. For the majority of the material traditional tomographic approaches provide insufficient internal resolution for digital extraction. We therefore employ an integrative imaging approach that combines high-resolution CT scanning and computer laminography (CL) to overcome common limitations. This technique helps to reverse taphonomic overprinting and is thus a crucial preliminary step for follow-up studies that assess the phylogeny, ecology, and functional morphology of the group.

We show that the crania of thalattosauroid thalattosauriforms are highly akinetic, with intricate interlocking and extensive bony contacts between skull elements. These likely helped thalattosauriform skulls sustain large stresses related to the durophagous aspects in their diets. In addition, *Thalattosaurus* displays a set of unique dental characteristics including variation in tooth orientation, degree of enamel covering and root dimensions. Overall, the morphological variability of dentigerous elements is much greater than previously assumed as illustrated by a thorough sampling of North American thalattosauroid thalattosauriforms.

REVISING THE NEGLECTED POST-CRANIUM OF JURASSIC RHYNCHOCEPHALIANS FROM THE SOLNHOFEN ARCHIPELAGO

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Keywords: *sphenodontian, Mesozoic, osteology*

The significant diversity of rhynchocephalians during the Mesozoic has been known for over a century and is getting increasing attention in the last decade. However, most studies of this group of lepidosaurs still focus mainly on the cranial anatomy, with emphasis on the jaws and dentition. This has led to a poor understanding of the postcranial anatomy of rhynchocephalians, and the implications this might have for their taxonomy, phylogeny, and palaeoecology. The high diversity and exceptional preservation of Jurassic rhynchocephalians from the Solnhofen Archipelago can provide new information on the postcranium of these animals. Taxa, such as *Kallimodon* and *Homoeosaurus*, have been formerly described, but still lack proper diagnosis, leading to disagreements over the validity and real diversity of rhynchocephalians during the Late Jurassic of Europe. Revisions of these taxa are long overdue and can help in identifying new species based solely on postcranial material, as well as to quantify morphological variation between specimens. In the last five years, the postcranium of rhynchocephalians has accounted from 0% to 30% of the total phylogenetic characters. In our preliminary works, we already observed new characters that may improve and resolve some issues of their evolution and relationships. The postcranial anatomy can also be used for palaeoecological inferences for the clade. Most of these inferences are, so far, based on teeth and jaw morphologies. However, the closest relatives of rhynchocephalians, squamates, show how important postcranial anatomy is, with studies that correlate the appendicular skeleton proportions and morphology to lifestyle and habitat use.

DISSCO PREPARE: TOWARDS A EUROPEAN INFRASTRUCTURE FOR SCIENTIFIC COLLECTIONS

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Keywords: *Natural Sciences Collection, Research Infrastructure, ICCD, Knowledge Graph, DiSSCo*

European Natural Sciences Collections (NSCs) consist of around 1,5 B specimens that are crucial for answering fundamental scientific questions about ecological, evolutionary, and geological processes. In the last decades the volume and diversity of information derived from NSCs are exponentially increasing due to the digital transformation and the progressive use of analytical instrumentation, remote sensing and molecular approaches. The Distributed System of Scientific Collections (DiSSCo) is a world-class Research Infrastructure (RI) for NSCs currently in its preparatory phase. The DiSSCo RI aims to create a new organisational model for collections that digitally unifies all European natural sciences assets under common access, curation, policies and

practices ensuring that all the data are easily Findable, Accessible, Interoperable and Reusable (FAIR principles). DiSSCo thus represents the largest ever formal agreement between natural history museums, botanic gardens and collection-holding universities in the world.

The NHM of the University of Florence represents the current Italian National Node of the DiSSCo Prepare Project and is playing a key role in establishing innovative relationships between its internal Collection Management System and: i) ArCo, i.e. the Knowledge Graph of the Italian Cultural Heritage promoted by the Italian Central Institute for Catalogue and Documentation and the Italian National Research Council, ii) the General Catalogue of Italian Cultural Heritage web portal created by the ICCD (3 M catalogue records) and, finally iii) the DiSSCo RI. In particular, ArCo ontology network, adopted by Agenzia per l'Italia Digitale (AgID), allows the representation on the semantic web of ICCD standards for natural heritage.

THE EMERGENCE AND EARLY DIVERSIFICATION OF THE PLACENTAL MAMMAL BRAIN

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Keywords: *Paleogene, mammal, endocast, neocortex, petrosal lobules*

Mammals have the largest brains among vertebrates, and boast a novel cerebral neocortex, center of sensory integration and complex behavior. The emergence and diversification of the mammalian brain remains challenging to decipher because fossil specimens that can provide brain endocasts are relatively rare. We used 34 new computed tomography scans of Paleogene fossils including 17 taxa from the Paleocene of the USA and France alongside previously published endocasts. Contrary to previous hypotheses that relative brain size increased continuously over time, our results show that following the end-Cretaceous extinction, body mass increased at a faster rate leading to a decrease in relative brain size in early Paleocene mammals. Ten million years after the extinction during the Eocene, greater encephalization independently emerged in several mammalian lineages. The neocortex and the petrosal lobules were substantially more expanded in early members of crown placental mammals. Intensified competition in increasingly saturated ecosystems might have triggered an arms race, in which greater encephalization and behavioral specialization promoted lineage survival. Indeed, predators and potential prey had low and indistinguishable phylogenetic encephalization quotients in the Paleocene, but both guilds encephalized in the Eocene, arming carnivores with significantly larger relative brain size than herbivores. Additionally, the Eocene experienced intense hyperthermal warming spikes, leading to higher precipitation and increased seasonality, during which behavioral flexibility and ability to disperse, linked to higher relative brain size, may have been beneficial. These findings indicate that increased ecological opportunity and guild interactions both were instrumental during the establishment of crown mammalian brains.

REDESCRIBING *LIBYCOSUCHUS BREVIROSTRIS* STROMER 1914 (CROCODYLIFORMES, NOTOSUCHIA)

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Keywords: *Crocodyliformes, Notosuchia, Cretaceous, tomography, digitalization*

The German palaeontologist Prof. Ernst Stromer discovered a striking bizarre vertebrate fauna during his expeditions into the Western Dessert of Egypt at the beginning of the 20th century. Among the species described by him is the crocodyliform *Libycosuchus*, being one of the few fossils of Stromer's collection that was not destroyed during the bombing of Munich in the Second World War (1944).

Libycosuchus is represented by an almost complete, articulated skull, lower jaws and four vertebrae found at the Gebel El Dist site (Cenomanian of Bahariya, Egypt). The skull is well preserved, but damaged at several points (right orbit and postorbital bar, left jugal, right pterygoid and palatines), which have been reconstructed. In the lower jaw, the anterior ends of both dentaries are damaged, and the area around the left mandibular fenestra is broken and reconstructed. We performed a CT-scan of these remains in order to improve the morphological descriptions and assess the internal anatomy.

When first described (1914), anatomical comparisons of *Libycosuchus* were limited, and the taxon was compared to *Notosuchus*, *Alligatorellus*, *Theriosuchus*, goniopholids, *Bernissartia* and *Crocodylia*. This led Stromer to consider *Libycosuchus* as a "highly-specialized form with ancestral features" closely related to *Notosuchus* and *Theriosuchus* and placed in its own genus and family. Since then, a vast number of newly discovered taxa has increased the complexity in the systematics of the Notosuchia, resulting in different interpretations of the position of *Libycosuchus*. Our aim is to update comparisons with taxa from different notosuchian clades, and discuss its phylogenetic relationships.

**A SINGULAR ASSEMBLAGE OF SMALL AMPHIBIANS AND REPTILES
FROM THE EARLY MIOCENE (RAMBLIAN, MN3) OF TURÓ DE LES
FORQUES 1 (VALLÈS-PENEDÈS BASIN, CATALONIA)**

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Keywords: *palaeoherpetofauna, amphibians, reptiles, squamates, crocodiles, Miocene*

Turó de les Forques 1 is a fossil vertebrate locality located close to Castellbisbal, in the Neogene Vallès-Penedès Basin, and correlated to zone A of the Ramblian regional age (MN3, Early Miocene) based on its rodent fauna. Here we report a diverse assemblage of small amphibians and reptiles that was recovered, together with other microvertebrates, using screen-washing techniques, and is currently housed at the Institut Català de Paleontologia Miquel Crusafont. The palaeoherpetofauna includes amphibians, lizards, snakes, and crocodiles, mostly represented by fragmentary material. Among the amphibians, the identified taxa correspond to alytid and ranid anurans, and possibly, but not certainly, to an indeterminate urodele. Among lizards, we report the presence of chameleons, scincoids, lacertids, and anguines. Snakes are represented by numerous but rather fragmentary vertebrae (mostly condyles), but we recognised at least the presence of “colubrines”. Finally, crocodylians are represented by scarce teeth and osteoderms,

whose morphology is reminiscent of that of *Diplocynodon*, although we regard this identification as tentative given the lack of more diagnostic material. Besides a relatively high diversity, the locality is interesting in providing the earliest evidence of many small amphibian and reptilian taxa typical of the Vallès-Penedès Basin, and a particular assemblage composition that lacks some typical elements found in other localities of the same basin, like blaniid amphisbaenians and the varanid lizard *Varanus*. On the other hand, it includes less common taxa such as chameleons and scincoids, representing the first record of the former in the basin.

EARLY MIOCENE REMAINS OF *MELISSIODON* FROM MOKRÁ-QUARRY (MORAVIA, CZECH REPUBLIC) SHED LIGHT ON THE EVOLUTIONARY HISTORY OF THIS RARE CRICETID GENUS

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Keywords: *Melissiodontinae*, *Melissiodon schlosseri*, *Melissiodon dominans*, *Burdigalian*, *Moravian Karst*.

The extinct genus *Melissiodon* is a cricetid considered endemic to Europe, known from the early Oligocene to the early Miocene. Among micromammal remains, its finds are usually very rare, and most of them are scarce and fragmentary. Currently, two species are considered taxonomically valid from the early Miocene: *Melissiodon schlosseri*, which is based on two teeth from the MN2 German locality of Haslach and only reported in two other sites coeval in age (i.e., Ulm-Uniklinik and La Chau; Germany and Switzerland respectively); and *Melissiodon dominans*, found in MN3 and MN4 localities across Europe, even though the scarce and fragmentary remains make some of these taxonomical assignments dubious. For this reason, *Melissiodon dominans* has become a “wastebasket” species. However, the Mokrý-Quarry site provided one of the best-documented findings of *Melissiodon* remains in MN4 localities of Europe. These new remains of *Melissiodon* have been identified as a new morphotype that clearly differs from *Melissiodon dominans* by its unique m1 morphology but still shows some resemblance to *Melissiodon schlosseri*. Based on that, the material presented here is referred to *Melissiodon* aff. *schlosseri*. We also propose the hypothesis of an evolutionary line starting from *Melissiodon schlosseri* that would have reached

the late early Miocene. Therefore, at least two different taxa of *Melissiodon* coexisted before the genus extinction. Thus, the evolutionary history of the genus is more complex than previously thought and a complete revision of the type material of *Melissiodon dominans* and *Melissiodon schlosseri* is required.

**MITOCHONDRIAL PHYLOGENY OF THE EXTINCT *PROLAGUS SARDUS*
(LAGOMORPHA, MAMMALIA): REIGNITING THE DEBATE ABOUT FAMILY
PROLAGIDAE**

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Keywords: *ancient DNA, Prolagus sardus, phylogeny, insular evolution*

Sardinian Quaternary palaeofauna potentially represents a gold mine for application of ancient DNA techniques. Dozens of small and large mammals, now extinct, populated the island in the recent past (sometimes until historical times). Palaeogenomic studies could cast a light on their phylogeny, often obscure due to the modifications acquired under insular evolution, and provide valuable data about past faunal diversity and dispersal routes.

The lagomorph *Prolagus sardus* is an emblematic Sardinian small mammal, and one of the last

survivors of the Plio-Pleistocene faunal assemblages. Archaeological evidence, as well as testimonies from historians, highlight that *P. sardus*, the last representative of a genus that can be traced back to ~20 Ma in continental Europe, survived in Sardinia (at least) until the Bronze Age. According to Western European taxonomic “tradition”, *Prolagus* is a member of family Ochotonidae. In this case, *Prolagus* represents, together with the extant *Ochotona*, the only ochotonid to survive in historical times. Other scholars, mainly from Eastern Europe and Asia, consider the existence of the family Prolagidae to include all the species of *Prolagus* and possibly *Ptychoprolagus*.

A femur of *P. sardus* from San Lussorio cave (Romana, NW Sardinia, early Neolithic, 4.7-2.4 ky BC) yielded DNA, providing promising results. Preliminary phylogenetic analyses based on a discrete mitochondrial DNA dataset show that *Prolagus* is a sister clade to extant family Ochotonidae. Further perspectives are: 1. clarify if *Prolagus* deserves to be included in a separate family (Prolagidae), and 2. provide the time of the divergence of the two clades.

POSTCRANIAL OSTEODERM MORPHOLOGY OF PERMIAN PAREIASAURS (PARAREPTILIA)

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Keywords: *Pareiasauria, osteoderms, morphology, middle-late Permian, Eastern Europe, South Africa*

Postcranial osteoderms are a characteristic feature of pareiasaurs. Developed usually as massive lens-shaped structures, they have a high preservation potential and, thus, frequently occur in localities, either isolated or associated with skeletons. Several tens (*Bradysaurus, Deltavjatia, Embrithosaurus, Nochelesaurus, Provelosaurus*) to several hundreds (*Anthodon, Pareiasaurus, Pumiliopareia, Scutosaurus*) of osteoderms could be distributed along the body of a pareiasaur. Three types of postcranial osteoderms are known in pareiasaurs: the platform type, most frequently found in Gondwanan and East European representatives, and two further types – the conical and the spherical – only observed in the East European genus *Scutosaurus*, in combination with platform osteoderms. Platform osteoderms exhibit a complex morphology, determined by the name-giving platform (*basis osteodermæ*), which has a rounded, oval or polygonal outline and a lens-shaped cross-section. Its ventral surface is smooth and bears openings and grooves of blood vessels, sometimes also irregularly shaped tubercles. The outside is characterized by a complex relief, composed of a distinct dorsal elevation (*tuber osteodermæ*) and a variety of pits, tubercles, ridges, furrows and foramina. The presence or absence of these characters and their combination frequently allows for determining the topological position of platform osteoderms within a pareiasaur skeleton. Furthermore, morphological differences between the platform osteoderms of both the East European and the South African pareiasaur genera demonstrate their huge potential for the systematics of the group.

HIGH MORPHOLOGICAL DISPARITY IN A BIZARRE PALEOCENE FAUNA OF PREDATORY FRESHWATER REPTILES

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Keywords: *Cretaceous-Paleogene, Choristodera, Depauperon, North America*

The Cretaceous-Paleogene mass extinction was a pivotal event that fundamentally changed global ecosystems and shaped extant biodiversity. However, the floras and faunas that appeared immediately after the extinction event were very different from ecosystems found today. Choristoderes are a phylogenetically problematic, species-poor reptile clade with a fossil record stretching from the Middle Jurassic to the Miocene. Members of one major choristodere clade, the Neochoristodera, seem to have their largest sizes and peak diversity right after the asteroid impact. I describe two new choristoderes from a ~60-million-year-old ecosystem in western North America based on complete skulls and partially articulated skeletons that deviate dramatically in morphology. *Kosmodraco magnicornis* gen. et sp. nov. possesses an extremely short snout, extensive cranial ornamentation, and a sacrum with enlarged muscle attachment sites reminiscent of some giant crocodylians. In contrast, *Champsosaurus norelli* sp. nov., is a longirostrine taxon with an unornamented skull. Together with the North American choristodere *Kosmodraco dakotensis* comb. nov., *K. magnicornis* substantiates a new clade of giant brevirostrine choristoderes endemic to the American West. The new taxa in turn increase Cenozoic choristodere richness and suggest that choristodere faunas showed trans-Atlantic divergences in the aftermath of the asteroid impact.

INFERENCE OF LIMB PHASE AS A CRUCIAL GAIT PARAMETER FOR THE PRODUCERS OF *ICHNIOTHERIUM* TRACKS FROM THE EARLY PERMIAN TAMBACH FORMATION, GERMANY

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Keywords: *Diadectomorpha*, *Cisuralian*, *Thuringian Forest Basin*, *locomotion*, *tetrapod ichnology*

The order of limb movements in symmetric gaits of quadruped tetrapods can be described as continuous spectrum between pace (limb phase at 0 and 100%) and trot (limb phase at 50%) with intermediates referred to as sequence walk. Given the availability of relatively long *Ichniotherium sphaerodactylum* trackways in larger numbers and of complete skeletons that belonged to a very likely trackmaker (*Orobates pabsti*), the well documented trackway sample of the early Permian Bromacker locality yields the unique possibility to infer the limb phase of the *I. sphaerodactylum* trackmakers via two independent approaches: (a) use of the along-track variability in stride length for calculation of an optimum order of limb movements that minimizes variability under the assumption of a homogeneous walking style, (b) comparison of the distance between the centers of hip and shoulder joints in *Orobates* with the so-called glenoacetabular distance (GAD) in *I. sphaerodactylum* of comparable size. The GAD represents a trackway measure that describes the distance between successive pairs of manus and pes footprints and is supposed to correspond to the trunk length of a skeleton. Approach (b) resulted in limb phases between 25% (single foot lateral sequence walk) and 60% (diagonal sequence walk with diagonal couplets) with a maximum between 40 and 50%. Approach (a) was inconclusive for most of the longer trackways, which were too homogenous, and only one specimen produced a well-constrained optimum limb phase of 40% (lateral sequence with diagonal couplets), a result in good agreement with an average limb phase

of 41% inferred by means of approach (b). Accordingly, *Orobates* probably employed a walking trot or a slightly deviating type of lateral sequence walk.

REVISION OF THE CROCODYLIAN *TOMISTOMA DOWSONI* FROM THE MIOCENE OF NORTH AFRICA PROVIDES NEW INSIGHTS INTO GAVIALOID NEUROANATOMY

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Keywords: *Tomistoma*, *neuroanatomy*, *phylogenetics*, *Gavialis*, *Crocodylia*

The interrelationships of the crocodylian species *Gavialis gangeticus* and *Tomistoma schlegelii* has been historically disputed. Whereas molecular analyses indicate a sister taxon relationship between the two species, morphological datasets typically place *Gavialis* as the outgroup to all other extant crocodylians. Recent morphological-based phylogenetic analyses have begun to resolve this discrepancy, with *Gavialis* more closely related to *Tomistoma* than to any other living species. However, several stratigraphically older fossil taxa are recovered as closer to *Gavialis* than *Tomistoma*, resulting in anomalously early divergence rates. This includes several species currently referred to *Tomistoma*. Here we present an anatomical revision of *Tomistoma dowsoni* from the Miocene of Egypt, known from a holotypic partial snout and a near-complete referred skull. This work demonstrates its validity as a distinct species, but, combined with its incorporation into a phylogenetic analysis, excludes it from the genus *Tomistoma*, which is restricted to the extant species. The referred skull is well preserved, allowing enhanced visualization of the braincase and thus an insight into the neuroanatomy of this species. The inner ear of *Tomistoma dowsoni* exhibits an intermediate morphology between *Gavialis gangeticus* and *Tomistoma schlegelii*, a starting point in understanding more about the evolution of ecomorphological features in gavialoids that might help resolve the group's interrelationships. Features such as the inner ear, cerebrum, pituitary fossa and olfactory tracts vary in size amongst crocodylians. By incorporating such previously inaccessible information from the neuroanatomy of extinct and extant crocodylians into phylogenetic analyses, we might be able to resolve remaining problems surrounding the *Tomistoma-Gavialis* debate.

ELLIPTIC FOURIER ANALYSIS VS FIXED LANDMARKS IN THE DENTITION OF *ANCHITHERIUM*

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Keywords: *geometric morphometrics, upper dentition, Anchitheriinae, Madrid Basin, Middle Miocene*

Anchitherium is a genus of equid (Equidae) belonging to the extinct subfamily Anchitheriinae. This subfamily is characterized by brachydont teeth and tridactyl limbs. Nevertheless, the isolated teeth of *Anchitherium* are difficult to differentiate because of the morphological similarities between the molars (M/m) and the premolars (P/p), and between the decidual and the definitive dentition especially in the upper cheek tooth rows. Therefore, comparisons between species and paleoecological reconstructions can be biased by this dental element determination problem. In order to identify the different dental elements, we use geometric morphometric analysis on upper molars applying Elliptic Fourier Analysis and a set of fixed landmarks. We use isolated and associated maxilla teeth from the Spanish Middle Miocene sites of Mahou and Los Nogales (MN5, Madrid) trying to interpret the observed distribution. Our geometric morphometric approaches consist of the digitization of the different dental pieces using TPSDig2. To do that, we used scaled photographs of the occlusal surfaces of each dental pieces and transformed them to have the same orientation. We use the RStudio packages Stereomorph to collect the data and Geomorph to perform different statistical analyses. The provisional results indicate that these techniques may be useful not only to distinguish between premolars and molars, but also to help identify each dental element in anchitherines.

THE AXIAL SKELETON OF THE HOLOTYPE OF THE SIMOSAURID *PALUDIDRACO MULTIDENTATUS* (EOSAUROPTERYGIA) FROM THE LATE TRIASSIC OF CENTRAL SPAIN

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Keywords: *Sauropterygia*, *Nothosauroidea*, *Simosauridae*, *vertebral series*, *Iberian Peninsula*

Simosaurids are Triassic eosauropterygians belonging to the clade Nothosauroidea. Its fossil record ranges from the Anisian or Ladinian (Middle Triassic) to the Carnian (Late Triassic) of Europe and the Middle East. Simosauridae was, until recently, a monospecific clade only including *Simosaurus gaillardoti* from the Ladinian (Middle Triassic) of France and Germany, due to the Austrian Ladinian '*Partanosaurus zitteli*' was considered as a *nomen dubium*. In 2018, a new simosaurid, *Paludidraco multidentatus*, from the Carnian (Late Triassic) fossil site of El Atance (Guadalajara, Spain) was described. It was interpreted as a bizarre taxon, showing adaptations for slow movement near the marine bottom of shallow littoral environments, thus, extremely different from its sister taxon, the active predator *S. gaillardoti*. *Paludidraco multidentatus* was briefly described based on a relatively complete skeleton (the holotype) and an isolated skull. The anatomy of the vertebrae of this taxon has not been hitherto described. Conversely, the skeleton of *S. gaillardoti* was described in detail in the literature, being well-known not only the skull but also the postcranium, including elements of the axial series from cervical to caudal vertebrae. The description in detail of the vertebral elements preserved in the holotype of *P. multidentatus* is proposed. Most of these elements are articulated, corresponding to the almost complete dorsal and sacral series but also some cervicals and, probably, the most proximal caudal vertebrae. Detailed comparisons with the vertebrae of *S. gaillardoti* are performed, along with those of some indeterminate simosaurids from other European palaeontological sites.

PEER INTO THE *PELECANIMIMUS* EYE: SCLEROTAL RING RECONSTRUCTION OF AN EARLY CRETACEOUS ORNITHOMIMOSAUR FROM SPAIN

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Keywords: *Theropod, Dinosauria, Visual capabilities, CT-Scan, Las Hoyas fossil site*

Ornithomimosaurids were a distinctive group of theropod dinosaurs. Some taxa have been suggested to be omnivores, unlike the vast majority of non-avian theropods. This is the case of *Pelecanimimus polyodon*, with slender mandibles with more than 200 teeth. But the dietary behaviour is not the only questioned issue in their palaeobiology. Diet could be strongly related to sensory habits such as visual capabilities. Non-avian theropod dinosaurs have been assumed as essentially diurnal, but recent studies have revealed probable nightlife capabilities for specific lineages. These studies correlated the relative dimensions of the scleral ring and the orbit with the probability of nocturnality. The results indicated that some ornithomimosaurids, such as *Ornithomimus*, had high probability of nocturnal vision capabilities while others such as *Garudimimus* would have had cathemeral activity (day and night habits). To test the vision capabilities of *Pelecanimimus*, an accurate reconstruction of its scleral ring was performed. The reconstruction was made using CT-Scans of the skull of *Pelecanimimus*. We carried out an accurate segmentation of the different ossicles of the slightly disarticulated scleral ring separately based on the tomography sections. Posteriorly, the scleral ring was virtually reconstructed, reintegrated and manually articulated.

With these reconstructions, we will be able to correlate statistically precise measurements of the scleral ring and orbit with the vision capabilities of *Pelecanimimus* in future approaches. Resolving if it was a nocturnal or cathemeral dinosaur will provide insight on the visual capabilities of early ornithomimosaur.

SPECIFIC SEPARATION OF *DICRAEOSAURUS HANSEMANNI* AND *DICRAEOSAURUS SATTLERI*: OSTEOLOGICAL AND TEMPORAL EVIDENCE

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Keywords: *Dicraeosaurus*, *taxonomy*, *sauropods*, *digitisation*

Dicraeosaurus is a flagellicaudatan sauropod from the Late Jurassic of the Tendaguru Formation in Tanzania that was originally described by Werner Janensch in 1914. It is divided into two species, *D. hansemanni* and *D. sattleri* based largely on the temporal distribution of the known material and the generally more gracile morphology of *D. sattleri*. Here we present a new comparison of the material with the aim of clarifying the differences between the two species, and determine whether they are sufficient to justify the separation of the genus. The holotype material for *D. hansemanni* is mounted at the MfN, Berlin and *D. sattleri* remains in the collections, all material, including specimens currently assigned to genus level, was digitised using laser surface scanning. We found that based on presented analyses and stratigraphy there is sufficient distinction between the specimens to justify the separation of the two species, with all material found in the Upper Dinosaur Member having a morphology akin to that of *D. sattleri* and that from the Middle Dinosaur Member with *D. hansemanni*.

REVISITING THE RADIATION OF HORSES

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Keywords: *macroevolution, diversification, equidae, phylogeny, phenotype*

Horses were common elements of Cenozoic communities and reached high diversity during the Neogene. Most research of their diversification has so far focused on the Early Miocene cladogenesis of the subfamily Equinae (equines, the so-called ‘grazing horses’), interpreting raw diversity counts at face value. Using occurrence data, diversification models and phylogenetic methods, we reconstruct speciation and extinction in horses and interpret these trends in the context of the evolution of body size and relative tooth crown height (hypsodonty). We found that fast species proliferation (speciation rate) was not restricted to equines but was a shared feature in both anchitheres and equines, likely stemming from the more variable environments of the Neogene. The fast early-phase radiation in the subfamily Equinae was likely the result of reduced extinction rates and higher lineage survival rather than a substantial acceleration in speciation. The evolution of body size and hypsodonty was not rapidly acquired in regions of the phylogeny with faster diversification, suggesting a broad-scale decoupling of ecomorphological and taxonomic diversification. Our phylogenetic modeling approach reveals that major phenotypic trends were not caused by phyletic progression, derived from sustained and ubiquitous directional selection, but more likely were the outcome of differential lineage-level survival and multiplication (species sorting).

NEW REMAINS OF NEOTROPICAL BUNODONT LITOPTERNS FROM THE MIDDLE MIOCENE, LA VENTA FAUNA: PALAEOBIOLOGY AND SYSTEMATICS

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Keywords: *Litopterna*, *South America*, *Neotropics*, *Mammalia*, *Morphological phylogenetics*

Litopterna is one of the most diverse and long-lived clades of the South American Native Ungulates (SANUs). *Megadolodus* and *Neodolodus* are bunodont litoptern genera recorded in the middle Miocene tropical fauna of La Venta (Colombia). Both taxa were initially identified as a didolodontid 'condylarths', but later transferred to Proterotheriidae, within Litopterna. Previous studies proposed their inclusion within Proterotheriidae, but possible affinities with early litopterns and didolodontids have not been properly tested in phylogenetic analyses. We report new material of *Megadolodus* and *Neodolodus* and reassess their phylogenetic relationships with Litopterna and Didolodontidae. In our phylogenetic analyses, we tested two alternative approaches of character construction for serial characters on the dentition. The reductive coding approach scores characters separately assuming the observed morphological variations are independent, whereas the composite coding approach favours the construction of a single character when the observed variation is hypothesized to be non-independent. Based on the new fossil material, our analyses with either one or the other coding approach support a close relationship between *Megadolodus* and *Neodolodus*, within Litopterna, and not a close relationship with Didolodontidae. At a less inclusive level, the relationships of Megadolodinae within Litopterna and its inclusion within Proterotheriidae vary depending on the coding approach used. However, all our analyses unambiguously support the monophyly of Megadolodinae as a clade of bunodont Neotropical litopterns. While the discovery of these new remains enlightens part of the litoptern phylogeny, the sensitivity of our analyses to coding approaches highlights the importance of critical evaluation of character construction in morphological phylogenetics.

NEW VERTEBRATE REMAINS FROM THE JURASSIC-CRETACEOUS TRANSITION OF THE EASTERN CAMEROS BASIN (SPAIN)

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Keywords: *Matute Alloformation, Crocodylomorpha, Pterosauria, Testudines, Osteichthyes*

The eastern Cameros basin is well known by the high number of dinosaur tracksites, although sites with osteological remains are scarce. One of the units that has yielded fossil bones is the Matute Alloformation, from where the freshwater aquatic turtle *Pleurosternon moncayensis* and the semionotiform actinopterygian *Camerichthys lunae* have been described. This geological unit is included within the upper part of the Tera Group and was deposited in shallow carbonate lakes. The most probable age of the Matute Alloformation is late Tithonian-earliest Berriasian. A new paleontological site, named Ribota, has been found close to the locality of Ágreda (Soria province, north-central Spain) in the lower part of this unit. The Ribota site is included in a carbonate-dominated interval outcropping over a large area of almost 10 hectares. There, three main areas with 36 small but rich, fossiliferous concentrations of isolated bones have been identified. The excavation of these areas has allowed to recover more than 75 vertebrate fossils. These mainly include crocodylomorph remains, such as isolated teeth, skull fragments, vertebrae and osteoderms, of different sized individuals with possible goniopholidid affinity. Other findings, although less abundant, includes testudine plates and few isolated cranial and appendicular pterosaur bones. In addition, cranial fragments and several articulated partial specimens of indeterminate osteichthyans have been recovered. Further systematic studies of these fossils will shed new light on these lacustrine vertebrate fossil assemblages from the Jurassic/Cretaceous transition, a poorly known time period in the Iberian Peninsula and Europe.

DEFORMATION MECHANISM AND RETRODEFORMATION OF INDIAN RHYTIDOSTEID TEMNOSPONDYL RESULTS IN A NEW COMBINATION OF BRAZILIAN TAXON

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Keywords: *Deformation mechanism, Retrodeformation, Rhytidosteids, India, Brazil*

Two discrete lacrimal-bearing temnospondyl amphibians of the Family Rhytidosteidae, *Indobrachyops panchetensis* and *Sangaia lavinai*, were erected in India and Brazil, respectively. Identification, illustration and interpretation of *Indobrachyops panchetensis* established by earlier workers are found to be biased by taphonomic deformation. The holotype of the Indian taxon is highly fractured and strained. The fossil has been deformed heterogeneously by both brittle and ductile deformation. Tectonic deformation rarely deforms rocks homogeneously and when diagenetically replaced fossil material has greater mechanical strength than the matrix, the fossil is deformed inhomogeneously by both brittle and ductile deformation. Brittle deformation generates fractures within the fossils which in turn displaces their structure along the fracture planes and ductile/plastic deformation changes the shape of the fossil without breaking or fracturing it. This resulted in a complex deformation pattern and distorted the shape of *Indobrachyops panchetensis*. A retrodeformation study, based on the mechanism of deformation, has been used to correct the shape outline. Morphological features of both *Indobrachyops panchetensis* and *Sangaia lavinai* were then compared. Both taxa share several features viz. the presence of lacrimals, interpremaxillary foramen and septomaxilla, short-faced trapezoidal skull, the lateral position of orbits, frontal and nasal of equal length, otic embayment instead of an otic notch, reduced tabular horn composed of both tabular and squamosal, widely spaced occipital condyles which justify their assignation to a single genus. As *Indobrachyops* is the senior synonym, *Indobrachyops lavinai*

comb. nov., for the Brazilian taxon *Sangaia lavinai* is erected, based on a detailed phylogenetic study.

A NEW, HIGH-SPEED PROTOCOL TO RUN MUSCLE-DRIVEN BIOMECHANICAL SIMULATIONS THROUGH FINITE ELEMENT ANALYSES

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Keywords: *Finite element analysis, simulation protocol, biomechanics, muscle-induced, muscle loading algorithm.*

Finite element analysis (FEA) is a computational method used to predict the behaviour (stresses, strains, and deformation) of a structure under predefined loading conditions. It can be applied to biological structures such as bone to study defined biomechanical scenarios. However, as muscle is an extremely complex structure to model, biologists usually model muscle forces indirectly. In 2007, the Boneload MATLAB routine was developed to distribute muscle forces on a surface defined by the user. This routine needs to be coupled with a pre-existing FEA software (e.g., Strand7) to perform the analyses, and has been widely used ever since. Here, we demonstrate a new method to run muscle-driven finite element simulations on bone by distributing muscle forces on their insertion areas within a single computational environment. We test this protocol on three different biomechanical systems linked to feeding and locomotion. Our automated script meshes the 3D model, applies the constraints, and distributes muscle forces within a single simulation software: Metafor. Metafor can perform the entire protocol on high resolution volumetric meshes (millions of tetrahedra) rapidly, outpacing the processing time of other widely used software by up to 12 times, all-the-while producing similar and congruent results. Our new protocol thus opens up the possibility to routinely and rapidly simulate the behaviour of high-precision, muscle-driven FE models and investigate a wide range of biomechanical scenarios at unprecedented resolution.

A COMPUTER-AIDED PROTOCOL FOR THE VIRTUAL RECONSTRUCTION OF THEROPOD DINOSAUR SKULLS. *TYRANNOSAURUS REX* AS AN ICONIC CASE STUDY

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Keywords: *retrodeformation, Tyrannosaurus rex, 3D model, R, virtual paleontology*

Taphonomic processes impact the physical preservation of fossil remains and often involve their deformation. Recently developed R-based virtual reconstruction protocols 'Retrodeformation' and 'Target Deformation' aim to reduce taphonomic distortion. These protocols have been tested and applied to Cenozoic fossil mammals and fossil human digital remains. Retrodeformation removes asymmetric alteration by applying a set of corresponding bilateral landmarks on the model. Target Deformation uses target specimens of the same species (less distorted, even if incomplete) as a virtual reconstruction guide, ideally permitting the protocol to reconstruct the original morphology. The procedure of undistorting the specimen thus follows two steps: 1. Retrodeform by applying bilateral landmarks to the target specimen; 2. warp the second original specimen onto the retrodeformed target 3D model. Here, we present the preliminary result of the application of Retrodeformation and Target Deformation on two iconic *Tyrannosaurus rex* skulls, FMNH PR2081 (informally known as 'SUE') and RGM.792000 (informally known as 'Trix'). 'SUE' is based on the

published raw CT-scans, which include considerable matrix around and within the skull, whereas the “Trix” 3D model was obtained by surface scanning. Retrodeformation was run on Trix first, then Target Deformation methodology was applied on “SUE”, using the better-preserved and retrodeformed “Trix” as the target specimen. The results are extremely positive, despite the matrix surrounding the skull of “SUE”. The result provides a baseline for deeper applications of the method to more *T. rex* specimens and other dinosaur skulls.

NEUROANATOMY OF *GROSSIUS*, AN EARLY PREDATORY LOBE-FINNED FISH FROM THE DEVONIAN OF SPAIN

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Keywords: *Computed microtomography, neurocranium, Onychodontida, Paleozoic, phylogeny.*

Onychodonts (Osteichthyes, Sarcopterygii) were an extinct group of predatory marine fishes from the Devonian traditionally characterized by kinetic skulls, hypertrophied parasymphysial teeth inserted in whorls on the dentary symphysis, and a modified ethmosphenoid region of the neurocranium to accommodate the tusks. The holotype and only specimen of *Grossius aragonensis* from the Moyuela Formation (Eifelian, Middle Devonian) of Aragón province (Spain) represents one of the most completely-preserved onychodont skulls but, despite its three-dimensional preservation, a detailed study of its internal anatomy was impossible, until now. The application of computed microtomography techniques has enabled to gain access to previously unknown cranial anatomical information and to virtually reconstruct the morphology of the braincase and its internal cavities for the first time. The neurocranium of *Grossius* shows differences with those of other onychodonts, such as a more acute angle between the otic-occipital region and the anterior-posterior axis of the ethmosphenoid than in *Onychodus* and *Qingmenodus*. Comparisons with other osteichthyan neurocrania revealed that onychodonts share features markedly different from other sarcopterygians such as *Dipnorhynchus* (dipnoans) or *Diplocercides* (coelacanth), like deep, large and ventrally-directed nasal capsules forming a broad angle between them.

The study of the neuroanatomy of *Grossius* highlights unique features, as well as new synapomorphies of Onychodontida. These new anatomical data constitute a rich source of morphological information for such an enigmatic group of early osteichthyans and will have a

broad impact on the study of sarcopterygian interrelationships and character evolution in future phylogenetic analyses.

**E UNUM PLURIBUS – THE FIRST HIGH-DIVERSITY KOGAIONID
(MAMMALIA, MULTITUBERCULATA) ASSEMBLAGE FROM THE
UPPERMOST CRETACEOUS OF THE TRANSYLVANIAN AREA, ROMANIA**

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Keywords: *Maastrichtian, Kogaionidae, multituberculates, diversity*

The latest Cretaceous Transylvanian record of kogaionid multituberculates is continuously growing, with over 25 currently known localities, concentrated primarily in the Hațeg Basin. Most of these yielded a small number of kogaionid fossils, although some were more specimen-rich, including the type-locality of the small *Barbatodon oardaensis* with several dozens of isolated teeth. Also, most localities contain monospecific kogaionid assemblages, including the rich *oardaensis* type-locality, while only a handful are reported to contain remains of two different taxa.

Here, we report a remarkable kogaionid locality (Fântânele1 in the northwestern Hațeg Basin) that is both specimen-rich and taxonomically diverse. It was discovered about 25 years ago, when isolated teeth from here had been tentatively referred to the Paleocene kogaionid *Hainina*. During the past two decades, over 50 isolated teeth have been recovered from this locality. Their survey suggests that at least three different taxa are represented in the local assemblage. Small-sized kogaionids dominate, including the probably first definitive, apomorphy-based report of *Barbatodon oardanesis* outside its type-locality. These are accompanied by less common medium- and large-bodied taxa, some of which are possibly related to the recently erected *Kogaionon radulescui*, while others are reminiscent of *Barbatodon transylvanicus* or *Litovoi tholocephalos*, all taxa known from other parts of the basin. Despite being taphonomically and lithofacially similar to the monotaxic *oardaensis* type-locality, the politaxic Fântânele1 locality documents in premiere the existence of diversified sympatric kogaionid assemblages in Transylvania.

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RANGE SIZE AND EXTINCTION RISK OF CUBAN MAMMALS: A CONSERVATION PALEOBIOLOGY PERSPECTIVE

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Keywords: *island, extinction risk, range size, Cuba, Quaternary*

Predicting why and when a species will become extinct is a crucial, yet challenging task in conservation research. Geohistorical data can provide essential information on how ecosystems reacted to disturbances, such as climate change and anthropogenic impacts, and have proven especially useful in understanding extinction risks.

Here, we used a newly assembled dataset of late Quaternary fossil occurrences on Cuba (1,522) and a new method of range size reconstruction based on co-occurrence analysis to analyze the relationship between extinction risk and geographic range size for mammals across four orders. Furthermore, we investigated changes in range size of extant and extinct species through the late Quaternary.

We found that the probability of being threatened or extinct was negatively and significantly related to range size for Cuban mammals. Moreover, we detected a significant decrease in range size since the Late Pleistocene across all species in our dataset. Finally, we recorded significant differences in range size shifts between taxonomic orders and between extant and extinct species. In particular, while range contractions were significantly associated with the extinction of mammals on Cuba, extant species experienced range expansions. We also discussed patterns of changes in range size in response to human arrival and climatic changes at the end of the Last Glacial Maximum.

Our results offer an insight into range size shifts of Cuban mammals through the late Quaternary, and highlight the importance of historical range contractions as predictors of extinction risk.

BRINGING THE DEVIL BACK HOME

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Keywords: *Conservation Paleobiology, Tasmania, Australia, SDM*

Tasmanian devil (*Sarcophilus harrisi*) is a marsupial carnivore widespread in Tasmania and contiguous islands. The current devil's population is listed as endangered because of an infective tumor disease that is dragging the species to extinction. The fossil record revealed the devil lived in continental Australia until about 3000 years ago. The rising of Rewilding is bringing new hopes on the future of the devil and healthy individuals have been already translocated to continental Australia to keep the population alive. Species distribution models have been used by conservation biologists and managers to detect areas of priority importance for conservation the introduction of the devil on the continent, but they only made use of current occurrences in Tasmania, thus providing a poor estimation of this species' environmental niche. Fossil occurrences of the species on the continental Australia, combined with bioclimatic variables of the past may, provide a more accurate depiction of the environmental needs of the species, thus helping in detecting better suitable territories for the species' translocation.

In this research, we show the results of integrating present and fossil species occurrences for modeling a more accurate devil's bioclimatic niche by using Machine Learning Algorithm. This niche estimation can be used to detect the suitable territories for the species in both Tasmania and continental Australia and to predict the available space under future scenarios of climatic change. This research revealed the importance of integrating paleontological information to have a better depiction of the fate of living species in a changing world.

TIME-SCALING OF CROCODYLIAN EVOLUTION AND THE CONTRIBUTION OF TOTAL EVIDENCE TIP-DATING ANALYSIS

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Keywords: *Crocodylia, tip-dating, time-scaling, divergence time, macroevolution*

A manageable number of living species and rich fossil record make Crocodylia, the crown group of Crocodyliformes, an excellent model clade for divergence dating analyses. Most time-scaling approaches of crocodylian evolutionary trees rely on often poorly established fossil calibrations in molecular divergence studies as well as on the *a posteriori* distribution of time among nodes and internal branches based on stratigraphic range of fossils and interspecific relationships. Tip-dating analyses, on the other hand, have the advantage of simultaneously generating a time-scaled phylogeny using both phenotypic and molecular rates and stratigraphic ages of fossils. In Crocodylia, only a single total evidence tip-dating analysis have been performed so far, contributing to the reinterpretation of character evolution and to well-supported divergence age estimates. Here we present an additional tip-dating study employing a different taxon sampling and focusing on the origination time of Crocodylia. Our results were overall consistent with the previous tip-dating analysis as well as with some published molecular clock estimates explicitly following best practices for fossil node calibrations. Inconsistency with estimates from published *a posteriori* methods is apparent on the other hand, as well as sensitivity of tip-dating to sampling, particularly autapomorphies. Finally, our analyses demonstrate the critical importance of integration of DNA and morphological data for estimating clade ages when morphology-based relationships among living taxa are robustly contradicted by genomic data.

PHYLOGENETIC SIGNAL OF CRANIAL CHARACTERS IN CLADISTIC ANALYSIS OF DIPLODOCOID SAUROPOD DINOSAURS

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Keywords: *Sauropoda, Diplodocoidea, cladistics, cranial, ontogeny*

Diplodocoidea is a highly diverse clade of sauropodomorph dinosaurs, which has been reassessed for its systematics in great detail in the past decade. Recent descriptions of new taxa (e.g. *Galeamopus*) and the reestablishment of *Brontosaurus* as a valid genus are just two outcomes of analyses with large datasets at both specimen- and species-level. However, several taxa included in these analyses are represented by small-sized individuals, which had raised doubts about the validity of phylogenetic analyses. Here, we test the impact of ontogeny onto two versions of a matrix with focus on flagellicaudatan Diplodocoidea with both presence and absence of postcranial characters. The matrix includes 86 operational taxonomic units, 38 of which preserve cranial remains at varying ontogenetic stages, and was analyzed with TNT. Using the cranial-only dataset, the traditionally recognized partition into Apatosaurinae and Diplodocinae was not recovered, and small-sized individuals appear to cluster at the base of a grade of diplodocid specimens leading towards a monophyletic Dicraeosauridae. Using the complete dataset, large skulls usually identified as diplodocines group with the large type specimens of *Apatosaurus ajax* and *A. louisae*, whereas smaller skulls group with the smaller type specimens of *Galeamopus pabsti*, *G. hayi*, and *Kaatedocus siberi*. Hence, body size, and thus possibly ontogeny, seems to impact tree structure, with skull-only specimens being particularly prone of being attracted to similarly-sized specimens.

It is therefore crucial to identify ontogenetically variable characters in the skull, and avoid scoring them in juvenile specimens to reduce directed noise in the phylogenetic analysis.

THE HYOID ARCH AND FEEDING IN TWO FISH-SHAPED MARINE TETRAPODS

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Keywords: *ichthyosaur, odontocete, hyoid, feeding*

The hyoid apparatus is essential for underwater feeding in marine tetrapods, but the extent of convergent adaptations is not well known. This study compares ossified hyoid elements in ophthalmosaurid ichthyosaurs and odontocetes, two groups with an overall similar body shape often interpreted to indicate a similar ecology, asking whether they also share a similar feeding mode.

Three sources of data were used: size, morphology and internal bone microstructure. Size and morphology data was collected from all ophthalmosaurid specimens (Middle Jurassic - middle Cretaceous) where at least one hyoid is preserved (n= 13). Inner bone microstructure was mapped via CT scanning of four ophthalmosaurid hyoid elements from the Late Jurassic Slottsmøya Member at Spitsbergen and two odontocete specimens (*Lagenorhynchus albirostris* and *Hyperoodon ampullatus*). By comparing the size data from ophthalmosaurids to earlier ichthyosaurs (Early Triassic – Middle Jurassic), we show that the relative size and shape of the hyoids did not change. With regard to the inner microstructure of the hyoid elements, the odontocetes have an overall less compact structure, whereas the ophthalmosaurids possess cancellous inner cones in an outer, more compact sheath. These are likely mechanical adaptations to feeding mode. Together with the consistently slender hyoid element, this indicates that ichthyosaurs never evolved the same type of suction feeding as extant odontocete whales.

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AEOLOSAURINE TRAITS IN VERTEBRAL CAUDAL SERIES FROM BELLEVUE LOCALITY (FRANCE): MORPHOFUNCTIONAL HOMOPLASY OR EVIDENCE FOR SOUTH AMERICAN TITANOSAURS IN THE LATE CRETACEOUS OF EUROPE?

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Keywords: *Titanosauria, Aeolosaurini, Late Cretaceous, France, Caudal Vertebrae*

Systematics and palaeobiogeography have always been controversial topics when dealing with Late Cretaceous European titanosaurs. Thanks to thorough works carried out in the last decades, the taxonomic diversity of this group of sauropods has significantly increased, but we are still far from perceiving the real image. The early Maastrichtian Bellevue site (Aude, France) is well-known for its dinosaur fauna, especially the titanosaur taxa, with *Ampelosaurus atacis* as the only species described to date. Among the sauropod material, interesting features were identified in a sequence of anterior caudal vertebrae associated with an incomplete sacrum: the caudal centra present an anterior margin tilted anteriorly, the neural arches are positioned on the anterior margin of the centrum, and the prezygapophyses are notably elongated. Besides these characters, other isolated anterior-middle caudal vertebrae show a neural spine, in which the distal tip is tilted anteriorly. These features are commonly recognized as synapomorphies of the South American clade Aeolosaurini, and some of them were reported in a caudal series from Lo Hueco site (Spain). With the current data at hand, two main hypotheses emerge: 1) aeolosaurines were present in Europe during the early Maastrichtian, or 2) the acquisition of such particular caudal features would reflect some kind of morphofunctional homoplasy between distant-related titanosaur taxa. The ongoing

study will shed light on the question as well as on a better comprehension of the complex evolutionary history of this clade of sauropods.

SMALL BRAINS PREDISPOSED LATE QUATERNARY MAMMALS TO EXTINCTION

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Keywords: *brain size, megafauna, Quaternary, extinction*

During the Late Quaternary, many of the world's largest terrestrial mammals went extinct. These extinctions are often attributed to either human hunting, climate change, or both. However, many large mammals similar in size to those that went extinct are still alive today, implying that body size was not the only predictor of extinction risk. We hypothesized that extant species have significantly larger brains than those that went extinct during the Late Quaternary which allowed them to cope with the changing environment and/or novel predators (humans). We created a dataset that included brain sizes of 291 extant mammals and 50 that went extinct during the Late Quaternary. We performed logistic and mixed effect models, controlling for phylogeny and body mass to test if extant mammals have larger brains than extinct ones and if this was correlated with extinction status. We found that extant species have brains on average 53% larger than those that went extinct, and 83% larger when a single regression line is fitted. We also found that brain size was a significant predictor of extinction status. We propose that small-brained species were predisposed to extinction during the Late Quaternary whereas their large-brained extant counterparts were better suited to cope with changing environments and human hunters. We propose that possessing a large brain was a crucial, yet so far, neglected characteristic of surviving megafauna species.

TETRAPOD ICHNOASSOCIATIONS, BIOSTRATIGRAPHY AND PALEOENVIRONMENTAL RECONSTRUCTION OF THE PERMIAN TERRESTRIAL SUCCESSION OF CASTELLAR DE N'HUG (CATALAN PYRENEES, SOUTHERN EUROPE)

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Keywords: *Tetrapod Ichnology, Volcanosedimentary succession, Dromopus biochron, Brontopus sub-biochron, Western Tethys*

The early–middle Permian in the Western peri-Tethys was marked by an aridification process, with environments changing from wet- to dry-dominant conditions. The evolution of tetrapod continental faunas in Southern Europe is unclear due to the remains scarcity, especially bones and teeth. However, tetrapod ichnites are better known from European Permian deposits, thus being a powerful tool to reconstruct ecosystems. The discovery of three new ichnosites from the lower and middle Permian volcanosedimentary terrestrial successions from the Catalan Pyrenees (NE Spain), together with stratigraphic and facies analyses, allows a better understanding of these ecosystems. Tetrapod ichnofossils were discovered in red-beds from the Lower Red Unit and Upper Red Unit, corresponding to alluvial deposits and building an almost 1000 m thick continuous succession, the longest of the Pyrenean Basin. The stratigraphic succession also includes volcanoclastic deposits, sometimes reworked by fluvial processes. The volcanoclastic deposits notably diminish towards the upper part of the succession, which is dominated by floodplain

deposits with desiccation cracks. The identified tetrapod ichnofossils correspond to the ichnogenera *Batrachichnus*, *Dromopus*, *Varanopus*, *Hyloidichnus*, *Brontopus*, *Pachypes* and *Charachichnos*. 3D photogrammetric models of selected footprints and trackways were generated, complementing morphological descriptions and biomechanical analyses. The composition of the ichnoassociations changes along the succession, as well as the accompanying invertebrate fauna, showing features of the *Dromopus* biochron in the volcanoclastic and fluvial deposits and features of the *Brontopus* sub-biochron in the floodplain deposits. The biostratigraphic and magnetostratigraphic results of this study suggest a late Cisuralian to early–middle Guadalupian age.

SYNCHROTRON SCANNING REVEALS THE UNIQUE ANATOMY OF A LATEST CRETACEOUS PADDLEFISH FROM TANIS (ND, USA)

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Keywords: *Acipenseriformes, paddlefish, Tanis, KPg, anatomy*

The Cretaceous-Palaeogene event deposit Tanis (North Dakota) yields fossils from yet undescribed Acipenseriformes. Propagation Phase-Contrast Micro-Computed Tomography was applied to study anatomical features preserved in a partial paddlefish from this assemblage. Comparison with the two extant paddlefishes *Polyodon* and *Psephurus*, and with fossil forms including the Maastrichtian *Paleopsephurus* shows that The Tanis paddlefish represents a new taxon.

The elongate cranial roof appears intermediate between the more robust *Polyodon* skull and the more slender *Psephurus* skull. It is distinctly curved anteroposteriorly, as is the parasphenoid, which trends parallel with the cranial roof up to its anterior margin. This differs from the condition in the extant forms, especially *Polyodon*, in which the parasphenoid is straight and converges on the skull roof anteriorly. The postorbital foramen features a unique interfenestral strut. The posttemporal widens posteriorly, whereas it narrows in both *Polyodon* and *Psephurus*. The parietal is significantly longer and intermediate in width relative to both extant genera. Its centre of ossification is positioned much further forward than in *Polyodon*. The gill rakers appear comparatively short and unlike those of the modern paddlefishes.

The cause of death was likely burial in the massive seiche wave and/or suffocation with impact spherules. The spherules are almost exclusively encountered between the second and the third gill arch, possibly indicating the main respiratory water flow path; since the gill arches are obscured by a gill cover that cannot be removed without damaging the specimen, such details would remain invisible without the use of synchrotron microtomography.

A STYRACOSTERNAN SACRUM FROM A NEW FOSSIL LOCALITY FROM THE ARCILLAS DE MORELLA FORMATION IN MORELLA (SPAIN)

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Keywords: *Dinosauria, Styracosterna, Early Cretaceous, Iberian Peninsula, Maestrazgo Basin*

An isolated styracosternan ornithopod sacrum from the new Barremian fossil locality of Fábrica Giner (Morella, Castellón, Spain) is described. This partial sacrum comprises six fused sacral centra including the badly preserved posterior end of a most anterior sacral vertebra. Additionally, some portions of the sacral ribs of the posteriormost sacral centra are preserved. The posteriormost sacral centrum is transversely broad and has a wider than deeper concave posterior articular facet. Its ventral surface is slightly eroded but seems to be flat. The base of the sacral ribs is positioned at the posterior half of the centrum. The two preceding sacral vertebrae are transversely broad and have flat ventral surfaces. In these vertebrae the sacral ribs are intervertebrally positioned. The most anteriorly positioned sacral centrum is spool-shaped and bears a well-defined ventral keel whereas the succeeding sacral centrum is not transversely constricted and present a modest ventral keel anteriorly placed.

To date, the styracosternan sacral material from the Arcillas de Morella Formation have been ascribed to *Iguanodon bernissartensis* and to *Morelladon beltrani*. The analyzed partial sacrum clearly differs from those of the *I. bernissartensis* by the absence of a ventral sulcus in the most posterior sacral vertebrae. Comparing it with those attributed to *Morelladon*, both differences (e.g. un-keeled penultimate sacral vertebrae, third last sacral centrum transversely broad) and similarities can be observed. Although some of these differences can be part of the intraspecific variability of *Morelladon*, it has been preferred to provisionally assign this new sacrum to an undetermined styracosternan ornithopod.

A NEW GNATHOSAURINE (ARCHAEOPTERODACTYLOIDEA, PTEROSAURIA) FROM THE LATE JURASSIC OF PORTUGAL

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Keywords: *Pterodactyloidea, Lourinhã Formation*

The known global distribution and diversity of pterosaurs demonstrates their success as a group, and yet their relatively sparse fossil record and often incomplete preservation (outside of Lagerstätten environments) pose a challenge for further understanding their palaeobiology, when compared with other vertebrates. Such is the case for the Lourinhã Formation of Portugal, which is largely recognized for its rich and taxonomically diverse fossil representation of dinosaurs, fishes, amphibians, marine reptiles, crocodylians, and eggs. Despite this abundance, up to now, pterosaur material recovered from this deposit has been restricted to scant and often fragmentary isolated bones and teeth, hindering any confident taxonomic assignments. Recently, a remarkably-sized dentated rostrum fragment and associated partial cervical vertebrae (ML2554) of a pterosaur were discovered from the Late Jurassic (Kimmeridgian-Tithonian) of Praia do Caniçal, Lourinhã. The specimen exhibits features such as a spatulated anterior expansion of the rostrum, a robust comb-like dentition, and pronounced rims of the tooth alveoli, indicating gnathosaurine affinities. The presence of this taxon adds yet another ecological niche element to the fluvio-deltaic lagoonal environment that has been suggested to be representative of Lourinhã Formation in the Late Jurassic, and contributes to the diversity and distribution of gnathosaurines worldwide.

Furthermore, based on its unique tooth and dentary morphology, ML2554 clearly represents a new taxon, the first named pterosaur species from Portugal.

FIRST APPROACH TO LIFE HISTORY OF THE ISLANDER *PROLAGUS SARDUS* (LAGOMORPHA) BY STUDYING FEMORAL BONE HISTOLOGY

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Keywords: *gigantism, insular regimes, paleohistology, Pleistocene, small mammals.*

Islands hold an outstanding potential for studying evolution due to their geographical isolation and singular ecological pressures (resource limitation, low extrinsic mortality and high intraspecific competition). In small mammals, the evolution in insular regimes entails later maturation and larger body sizes. We decided to evaluate the life history strategy of the islander *Prolagus sardus* (Ochotonidae) assessing the femoral bone histology of an ontogenetic series (N = 11), recovered from the Late Pleistocene Dragonara Cave faunal assemblage (22.39-21.94 ka, Sardinia). Bones were categorized into 3 ontogenetic groups (juvenile, young adult, and adult) according to the epiphyseal plates fusion, and bone thin sections were examined under polarized microscopy. The osteohistological analysis revealed rapid growth rates in juveniles, characterized by fibrolamellar bone, whereas a decrease in growth rate (parallel fibered and lamellar bone) with secondary remodeling (Harvesian systems) was noted in adults. Young individuals showed smaller medullar area, because of its smaller size ($p < 0.05$). LAGs were identified in the outer cortex of juvenile to adult specimens. In young adults (with at least one unfused epiphysis) a range of 1-3 LAGs was determined, pointing to a delayed achievement of skeletal maturity. In the larger specimen 8 LAGs were identified, hinting an

approximated longevity of 8 years. Considering the size of the Dragonara population (700-750 g), the observed lifespan is longer than the expected, suggesting a shift towards the slow end of the life history continuum. This study contributes to understanding the eco-evolutionary responses of small mammals to insular regimes.

SMALL-MAMMAL ASSEMBLAGES FROM THE LATE PLEISTOCENE IN NORTHERN IBERIA (SOUTHWESTERN EURASIA): ENVIRONMENTAL CLUES FOR ASCERTAINING NEANDERTHALS' ECOLOGY

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Keywords: *rodents, paleoclimate, paleoecology, Middle-to-Upper Paleolithic transition*

Small mammals' record preserved in archeo-paleontological assemblages allow reliable regional paleoenvironmental characterization in the terrestrial domain. During the Pleistocene these remains are useful to reconstruct the climate experienced by past human populations. Within the SUBSILIENCE project (ERC CoG No. 818299), a compilation of 80 levels containing high-quality small mammals' data coming from 17 different sites from northern Iberia during the Late Pleistocene, focusing on the transition from the Middle to Upper Paleolithic, has been achieved. In these assemblages, the most common species have Euro-Siberian requirements (*Microtus arvalis-agrestis*, *Talpa europaea*, *Arvicola terrestris*), whereas Mediterranean species (*M. T. duodecimcostatus*, *M. cabreræ*) are scarcely present and woodland dwellers (*Apodemus sylvaticus-flavicollis*) abundance oscillate. Based on the habitat weighting method, humid meadows predominate, in combination with open forest, grassland and punctual dry shrubland; but a noticeable shift through time is not observed. Considering the species composition of each sedimentological unit, the Bioclimatic Model method allows the paleoclimatic estimation in terms of temperatures and precipitations. The results suggested colder and drier conditions than nowadays, with a decrease of rainfall and temperatures from Middle-to-Upper Paleolithic, after the Heinrich Event 5 and coincident with late Neanderthal settlements, which are followed by a populational hiatus. These considerations must be taken cautiously considering that sometimes assemblages have scarce individuals, were recovered through unappropriated techniques, present little taphonomic information and certain taxonomic groups could hidden environmental information. Nevertheless, conclusions are consistent with stadial-interstadial oscillations and with other regional climatic proxies, such as pollen, stable isotopes on large mammals, and glacial records.

NEW SPECIMEN OF DRYOMORPHAN (ORNITHISCHIA, IGUANODONTIA) REMAINS FROM THE UPPER JURASSIC OF PORTUGAL

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Keywords: *Ornithopoda, systematics, Jurassic, Europe*

Upper Jurassic Lourinhã Fm. has yielded a diverse vertebrate fauna dated to the Kimmeridgian/Tithonian interval. Extremely common are saurischian dinosaurs, although recent work made by the working team highlighted an over-looked diversity and abundance of ornithischian and ornithopod dinosaurs. Fieldwork activities of Museu da Lourinhã have unearthed ML 2700, a partially articulated left hind limb and associated carpal elements. The specimen is fractured and distorted, however several elements are identifiable and provide a useful taxonomic signal. The hind limb of ML 2700 comprises a partial tibia, an almost complete fibula, a complete metatarsal (MT)-I, a complete MT-II, partial MT-III and several phalanges, which articulate with one another, including three pedal claws. The carpal elements include an isolated partial metacarpal, and an ungual phalanx. The diagnostic characters of ML 2700, include: a rounded and well distinguishable cnemial crest that projects cranio-laterally; fibular condyle that projects laterally and forms a 90° structure together with the caudal condyle; symmetric margins of the proximal end of fibula and enlarged distal one; reduced splint-like MT-I; MT-II overlaps MT-III dorsally; extremely

shortened pedal phalanx III-3 and claw-like pedal claws with well-developed lateral and medial flanges. Furthermore, the manual ungual is claw-like and strongly arched. This combination of characters indicates a basal iguanodontian affinity for ML 2700, and it is not consistent with two taxa identified in Lourinhã Fm, *Eousdryosaurus nanohallucis* and *Draconyx loureiroi*. Phylogenetic analyses, employing Maximum Parsimony and Bayesian Inference, confirmed these results, recovering ML 2700 at the base of Dryomorpha.

A GIANT FRESHWATER TURTLE FROM THE PLEISTOCENE OF BRAZILIAN AMAZON

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Keywords: *Podocnemididae, giant reptiles, Quaternary, Amazon, body size*

Large reptiles are common among the Neogene fauna of the Amazon region but disappear after the Miocene. The giant podocnemidids, including the largest freshwater turtle, *Stupendemys geographicus*, are all closely related to the extant *Peltocephalus dumerilianus*, also from the Amazon. Here, we present an isolated 25 cm long dentary from the Rio Madeira Formation, northwestern Brazil, well beyond the 16 cm of the largest known dentary of *Stupendemys*. The morphology of the symphysis and extension of the lingual ridge suggest a closer affinity to *Peltocephalus* among extant taxa. We took a set of linear measurements from 42 specimens sampling all the eight extant podocnemidid species, *S. geographicus* and performed a Principal Component Analysis (PCA) to further assess its affinities. The PCA results confirm its similarity to *Peltocephalus* and *S. geographicus*, but also support its distinctiveness. Carapace maximum length estimates (as a proxy for body size) show great uncertainty due to the lack of other giant specimens with associated lower jaw and carapace, ranging from 2114 to 697 mm, with a median at 1406 mm ($p = 0.0162$, $R^2 = 0.8893$). Radiocarbon (^{14}C) dating using three samples with preserved bioapatite provided an age between $14,290 \pm 45$ and $9,060 \pm 50$ cal BP, potentially

placing this gigantic turtle within the set of megafauna extinctions coincident with the human occupation of the Amazon. The paleontological and stratigraphical context of the region is still poorly understood, and we hope our results provide an exciting trigger to expand research about the Quaternary of the Amazon.

EARLY PLEISTOCENE HIPPOS FROM BARRANC DE LA BOELLA (TARRAGONA, SPAIN): PHENOTYPIC AFFINITIES AND PALAEOECOLOGY

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Keywords: *Quaternary, Europe, Hippopotamus antiquus, biogeography, geometric morphometrics*

The study of European hippopotamus (recorded throughout the Quaternary from the Early to the Late Pleistocene) presents several unresolved questions and a lack of consensus among specialists. The number of identified taxa, their geographical and chronological distribution, and the palaeobiological changes in their populations are still hotly debated. This work presents comparative analyses using descriptive anatomy, linear biometry and geometric morphometrics of hippo specimens unearthed in the archaeo-palaeontological outcrops of Barranc de la Boella (Francolí River basin, Spain), in the context of the record of the genus *Hippopotamus* in Europe and its putative migrations from Africa. The deposits from these localities attest the presence of hominids and hippos during the Early-Middle Pleistocene Transition (EMPT), a period of great climatic shifts. The evaluation of the studied specimens supports the consideration of *Hippopotamus antiquus* as the only taxon recorded in Europe from the Early Pleistocene (ca. 2.1

Ma) to the mid-Middle Pleistocene (ca. 0.4 Ma), when the current species of common hippo (*Hippopotamus amphibius*) dispersed from Africa. Even so, a more detailed understanding of the large intraspecific variability reported in the genus *Hippopotamus* is needed in order to characterise the variation in its populations across different chronologies, geographic locations and environmental conditions. The detailed review of the distribution of *H. antiquus* at the EMPT raises the possibility that the Iberian and Italic peninsulas acted as climatic refugia for its populations since ca. 0.94 Ma when a substantial increase in global ice volume accompanied the increasing severity and duration of cold stages.

FIRST APPROACH TO THE PALAEOENVIRONMENTAL AND BIOCHRONOLOGICAL CONTEXT OF THE NEW QUATERNARY SITE OF CUEVA DE LLAMAZARES (LEÓN, SPAIN) THROUGH THE STUDY OF MICROVERTEBRATES

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Keywords: *Micromammals, Herpetofauna, Palaeoclimate, Cantabrian Mountains, Quaternary*

Cueva de Llamazares is a karstic cavity located at 1400 m above sea level, in the southern part of the Cantabrian Mountains (León, Spain). Initial geochemical evidence and the estimated chronological range for the formation of the cavity and the sedimentary deposits suggest a good record of the changes in the climate and landscape. Among the study materials of the cave, a series of sedimentary levels containing skeletal elements of different vertebrates stand out. In this work, we focus on the study of the 264 microvertebrate specimens collected during the 2020 field campaigns. The work carried out has generated a digital catalogue; taxa from orders Rodentia, Eulipotyphla, Chiroptera, Anura and Squamata were identified. The microvertebrate association has been characterised by calculating the minimum number of individuals, considering the environmental range for different biological, physical and chemical parameters and reviewing the biochronology of each taxon. As a result, the presence of this association reveals climatic and environmental conditions similar to those present nowadays in the area of Cueva de Llamazares and that the chronological framework of the deposits is between the Upper Pleistocene and the Holocene. Although this work has limitations,

such as the lack of precise geophysical dating of the sedimentary deposits, it opens up a research path for new studies. The study of the faunal associations from Cueva de Llamazares and other caves in the north of León will help to gain a deeper understanding of the ecosystems, faunas and human occupations in the past of this territory.

PERISSODACTYLA DIVERSITY IN THE NEW EXCAVATIONS AT THE UPPER MIOCENE LOCALITY OF PIKERMI (ATTICA, GREECE)

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Keywords: *Pikermi, Perissodactyla, Equidae, Rhinocerotidae, Chalicotheriidae*

Pikermi is a renowned reference locality for the study of late Miocene vertebrates, its long history of excavation and research activity dating back 1835. Since 2008, a new series of recurring and stratigraphically controlled excavations has been conducted under the auspices of the National and Kapodistrian University of Athens and the municipality of Rafina-Pikermi (NKUA-SARG Project 70/3/12977), revealing several new sites numbered PV1 to PV4 (“PV”=“Pikermi Valley”).

Perissodactyls exhibit a notable degree of diversity and population density at the new sites. Equids are the most common representatives of the group and account for a large portion of the mammalian remains found. They are commonly attributed to two hipparionine species, the slender *Cremohipparion mediterraneum* and the more robust *Hippotherium brachypus*. The potential occurrence of additional hipparionine species has been frequently discussed, although based on limited and debatable evidence; the ongoing study combining both old and new material may offer valuable insights on this matter. Rhinocerotids, although less common, are rather diverse and represented by two tandem-horned species, *Dihoplus pikermiensis* and *Miodiceros neumayri*, as well as by the relatively scarce hornless species *Acerorhinus neleus*. Chalicotheriids are the rarest among the locality’s perissodactyls. At the new excavations, the typical Pikermian schizotheriine chalicothere *Ancylotherium pentelicum* is hitherto represented only by a few postcranial elements. Based on a handful of specimens, the rare occurrence of a chalicotheriine chalicothere (formerly referred to as *Chalicotherium goldfussi*) is currently known from old collections and the Pikermi-Chomateri site, but remains thus far absent from the new PV-sites.

A ROOM OF CIRO'S OWN - BUILDING A HYBRID DIGITAL PALEO SPACE

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Keywords: *Pietraroja, Scipionyx samniticus, Interaction design, immersive installation, virtual reality tour*

The developed project, using the potential of an immersive and interactive experience, has been envisaged for the paleontological site of Pietraroja, a unique paleontological site in the world that can significantly contribute to the education, and development of the surrounding area, and the promotion of the paleontological heritage.

This technology, which allows a reconstruction of the environmental context, is useful in creating an immersive environment by using integrated digital tools such as interactive devices, projection mapping, and web technology.

The integrated use of different digital tools and software allows transferring the knowledge content through an immediate, real-time, and non-conventional perception to the user. To create the CIRO digital model it is necessary to obtain complete information on the anatomical structure of *Scipionyx samniticus* and, through an accurate 3D modeling, generate the digital model of the dinosaur. The same approach it's used to recreate the landscape and the vegetation species. The complete reconstruction process is constituted by steps that allow, starting from the 3d modelling process, to create a web based virtual live environment, that it could be streamed in different amplitude and context: from a personal mobile device to an immersive multi projection system. The aim is to build an immersive digital space in which the visitor will perceive the original environment of the *Scipionyx samniticus* and will interact with the Ciro virtual avatar. Furthermore, the application, relying on web technology, it's accessible from all kind of device, each feature will be available according with the device capability.

HOW DOES A GIANT INSULAR LIZARD FEED? A 3D FINITE ELEMENT MODEL OF *GALLOTIA STEHLINI* AND ITS IMPLICATIONS FOR FOSSIL GIANT LIZARDS

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Keywords: *Computational Biomechanics, Gallotiinae, Lacertidae, Insularity*

The endemic giant insular lizard *Gallotia stehlini* (Lacertidae, Gallotiinae) lives in Gran Canaria (Canary Archipelago, Spain). Different extant and extinct *Gallotia* taxa are known from each Canary Island, with *Gallotia stehlini* the largest living taxon. Pleistocene fossil occurrences of this gigantic species are also known, being surpassed in size only by the extinct *Gallotia goliath*. To understand how the gigantic size of *G. stehlini* affects its functional cranial structures, here we present a high-resolution 3D Finite Element model of its skull. Different scenarios of symmetrical biting, bite position, and muscle actions have been tested in order to investigate the feeding behavior of this taxon. Our preliminary results suggest that the palate, and particularly the articulations of the epipterygoid with the pterygoid as well as the quadrate, plays a key role in cranial stress patterns, but possibly also on bite power and protection of the braincase. Our results shed light on the feeding ecology of this gigantic reptile, enabling a better understanding of the effects of increasing cranial bones size, muscle volume and insertion attachment area. Additional analyses will be required to assess the role of other structures such as the protractor musculature and cranial sutures. Overall, our analysis opens the door to future inferences on the cranial mechanics and the paleoecology of the extinct giant *Gallotia goliath*.

THE POSTERIOR BRAINCASE OF A SMALL TYRANNOSAURID

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Keywords: *Nanotyrannus*, *Palaeoneurology*, *Endocast*, *inner ear*, *Arcovenator*

In 1988, *Nanotyrannus lancensis* was described as a new tyrannosaurid taxon. However, the validity of this enigmatic species has been controversial since. Today, *Nanotyrannus lancensis* is generally considered to represent either a separate taxon or a juvenile *Tyrannosaurus rex*. Although numerous diagnostic apomorphies have been proposed to distinguish *Nanotyrannus* from *Tyrannosaurus*, many of these have been demonstrated to be ambiguous or susceptible to ontogenetic variability. As such, distinguishing true taxonomic diversity from ontogenetic, sexual, and intraspecific variability represents a notorious challenge in vertebrate palaeontology that is exemplified by the case of *Nanotyrannus*.

A partial posterior braincase representing putative *Nanotyrannus lancensis* (BHI-6430) was scanned at the European Synchrotron Radiation Facility (Grenoble, France) to reveal its internal osteology. Additionally, the distribution, shapes, and dimensions of osteological correlates of neural and sensory structures were visualised, including the endosseous labyrinths. This allowed us to non-destructively visualise the sutures within the braincase as well as create three-dimensional visualisations of the endocast and endosseous labyrinths. Additionally, the endosseous labyrinths of *Arcovenator escotae* were visualised for comparative reference. The referred methods and materials will allow for interpretation and differentiation between ontogenetic and functional conditions in the posterior braincase of *Nanotyrannus lancensis*. The states of the sutural openings have already indicated that BHI-6430 represents a juvenile. In

addition, the neural and sensory structures preserved in the specimen will aid in illuminating its ecomorphological affinity. Reflected on the diagnostic cranial anatomy of *Tyrannosaurus rex*, these insights will provide new information on the taxonomic identity and palaeobiology of *Nanotyrannus lancensis*.

THICK TAILS! NON-AVIAN DINOSAUR CAUDOFEMORAL MUSCLE ESTIMATION FROM CT-SCAN OF EXTANT TAXA

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Keywords: *muscle volume, dinosaur, caudal region, CT-scans, area of insertion.*

A precise estimation of extinct dinosaur musculature is a key to a better understanding of dinosaur biomechanics. However, most evidence of muscular tissue in dinosaurs is restricted to the scars left where its origins and insertions were in the bones. This constraint complicates the estimation of caudal muscle volume of extinct animals, resulting in wide error margins of biomechanical properties (e.g. centre of mass). The musculature in the caudal region is one of the most debated. The earliest reconstructions of dinosaur caudal musculature limited the lateral extension of the muscles to the lateral limits of caudal ribs. Resulting estimates were too conservative in volume, particularly *M. caudofemoralis longus* (CFL). Most recent research resorts to comparisons with extant groups, with muscle volume greater than the limits of bone contour. This presents a problem: with different criteria for the reconstruction of CFL, differences in volume estimation can be up to 50% between maximum and minimum estimates. With the aim of narrowing this interval, we segmented CT-scans of 42 specimens from 19 species of extant crocodiles and lepidosaurs. Once segmented, a 3D digital mesh of CFL and caudal vertebrae were generated. These 3D models were measured for volume (CFL) and area of origin (vertebrae and chevrons). Data collected was later analyzed with statistic software, showing a strong correlation between CFL volume and its area of insertion, with values of R^2 over 0.9. Using regression equations, we estimate CFL volume for several saurischian dinosaurs, comparing them with previous reconstructions.

BIOMECHANICAL AND GROWTH REMODELLING DIFFERENCES BETWEEN MODERN HUMANS AND NEANDERTHALS

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Keywords: *Paleoanthropology, Finite element analysis, Virtual anthropology, Modern human, Neanderthal*

Modern human and Neanderthal faces present a clear divergence in their post-natal ontogenetic trajectories. Differences in patterns of bone growth remodelling have also been found in these two species with modern humans presenting bone resorption on the anterior subnasal surface, while Neanderthals present extensive bone deposition. These differences have been hypothesized to be related to genetic signals that differ between these species, or to differences in the forces arising from differences in food processing during post-natal development. Here we test the mechanical hypothesis.

Using geometric morphometrics and finite element analysis, we assessed the association between masticatory loadings, facial strains and facial remodelling during postnatal growth and development in modern humans and Neanderthals.

During biting simulations, strain contour plots show that, in both species, the highest strains are localised on the anterior maxilla, orbital, and anterior subnasal surfaces and decrease between infancy and adulthood. However, strains show differences in distribution and magnitude among age stages and species. Further FEA shows that biting performance varies with age and differs between species.

These findings confirm that differences exist in loading history throughout post-natal ontogeny between Neanderthals and modern humans and these partially reflect differences in remodelling maps. Therefore, we cannot exclude the possibility that differences in the ontogeny of masticatory

system performance and load resistance underlie the differences in the distribution of craniofacial growth remodeling features. Further work is needed to more directly compare cumulative strains arising from diverse masticatory system loads in both taxa and facial growth remodeling maps.

BIAS IN EXTINCT LION RECORD AFFECTS OUR UNDERSTANDING OF THE SPECIES

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Keywords: *Panthera spelaea*, *Panthera atrox*, *fossil record*, *distribution*, *paleoecology*

Eurasian and American lions faced extinction at the end of the late Pleistocene. Both disappeared right before the Younger Dryas (12.9 ka BP), concomitant with the extinction of other megafauna in the Northern Hemisphere. Because these two species shared morphologies and adaptations, doubts about their taxonomy persisted until genetic analyses demonstrated that indeed, these species were distinct.

Currently, most of the defining characteristics of the two species are accepted by the scientific community, but some of them were built on assumptions that are no longer valid. For example, in comparison to its closest relative in Eurasia, the American lion record is generally poor. Many specimens lack precise locality data or even a representation of the specimen, and only a few have been directly dated. Therefore, any attempt at comparison should be taken with caution. In the present contribution, analogies and differences observed in the datasets of these two extinct species were described. Data were analyzed with a particular focus on how the biased record is affecting our understanding of their distribution over North America and Eurasia, interaction with other species, and resilience to changing climatic conditions.

We noticed that the estimated distribution of Eurasian lion was less purely defined after the Last Glacial Maximum, where occurrences associated with any absolute ages are only one fifth of older periods. The American species has only four localities reporting any absolute dates and it is frequently reported as a single recovery, forcing a range estimation averaged through multiple local climatic conditions and preventing correlations with other species.

STUDY OF THE LATE MIOCENE RHINOCEROTIDAE FROM PIKERMI AND SAMOS (GREECE) AT THE COLLECTIONS OF THE NATURAL HISTORY MUSEUM OF VIENNA: PRELIMINARY RESULTS

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Keywords: *Rhinocerotidae*, *Late Miocene*, *Pikermi*, *Samos*, *Greece*

The celebrated Pikermi and Samos localities have been extensively excavated and studied since the 19th century, serving as reference faunas for the systematic, biostratigraphic and biogeographic assessment of Eurasian Late Miocene mammals. The Natural History Museum of Vienna hosts significant material from both localities. The Pikermi collection (acquired 1854-1863) comprises 82 rhinocerotid specimens, 89% identifiable at species level. The Samos collection (acquired in 1911) comprises 76 rhinocerotid specimens, 88% identifiable at species level. The majority of the material from both localities consists of postcranial elements (87% in Pikermi and 89% in Samos), clearly suggesting an origin from dedicated excavations and not selective purchases, which are biased towards well-preserved craniodental specimens. The most notable craniodental specimens include a relatively well-preserved cranium of *Dihoplus pikermiensis* from Pikermi; two fairly complete crania of *Chilotherium schlosseri*, a partial juvenile cranium of *Miodiceros neumayri*, and an exceptionally well-preserved juvenile maxilla of *Dihoplus pikermiensis* from Samos. The Pikermi collection comprises only the two tandem-horned species *Dihoplus pikermiensis* and *Miodiceros neumayri*; the rare hornless rhinocerotid *Acerorhinus neleus* is not represented. The Samos collection includes both aforementioned horned taxa and the hornless *Chilotherium schlosseri*. The marked differences observed in the relative distribution and abundance of both horned and hornless rhinocerotid taxa among the Turolian localities of Greece seem to have been influenced by environmentally controlled provincial differences. The relatively slenderer and lower-crowned *Dihoplus* and *Acerorhinus* seem to have preferred more closed and temperate niches, whereas the more robust and higher-crowned *Miodiceros* and *Chilotherium* have favored more open habitats.

CLIMATIC NICHES AND DISPERSAL OF MIOCENE HOMINIDS

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Keywords: *Niche Modelling, Miocene hominids, Dispersal, Macroecology, Paleoclimatic reconstruction*

Several scenarios for the dispersal of Miocene hominids from Africa to Eurasia still coexist. The reason why it remains impossible to decide between these scenarios, and why some fundamental questions about the biogeographic history of Miocene hominids are so difficult to address, lies in a fragmented fossil record and uncertain dating. In order to overcome these problems and to measure the potential effect of climate on the dispersal of Miocene hominids, we use ecological niche models (ENM) based on palaeoclimatic reconstructions of Early, Middle and Late Miocene. Using ENM, we demonstrate that the Eurasian climate during the Lower Miocene was not compatible with the climatic conditions required for the installation of hominids living in East Africa at the same time. Consequently, while the connection between Africa and Eurasia was active since the *Gomphoterium* Datum Event (PDE, ca. 19 myr), the presence of hominids in Eurasia appears unlikely during Early Miocene. In the Middle Miocene, the long-term cooling following the Middle Miocene Climatic Optimum profoundly modified the Earth's climate, notably in Eurasia. South Asia and Southeast Asia, as well as the Mediterranean coastline, became suitable for the presence of Late Miocene East African hominids. Finally, we provide a case of ecological niche displacement. The estimated climatic niches for European hominids in the Middle Miocene are

distinctly different from those of their Lower Miocene ancestors from East Africa. These arising taxa found in Europe did not simply 'track' their climatic niche, but adapted to the new climatic conditions of the European continent.

A REVIEW OF THE *URSUS ETRUSCUS* REMAINS FROM THE LATE VILLAGRANCHIAN OF EUROPE WITH EMPHASIS ON NEW FINDS

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Keywords: *Ursus etruscus*, Cave bear, Early Pleistocene, Quaternary.

Since the pioneering works of Björn Kurtén from the middle of XX century, the Eurasian Early Pleistocene species *Ursus etruscus* is considered the putative ancestor of both cave and brown bears. However, in the last two decades the remains of the late Early Pleistocene has been in a hotly phylogenetic and taxonomic debate and several authors included it alternatively in the brown or cave bear lineage.

Here we provide a complete synthesis of the latest published remains from *U. etruscus* from Taurida cave, the Orce sites, Dmanisi, Pietrafitta and Pirro Nord comparing it with the classical material of Saint Vallier, Olivola, Upper Valdarno and Kuruksai.

Our results support the distinction of two different morphotypes of *U. etruscus* throughout its long chronologically record, as stated by previous authors: an early forms from the Middle Villafranchian (e.g. Saint-Vallier or Kuruksay) and late forms from Olivola, Dmanisi, Taurida cave, Pietrafitta, Upper Valdarno or Venta Micena. Later on, at the end of the Early Pleistocene and roughly coeval with the climatic shifts associated with the 'Early-Middle Pleistocene Transition' the earliest large and stout specimens of speleoid bears (*Ursus deningeri*) were recorded in Europe at sites such as Le Vallonnet, Vallparadís Section or Untermassfeld as exemplified by their more derived characters an overall larger dimensions.

UNRAVELLING THE LOCOMOTION OF REPTILES: CONTRIBUTION OF FEMORAL MICROANATOMY AND PALEOBIOLOGICAL IMPLICATIONS

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Keywords: *reptile, locomotion, microanatomy, paleobiology, functional morphology*

The water-to-land transition represents a key event in the evolution of tetrapod vertebrates. The mechanical constraints inherent to this new environment led amniotes to develop novel locomotor strategies that granted them access to new ecological niches, thus contributing to the evolutionary success of the clade. Today, amniotes show great locomotor and postural diversity, especially in reptiles, whose extant representatives include erect bipeds (birds), "semi-erect" quadrupeds (crocodilians) and sprawling quadrupeds (lepidosaurs and turtles). But the various events that led to such diversity remain enigmatic and the locomotion and posture of many extinct species, such as the Triassic *Euparkeria capensis* (archosauriform) and *Marasuchus lilloensis* (dinosauriform), raise questions. The study of reptile microanatomy can help address these uncertainties. Indeed, this locomotor and postural diversity is accompanied by great microanatomical disparity. We show how microanatomical parameters measured in cross-section, such as bone compactness and the position of the medullo-cortical transition, can be related to locomotion and posture in reptiles. Using statistical methods accounting for phylogeny (phylogenetic flexible discriminant analyses), we develop several inferential models from a sample of femur cross-sections belonging to 51 reptilian species. We use these models to infer the locomotor mode and posture of 7 extinct reptile taxa. Our study contributes to the understanding of the evolution of locomotion in various early reptile species. Our models and methods could be used by palaeontologists to infer locomotion, including posture, in other extinct reptilian taxa, especially when considered in combination with other lines of evidence.

EVOLUTION OF CRANIOCERVICAL MUSCULATURE IN ABELISAURIDAE (DINOSAURIA: THEROPODA)

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Keywords: *neck, dinosaurs, specialization, myology, range of movement*

Abelisaurids were dinosaurs that diversified specially in Gondwana during the Cretaceous. They were medium to large sized theropods, with reduced forelimbs, highly modified cervical vertebrae and sometimes had horned skulls. Their fossil record is abundant and well-represented making possible to assess the evolution of craniocervical musculature in Abelisauridae.

We have mapped eight characters, corresponding either to correlates of musculature or to the motion capacities (moment arms, range of motion...) in recent phylogenetic hypotheses. Five of these characters are related to cervical ribs and vertebrae and three more to the skull. Characters were optimized following the principle of maximum parsimony considering *Ceratosaurus* as the taxon with the simplesiomorphic condition. These conditions are basal, derived or unknown. First derived characters occur in Carnosaurinae: (i) epiphyses taller than neural spine, (ii) paraoccipital processes inclined less than 45 degrees (dorsal view) that provide a big moment arm for dorsiflexion and dorso-lateroflexion, (iii) absence of ventral keel in posterior cervical and anterior dorsal vertebrae which implies a smaller insertion for neck ventriflexors, and (iv) the presence of aliform process in cervical ribs. Range of motion for torsion movements increased due to (v) wider prezygapophyseal facet joints.

These derived characters were present in Brachyrostra and there were indications of (i) widening of neck base, producing greater levers for lateroflexion and (ii) subhorizontal paraoccipital processes, granting greater moment arms. Finally, Furileosauria evolved (i) nuchal crests taller than wide. Craniocervical region evolution enabled abelisaurids greater moment arms for torsion, dorsiflexive and lateroflexive movements than their earlier branching relatives.

NOT ALL ARE CROCODILE BITES: SHELL PITTING ON A *NEOCHELYS* TURTLE FROM THE EOCENE OF ZAMORA (SPAIN)

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Keywords: *Testudines, Pleurodira, Lutetian, Corrales del Vino, paleopathology*

Shell pitting is one of the most common abnormal condition identified in extinct turtles and, at the same time, one of the less understood. References to shell pitting in extant turtles do not usually include morphological descriptions, illustrations, or data concerning causal agents, etiology or pathogenesis. In the case of the fossil record, available interpretations on shell pitting are generally speculative or poorly justified. In this sense, in the literature regarding extinct turtles, pre-mortem bite marks are the most frequently proposed causative agent to explain shell pitting. As a consequence, other potential causative agents (e.g., parasitism or bacterial and fungal infections) have rarely been contemplated.

The anomalies on the shell of an individual determined as *Neochelys* sp. (Pleurodira, Podocnemididae) from the middle Eocene (Lutetian) of Corrales del Vino (Zamora, Spain) are discussed in detail. The anomalies of the specimen were interpreted in a previous study as traumatic injuries result from a crocodile attack. The lesions produced by the predator were interpreted as non-fatal for the turtle specimen. The re-study of these anomalies through physical examination and differential diagnosis procedures, allows proposing alternative causal agents. This type of analysis indicates an increase in the complexity in the interpretation of the shell pits in fossil remains of turtles than that which can be generally deduced from the available literature.

THE IMPACT OF GIANT GROWTH: A COMPARATIVE FINITE ELEMENT STUDY OF EXTANT AND EXTINCT INSULAR DORMICE

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Keywords: *Finite Element Analysis, Insular Gigantism, Gliridae, Functional Morphology, Island Evolution*

Rodents on islands often drastically adjust their body size and shape as a response to their isolated environment. Small mammals, like dormice (Gliridae), appear to increase in size significantly on various Mediterranean islands. The largest extant dormouse population (*Eliomys quercinus ophiusae*) is present on the Balearic island of Formentera, Spain. Although significantly larger than its mainland relatives, these insular giants are relatively small in comparison to fossil dormice on islands like Mallorca (*Hypnomys* spp.) and Sicily (*Leithia* sp.). The mandibular shape of these dormice vary significantly, and statistical shape analyses indicate only part of these morphological variations can be explained by allometry. Variation in preferred diet and foraging techniques are expected between insular populations and could influence skull morphology. MicroCT data of both giant and normal sized dormouse mandibles used in this study allowed for evaluating the effects of shape change on the biomechanical performance within the masticatory apparatus. Finite Element Analyses specified which mandibular morphologies are better adapted to either chewing or gnawing at the incisors. Our results indicate the mandibular shape to have a direct effect on the masticatory apparatus, predicting faunivory in some giants and herbivory in others.

FINDING THE TRACEMAKER OF LARGE-SCALE CISURALIAN VERTEBRATE BURROWS

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Keywords: *burrow, Cisuralian, osteological correlates, trace fossil, fossorial lifestyle*

Burrowing is one of the most widely distributed behaviors among extant terrestrial vertebrates, yielding several ecological benefits, such as providing microhabitats with stable environmental conditions for aestivation and breeding, or subterranean foraging. In the fossil record fossorial lifestyles are best documented by the presence of burrowing structures. Evidence for fossorial lifestyles among vertebrates ranges as far back as the Devonian. However, large scale tetrapod burrows, especially in the Cisuralian are scarce, and information about possible producers are practically non-existent. The Cisuralian Bromacker locality near Tambach-Dietharz (Thuringia, central Germany) with its exceptional preservation of both trace- and body fossils, presents unique insights into terrestrial ecosystems of the early Permian. Among the trace fossils are one of the oldest known large-scale vertebrate burrows (width up to 50 cm). The observed structures, previously informally named “*Megatambichnus*”, include helical shafts, horizontal tunnels, and terminal chambers. The infilling is almost identical to the host rock and burrow walls are often not clearly visible. These burrows show extensive scratch marks, including bilaterally-arranged sets of up to 5 scratches. We try to find possible tracemaker candidates for those burrows, by (1) comparing scratch set and burrow measurements with body measurements of the taxa found in the Bromacker locality, and (2) discussing possible fossorial lifestyles in those taxa based on comparisons with osteological adaptations for fossoriality found in extant and extinct fossorial animals.

MOSASAUR FEEDING ECOLOGY FROM THE BEARPAW FORMATION, ALBERTA, CANADA: PART II

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Keywords: *Cretaceous, Bearpaw, mosasaur, feeding, geochemistry*

The Campanian Bearpaw Formation of southern Alberta, Canada, holds very well preserved specimens of mosasaurs (*Mosasaurus missouriensis*, *Prognathodon overtoni*, and *Plioplatecarpus primaevus*) and well-preserved specimens of elasmosaurs, turtles, *Enchodus*, lobsters, cuttlefish, and bivalves, representing a relatively complete ecosystem north of the Western Interior Seaway. Here, the ecosystem interrelationships of all these animals, and particularly those of the most common mosasaurs, are studied via two-dimensional dental microwear analysis, Energy-dispersive X-ray spectroscopy, and isotope analysis. Teeth of all vertebrates, as well as turtle carapace, and lobster, cuttlefish and bivalve shells were selected for analysis from the collections of the Royal Tyrrell Museum of Palaeontology in Drumheller,

The 2D dental microwear analysis reveals a generalist tooth wear for *Mosasaurus* (equal amounts of pits, gouges, and scratches), a more heavy wear for *Prognathodon* (more gouges and pits) and a variety of both softer wear (fine scratches) and moderate wear (gouges and pits) for *Plioplatecarpus*. Coupled with EDX Sr/Ca and Ba/Ca measurements, *Mosasaurus* pairs with piscivorous *Plioplatecarpus*, elasmosaurs and sharks, while *Prognathodon* pairs with durophagous sawfish.

Carbon and Oxygen isotope analysis shows, interestingly, the smallest range for *Mosasaurus*, indicating a less wide array of prey than its microwear and EDX results predicted. *Prognathodon* shows the widest range. *Plioplatecarpus*, elasmosaurs, and *Enchodus* show similar $\delta^{13}\text{C}$ values; sharks and sawfish less negative values, and lobsters and cuttlefish more negative values. *Prognathodon* shows the highest range and slightly higher measurements of $\delta^{18}\text{O}$, indicating perhaps different ingested salinity levels, and therefore a different foraging area for this mosasaur.

EARLIEST EVIDENCE FOR FRUGIVORY AND POTENTIAL SEED DISPERSAL BY BIRDS

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Keywords: *Early Cretaceous, Jehol Biota, Jeholornis, diet, bird-plant interactions*

The Early Cretaceous diversification of birds was a major event in the history of terrestrial ecosystems, occurring during the earliest phase of the Cretaceous Terrestrial Revolution. Frugivorous birds play an important role in seed dispersal today, and may have done so since their origins. However, evidence of this has been lacking. *Jeholornis* is one of the earliest-diverging birds, only slightly more crownward than *Archaeopteryx*, but its cranial anatomy has been poorly understood, obscuring diet-related functional interpretations. Originally hypothesised to be granivorous based on seeds preserved as gut contents, this interpretation has become controversial. We conducted high-resolution synchrotron tomography on an exquisitely preserved new skull of *Jeholornis*, revealing remarkable cranial plesiomorphies combined with a specialised rostrum. We use this to provide a near-complete cranial reconstruction of *Jeholornis*, and exclude

the possibility that *Jeholornis* was granivorous, based on morphometric analyses of the mandible (3D) and cranium (2D), and comparisons with the 3D alimentary contents of extant birds. We show that *Jeholornis* was at least seasonally frugivorous, providing the earliest evidence for fruit consumption in birds, and indicating that seed dispersal was more likely to be present from early in the avian radiation. As highly-mobile seed dispersers, early frugivorous birds could expand the scope for biotic dispersal in plants, and may explain, in part, the subsequent evolutionary expansion of fruits, indicating a potential role of bird-plant interactions in the Cretaceous Terrestrial Revolution.

MEDIUM AND SMALL-SIZED SUINES (SUIDAE, MAMMALIA) FROM THE LATE MIOCENE TO EARLY PLIOCENE OF EUROPE

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Keywords: *Suinae, Artiodactyla, large mammals, faunal turnover, Euro-Mediterranean*

Suids (Suidae, Mammalia), or simply the pigs, are a primitive-looking family of even-toed hoofed mammals widespread across the Old World. Most, if not all, living species belong to Suinae, a subfamily that originated during the late Miocene and became dominant soon thereafter. The late Miocene to early Pliocene is therefore a crucial period for investigating the dynamic of the success of Suinae, which occurred within a broader context of renewal of mammalian paleocommunities. Nonetheless, the paucity of complete cranial remains and the overall plesiomorphic anatomy of suids pose challenges in elucidating their evolution. Here, I present the results of an ongoing research focused on small and medium-sized species of European Suinae, including the description of new material as well as the revision of historical collections. Three good species are recognized during the late Miocene to early Pliocene of continental Europe, with no convincing evidence of chronological overlap between them: *Propotamochoerus palaeochoerus*, *Propotamochoerus provincialis*, and *Sus arvernensis*. *Propotamochoerus palaeochoerus* was a typical element of early Vallesian (MN 9) ecosystems of Europe, but it disappeared after the so-called (mid-)Vallesian Crisis (~9.7 Ma), along with many other species. *Propotamochoerus provincialis* is recorded in Turolian (MN 11-MN 13) assemblages, which document the presence of faunas adapted to open environments. The early Pliocene (Ruscinian) witnessed a return to more humid condition and the concurrent spread of *Sus arvernensis*. During the considered period, European suids experienced a significant decline in diversity, especially at the expense of non-Suinae.

UPDATING THE THEROPOD RECORD FROM THE EASTERN CAMEROS BASIN: SPINOSAURID REMAINS OF THE LOWER CRETACEOUS ENCISO GROUP (LA RIOJA, SPAIN)

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Keywords: *Early Cretaceous, Theropoda, Spinosauridae, Baryonychinae, Igea.*

The La Rioja sector of the Cameros Basin (northern Spain) is world-renowned for the abundance and good quality of preservation of its Lower Cretaceous dinosaur tracksites. In addition, explorations and digs carried out in recent years have led to new finds of theropod skeletal material. Nearly all theropod fossils recovered in Eastern Cameros so far come from the Enciso Group of near Igea village, which is dated as late Barremian-Aptian. These remains consist of three partial skeletons that can be confidently assigned to Spinosauridae, most likely to Baryonychinae, from Costarrey-1, Marino-2 and Virgen del Villar-1 sites. The specimen recovered from Costarrey-1 consists of some caudal vertebrae, ribs and fragments of the pelvic girdle; and that from Virgen del Villar-1 mostly comprises appendicular bones from the left hindlimb. The Marino-2 fossil is the most complete specimen. It preserves several cranial bones and elements from the axial skeleton, pelvic girdle and hindlimbs. Aside from these remains, more fragmentary material found in the Enciso Group in Igea consists of a partial maxilla and isolated teeth. Studies based on the maxilla and teeth suggest that they belong to a baryonychine spinosaurid different

from *Baryonyx*. Furthermore, two tooth morphotypes have been distinguished among the sample, which could indicate dental variation or the presence of two different species. Therefore, future research may lead to the description of new spinosaurid taxa and to better understanding of the diversity of Spinosauridae not only in the Cameros Basin, but also in Europe as a whole.

INVERTEBRATE BIOEROSION ON MESOZOIC MARINE REPTILE FOSSILS

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Keywords: *marine reptiles, Mesozoic, trace fossils*

Invertebrate assemblages have been recovered in association with whale carcasses in both the present day and in the fossil record. These whalefall communities are highly specialized for exploiting the nutrient influx produced by a large vertebrate fall. A few instances of organisms occupying this type of environment have been described from Mesozoic marine reptiles. Although it is possible that marine reptile falls provided a similar environment to whalefalls for specialist invertebrate taxa, there has been little focus on these Mesozoic faunas. Several whalefall taxa likely originated in the Cretaceous, raising questions of how the community of invertebrates associated with a vertebrate fall changed across the Jurassic-Cretaceous and Cretaceous-Paleogene boundaries. In this study, marine reptile fossils from three major UK collections were examined for traces of bioerosion. A variety of borings and surface traces were consistently identified on these fossils. Echinoid and gastropod grazing traces are present through the Jurassic and Cretaceous, and microborings emerge in more oxygenated Jurassic formations, while bivalve borings are more common in the Cretaceous specimens. This preliminary identification of ichnotaxa associated with Mesozoic marine reptiles lays the groundwork for describing and identifying taxonomic assemblages associated with marine reptile dead falls more widely. This study and those that follow will provide a snapshot of the invertebrate taxa present at a Mesozoic marine reptile fall and inform us on the ecological niche occupied by these specialist taxa through deep time.

TRACKWAY-DATA-BASED RECONSTRUCTION OF LOCOMOTION EVOLUTION IN EARLY TETRAPODS

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Keywords: *Carboniferous, Cisuralian, Reptiliomorpha, Amniota, footprint ichnotaxa*

Considering the large anatomical range of known late Paleozoic tetrapod postcrania, some of the variability among contemporaneous tetrapod tracks can be attributed to evolutionary changes in trackmaker locomotion style close to the origin of amniotes. In a study including Carboniferous (10%; 19 out of 186) and early Permian trackways, we tried to infer steps of locomotion evolution close to the origin of amniotes from trackway measurements by means of ancestral state reconstruction. Due to the imbalanced sample, imperfect track-trackmaker correlation and certain unresolved controversies about tetrapod phylogeny, many of our preliminary results regarding the timing, correlation and presumable convergence of locomotion evolution steps were not conclusive. With the inclusion of additional Carboniferous records of the ichnotaxa *Hylopus*, *Notalacerta*, *Dromopus* and *Varanopus*, we gain a better data coverage for the earlier part of the trackmaker tree, while consideration of several alternative trackmaker phylogenies provides an indication for the robustness of our conclusions about character evolution. Furthermore, the ages assigned to certain track assemblages and node ages of our trackmaker trees have been updated according to recently published data. Our new results suggest that some functionally relevant features, such as the appearance of narrow gauges, large body sizes and gaits without ground contact of the belly or tail, are seemingly not as clearly linked to evolutionary change within the series of common amniote ancestors as we had assumed before. Instead, group-specific patterns and convergent evolution in diadectomorph, synapsid, parareptile and eureptile track producers contributed greatly to the observed variability.

THE “GHOST” THEROPODS OF THE BAHRIYA OASIS AND THEIR BEARING ON CRETACEOUS AFRICAN THEROPOD FAUNAS

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Keywords: *Theropods, North-Africa, Cenomanian, Carcharodontosauria, Ornithomimosauria*

The Cenomanian of North Africa is famous for its large theropod taxa. Several of these, such as the iconic *Spinosaurus* and *Carcharodontosaurus*, were first described from the Egyptian Bahariya Formation. In recent years, new material from the presumably roughly contemporaneous Moroccan Kem Kem Group was claimed to be conspecific with some of the Egyptian taxa. Taxa claimed to be present in both units include *Deltadromeus*, *Carcharodontosaurus*, *Sigilmassasaurus*, and *Spinosaurus*. However, no detailed comparisons were presented between the Moroccan and Egyptian fossils, as the latter were destroyed during World War II. A detailed reexamination of the North African theropods, with an emphasis on the carcharodontosaurids and the Moroccan *Deltadromeus*, reveals that the two faunas are not as similar as previously thought. The Egyptian carcharodontosaurid is recognized as a basal carcharodontosaur distinct from the Moroccan neotype of *Carcharodontosaurus saharicus*, with the latter being recovered within the traditionally South American clade Giganotosaurinae. *Deltadromeus* is here recognized as distinct from any of the Egyptian theropod specimens. Instead, it is recovered as a sister taxon to the South American *Gualicho* and both were found to be basal ornithomimosaurids. These results emphasize the connection between Moroccan and South American theropods while calling previous comparisons between Egyptian and Moroccan theropods into question. This is consistent with the paleogeographical situation in the early Late Cretaceous of Gondwana, as Morocco and Egypt were separated from one another by the Trans Saharan Seaway, while Northwest Africa remained connected to South America until about 100 million years ago.

**NEW TETRAPOD TRACKSITE WITH EXTENSIVE TRACKWAYS FROM THE
MOENKOPI FORMATION (MIDDLE TRIASSIC, ANISIAN) OF
NORTHEASTERN ARIZONA: IMPLICATIONS FOR ICHNOTAXONOMY,
ARCHOSAUR COMMUNITIES AND PALEOECOLOGY**

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Keywords: *Moenkopi Formation, Chirotherium, Synaptichnium, Isochirotherium, Rotodactylus*

The Moenkopi Formation in the North American Southwest yielded a diverse tetrapod fauna with body and ichnofossils, being a famous reference for Triassic vertebrate paleontology and ichnology since the mid-twentieth century. Here we document a recently discovered large tracksite in the Holbrook Member (Anisian) of northeastern Arizona comprising the most extensive Middle Triassic footprint material from North America, about 50 trackways and 5000 imprints on a surface of 75 m². The site is about 5 m above the base of the Holbrook Member and 18 m below the overlying Upper Triassic (Carnian) Shinarump Formation of the Chinle Group. The footprint assemblage consists of *Chirotherium barthii*, *C. rex*, *Isochirotherium marshalli*, *Synaptichnium diabloense*, *S. pseudosuchoides* and *Rotodactylus cursorius*. *Synaptichnium* and *Rotodactylus* are most abundant at the site. The presence of different size-classes of all chirothere taxa suggests a mixed archosaur community with individuals of different age. The assemblage confirms the Holbrook Member to belong to the *Chirotherium barthii* biochron, and the lack of *Chirotherium sickleri* is further evidence of paleobiogeographic peculiarities in the composition, if compared to

European early Anisian ichnoassociations. Remarkable is the lack of non-archosaur footprints, for example *Rhynchosauroides* and therapsid tracks. Associated invertebrate traces are *Arenicolites*, *Gordia*, *Scoyenia* and *Taenidium*, indicating the *Scoyenia* ichnofacies and an intermittently subaerial/subaqueous setting on a nonmarine riverine floodplain environment. The track-bearing stratum is a 0.2-0.4 m thick bed of sandstone with climbing ripple laminae. This thin, tabular and extensive bed with ripples is interpreted as a sheetflood (unchannelized flow) deposit on the floodplain.

ORAL PROCESSING IN EARLIEST TERRESTRIAL HERBIVORES RECONSTRUCTED THROUGH TOOTH WEAR AND 3D MODELING

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Keywords: *ecology, feeding, herbivory, OFA.*

Diadectids are among the earliest clearly identified tetrapod herbivores in the fossil record. This diagnosis is mainly based on their suspected capability for efficient oral processing of plant fodder using strongly widened posterior (molariform) teeth and heavy jaws. While coeval localities preserve mostly faunivorous tetrapods, diadectids are the most abundant vertebrate fossils at the Cisuralian (lower Permian) Bromacker Locality (Thuringia, central Germany), with Bromacker representing the earliest example of our modern herbivore-dominated ecosystem structure. However, evidence for oral processing and thus herbivory in diadectids has never been demonstrated beyond morphological descriptions. Here we present a hypothesis for the movement of diadectid jaws in oral processing based on an analysis of attrition marks and wear facets evaluated using scanning electron microscopy (SEM) on both molariform and incisiform teeth as well as 3D reconstruction of skull bones and teeth. While the main orientation of attrition marks is focused in the orthal direction, a minor component of tooth wear supports a fore-aft movement (proal or palinal). Retrodeformed 3D skull reconstructions of the two exceptionally preserved Bromacker species *Diadectes absitus* and *Orobates pabsti* allow for more detailed reconstruction of the jaw movements. These results suggest that the origin of efficient oral processing might have to be predated at least 30 Ma, close to the origin of high fiber herbivory itself and outside the mammalian lineage. Further studies on metabolic costs might explain why oral processing is not more widespread among modern herbivorous reptiles and instead mostly restricted to mammals among tetrapods today.

DEFINING AGE AT MATURITY IN THE INSULAR GIANT LEPORID *NURALAGUS REX* FROM BONE HISTOLOGY

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Keywords: *gigantism, Balearic Islands, Pliocene, palaeohistology, life history*

Insular dwarfs consistently show a much later age at maturity than predicted from body size scaling. Little, however, is known about the life history traits that evolve associated to insular gigantism. Some theoretical works have predicted an increase in age at maturity with increasing body size in insular giants, but whether these taxa mature later than predicted from body size scaling remains unknown. To answer this question, we analyzed the bone histology of the tibiae (n=13) and femora (n=12) of the Menorcan giant leporid *Nuralagus rex* (Pliocene, Spain). We also studied *in-vivo* labelled bones of European brown hare (*Lepus europaeus*) to calibrate bone tissue types and bone growth marks with sexual maturity in a close-related extant species. Our results show that a slow-growing lamellar bone appears in *N. rex* around the second year of life. The External Fundamental System, however, is only deposited some years later, which suggests that the extinct giant leporid grew slower and for a longer time as compared to extant taxa. Indeed, growth curves obtained from measurements of bone growth marks show that females of *N. rex* achieved sexual maturity around the age of four. In an allometric context, this extinct taxon (body mass of around 8 kg) is an outlier that reached sexual maturity extremely late for leporids, and even late for slow-developing bovids of the same body mass. This is the first evidence that giant insular mammals mature later than predicted from body size scaling, mirroring the pattern of delayed maturation in insular dwarfs.

DEEP TIME INVENTION AND HYDRODYNAMIC CONVERGENCES THROUGH AMNIOTE FLIPPER EVOLUTION

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Keywords: *network analysis, Cryptoclidus eurymerus, plesiosaur, foreflipper, flipper twisting*

Plesiosauria (Sauropterygia) are secondarily aquatic diapsids. From the Late Triassic to the end of the Cretaceous, plesiosaurs inhabited the oceans globally. A special feature of plesiosaurs are their four hydrofoil-like flippers. It has been suggested that plesiosaurs swam by rowing, combinations of rowing and underwater flying (like Otariinae, *Carettochelys insculpta*), or by underwater flying (like Spheniscidae, Chelonioidea, and possibly Cetacea). Rowers use water drag, while underwater fliers are energy efficiently using lift but at the cost of manoeuvrability. It is largely accepted that plesiosaurs were underwater fliers. Recently, it has been suggested that for efficient use of lift during underwater flight, plesiosaurs were able to twist their flippers along the long axis actively with a special muscular mechanism. Here, the convergent evolution of flipper twisting in the foreflippers of a plesiosaur and its functional analogues were investigated by employing anatomical network analysis (AnNA). As functional analogues, taxa with substantial lift-based propulsion phases were chosen: *Caretta caretta* (Chelonioidea, Testudines), *Spheniscus demersus* (Spheniscidae), *Megaptera novaeangliae* (Cetacea), *Zalophus californianus* (Otariinae), and *C. insculpta* (Carettochelyidae, Testudines). The AnNA is based on literature data. Bone to bone and muscle to bone contacts were coded in N x N data matrices. Morphofunctional modules were detected by running “igraph” in “R” and using a walktrap algorithm. Foreflipper AnNA revealed that *C. eurymerus*, *C. caretta*, and *Z. californianus* convergently evolved myological mechanisms for active foreflipper leading and trailing edge twisting. *S. demersus* actively twists the leading edge, and *C. insculpta* and *M. novaeangliae* cannot actively twist their foreflippers.

EVOLUTIONARY HISTORY OF BIRD ECOMORPHOLOGY: USING 3D SCANS TO ESTIMATE ANCESTRAL STATES OF THE GALLOANSERAN QUADRATE

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Keywords: *Geometric morphometrics, birds, quadrate, Galloanserae, ancestral state reconstruction*

In birds and other reptiles, the quadrate acts as a hinge connecting the lower jaw and the cranium, and plays an important role in avian cranial kinesis. Though previous studies have qualitatively described its substantial morphological variability, none have tried to quantify evolutionary changes in its shape. Here, we investigate shape changes of the quadrate in Galloanserae, a major clade of extant birds uniting relatives of living chickens and ducks. We quantified morphological variation in the quadrate across 50 extant galloanseran taxa covering all major extant subclades using three-dimensional geometric morphometrics, and performed ancestral shape reconstructions in the context of an up-to-date neornithine phylogeny. We find that ancestral state reconstructions based only on modern quadrates failed to recover plesiomorphic features observed in stem groups, and instead merely represented the average shape derived from the extant dataset. Therefore, we strongly encourage adding fossil taxa into three-dimensional geometric morphometric datasets for ancestral state reconstructions when possible. After incorporating several early fossil galloanseran quadrates into our analyses (*Asteriornis*, *Presbyornis*, and *Conflicto*), our reconstructed ancestral galloanseran quadrate approximates aspects of quadrate morphology observed in galliforms, indicating that the ancestor of Galloanserae might have resembled extant galliforms in its quadrate morphology and aspects of its jaw biomechanics. The quadrate morphology of Pelagornithidae—an enigmatic clade of fossil birds potentially allied with Galloanserae—does not closely resemble our ancestral reconstructions, suggesting that pelagornithids may have exhibited divergent quadrate mechanics unseen in any other members of total-clade Galloanserae.

THE PHYLOGENY OF THE EARLY PALAEOCENE ORDER TAENIODONTA USING NEW SPECIMENS FROM NEW MEXICO, USA

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Keywords: *Palaeogene, mammals, extinction, anatomy, phylogeny*

After the Cretaceous-Palaeogene (K-Pg) mass extinction mammals thrived in the Cenozoic. However, the phylogenetic affinities of early Palaeogene 'archaic' mammals that lived immediately after the extinction remain unresolved. Taeniodonta is a group of puzzling 'archaic' mammals that appeared in the early Palaeocene of North America. They are arranged into two subgroups; the Conoryctidae and Stylinodontidae and are characterised by their extreme degree of dental wear, indicating an abrasive diet, which led to hypsodonty in the most derived species. Due, in part, to their worn teeth and their rarity in the fossil record, the position of taeniodonts in the mammalian phylogenetic tree remains unresolved. New fossils from San Juan basin, New Mexico, USA, including unworn teeth of four genera and postcranial elements of an early taeniodont, *Conoryctes*, shed light on their dental and postcranial anatomy. Both in the forelimb and hind limb of *Conoryctes*, there are anatomical adaptations towards fossoriality. Using these specimens, we scored taeniodonts and other Palaeogene mammals into a phylogenetic data matrix (620 characters, 135 taxa). We then conducted a phylogenetic analysis using parsimony. Our results show that Taeniodonta is a monophyletic group within Eutheria. We also found that *Onychodectes* is basal to the two subgroups previously proposed. Based on the new postcranial fossils and revised phylogeny, we concluded that digging behaviours were likely ancestral for taeniodonts. Therefore, a more fossorial mode of life may have been beneficial for their surviving and thriving in the wake of the K-Pg extinction.

FIGHTER OR BLUFFER: COMPARISON OF BENDING AND COMPRESSION IN MODELS OF THE CAUDAL SPINES OF DACENTRURINE AND STEGOSAURINE STEGOSAURS

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Keywords: *Stegosauria, Spines, Bending, Compression, Dacentrurinae*

Stegosaurian dinosaurs have a double row of parasagittal osteoderms and a ubiquitous and iconic set of two pairs of spines at the end of the tail, often referred to as thagomizer. Most derived stegosaurian taxa are members of two sister clades: Stegosaurinae and Dacentrurinae. Stegosaurinae includes *Stegosaurus stenops*, with large dorsal plates; and Dacentrurinae is represented by *Miragaia longicollum* and *Miragaia longispinus*, both characterized by the largest caudal spines, up to one meter long. The cross-section of the thagomizer spines is different between these taxa, as the stegosaurine spines are elliptical in cross-section while dacentrurine ones have a thick sigmoid-like section. These two different morphologies have been compared and used to estimate the forces withstandable by the spines, under compression and bending loadings, using a rhomboid shape as a proxy for dacentrurine spines. One estimate was carried out by attributing the same length and proportions to the two spines and a second one was carried out by attributing the spines' real length. The two models tested showed that stegosaurine spines have better performances in withstanding a higher force in bending and compression than dacentrurine ones. This difference can be explained by the spines of stegosaurine stegosaurs being better suited for combat than dacentrurine ones, while the latter may have been better suited for other functions, such as display or intimidation.

SIZE REDUCTION AND ITS MORPHOLOGICAL CONSEQUENCES IN MAMMOTH MOLARS FROM THE PLEISTOCENE OF BRITAIN

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Keywords: *elephant, molars, lamellae, enamel, size reduction*

The late Middle to Late Pleistocene saw the transition from *Mammuthus trogontherii* ('steppe mammoth') to *M. primigenius* ('woolly mammoth') in Europe, with increase in lamellar number in the molars, and reduction in lamellar and enamel thickness. There were also, in each species, episodes of significant size reduction, particularly well-documented in Britain. With a metric dataset of molars from over 40 localities I explore the pattern of size reduction and the consequences on molar morphology, a complicating factor in tracing the evolutionary transition. Shortening of molars increases lamellar packing but its effect on the number of lamellae appears variable across populations. The interplay of size reduction and additional developmental modifications in the transition between *M. trogontherii* and *M. primigenius* is explored. The sporadic occurrence of analogously small-sized populations in permanently continental areas (mainland Europe and Siberia) indicates that this is not always technically an 'island' phenomenon, but the exploration of developmental mechanisms in all these instances is relevant to the interpretation of size-related changes in the island syndrome.

THE MIDDLE PERMIAN TRACKSITE OF GONFARON: A COMPLEX ECOSYSTEM IN THE MIDST OF THE END-GUADALUPIAN MASS EXTINCTION

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Keywords: *Capitanian, ichnology, locomotion, captorhinomorph, full-body impression*

The Permian outcrops of Provence yield one of the most extensive records of continental ichnofossils, reaching from the Kungurian through the Capitanian (early-middle Permian). The Pélitique Formation of the Gonfaron site (Provence, France) has recently been revised and is marked by a diverse vertebrate ichnofauna: *Batrachichnus salamandroides* (temnospondyls/lepospondyls), *Capitosauroides talus* comb. nov. (therocephalian therapsids), *Dicynodontipus* isp. (cynodont therapsid), *Varanopus* isp. (bolosaurian parareptiles), *Hyloidichnus bifurcatus* (captorhinomorph eureptiles) and *Rhynchosauroides* isp. (neodiapsid eureptiles). This ichnoassociation has been dated to the late Capitanian and assigned to the newly introduced *Dicynodontipus* sub-biochron. It is also the earliest evidence of the post-dinocephalian extinction recovery at low latitudes of Pangaea. Moreover, the Gonfaron site is an excellent site for the study

of Permian ecosystems: it yielded two rare full-body impressions of Hexapoda that testify certain ecological strategies, such as mimetics and jumping adaptation, possibly indicating high trophic pressure in harsh palaeoenvironmental conditions. The trophic pressure was investigated through the analysis of co-occurrences of fossil traces (arthropod and tetrapod tracks and trackways), which show that the association of tetrapod and hexapod imprints was relatively common. Also, the good preservation of the tetrapod tracks of the Pélitique Formation allowed the first synapomorphy-based correlation between *Hyloidichnus* tracks and captorhinomorph trackmakers and a precise reconstruction of the locomotion of captorhinomorph eureptiles. Further studies and new excavations on the site are planned to provide more data/material and strengthen our knowledge of this crucial period in the evolution of tetrapods and hexapods.

THE FIRST DUCKBILL DINOSAUR (HADROSAURIDAE: LAMBEOSAURINAE) FROM AFRICA AND THE ROLE OF OCEANIC DISPERSAL FOR LATE CRETACEOUS AND PALEOGENE VERTEBRATE BIOGEOGRAPHY

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Keywords: *Cretaceous, Lambeosaurinae, Hadrosauridae, Biogeography, Macroevolution*

Following the breakup of Pangaea in the early Jurassic, continents became increasingly fragmented over the course of the Cretaceous and isolated by a combination of continental drift and high sea levels, leading to distinct and endemic dinosaurian communities in Northern, Laurasian continents and the southern, Gondwanan continents. Late Cretaceous Laurasian communities were dominated by hadrosaurids, ceratopsians, and tyrannosaurs; Gondwanan communities by titanosaurs and abelisaurids. The presence of hadrosaurids, a lineage endemic to North America, in the Maastrichtian of Africa raises questions about processes driving biogeography in the late Cretaceous and early Cenozoic. Similar patterns are seen in other dinosaur lineages including hadrosaurids and titanosaurs, and in Paleogene mammals. Long-range oceanic dispersal, via swimming, drifting, or rafting appears to play an infrequent but central role in structuring dinosaurian communities. Low-probability, high impact “Black Swan” events, including oceanic dispersal, mass extinction, and complex adaptations, all play a major role in driving evolution over long timescales. Microevolutionary processes observable on historical timescales are necessary but insufficient to explain macroevolutionary patterns: macroevolution is not just lots of microevolution.

NEW INSIGHTS INTO *TRICERATOPS* LIMB BONE HISTOLOGY: REVEALING SKELETAL UNITY THROUGH PATTERNS IN HISTO-VARIABILITY

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Keywords: *Triceratops*, *bonebed*, *ceratopsians*, *bone remodelling*, *histology*

Annual field expeditions from 2013-2019 to eastern Wyoming, USA by Naturalis Biodiversity Center yielded a monospecific bonebed comprising disarticulated remains of at least four individuals of *Triceratops* (Dinosauria: Ceratopsia). Hitherto, little research has been done on *Triceratops* growth. The abundance of post-cranial elements provides an opportunity to study *Triceratops* osteohistology in detail. Drill core samples were taken from multiple hindlimb elements (tibiae and femora) which were subsequently processed into thin sections and studied using polarizing light microscopy. All elements show laminar parallel-fibred bone and a lack of cyclical growth marks, a combination of histological traits similar to that seen in (derived) sauropod dinosaurs. However, there is significant variation in the degree of bone remodelling, despite minor variation in element size. Semi-quantification of remodelling patterns allows for the assessment of inter-elemental variation between the different limb bones and histovariability within *Triceratops*. The skeletal disarticulation of the site poses challenges when reconstructing the skeletons. The assessment of histovariability between different elements helps to reconstruct the individual skeletal unity of the disarticulated remains from the mass death assemblage. Elements from the same individual are connected through similarities in histological patterns. This study provides a first detailed analysis of *Triceratops* limb bone histology and allows for the opportunity to compare its histology with that of other ceratopsian dinosaurs. Comparisons with the closely related members of the Chasmosaurinae and more distantly related Centrosaurinae improve our understanding of ceratopsian growth and development in general.

REVIEW AND COMPLETENESS OF THE FOSSIL RECORD OF PALEARCTIC CAUDATA

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Keywords: *amphibians, sampling biases, Urodela, Eurasia, salamanders*

The absence of an up-to-date, taxonomically and spatiotemporally inclusive dataset of the fossil record of Palearctic caudates limits our ability to synthesize information, precluding an evaluation of the macroevolutionary and biogeographical history of this group. Here, we provide a critical reappraisal of the published fossil occurrences of caudates from the Palearctic and quantitatively evaluate the quality of the group's fossil record. By contrast with the depauperate nature of extant biodiversity (especially compared to that of the Nearctic), Palearctic Caudata were much more diverse in the past, with more than sixty extinct species currently recognized. Stem-Urodela were already widespread during the Middle Jurassic in Eurasia. Cryptobranchoidea, the earliest-branching sub-order of Caudata, appear to have radiated in Asia, whereas the origin of the other sub-order of Caudata, Salamandroidea, is unclear. Not all time bins are equally represented in the record, which is probably a combination of real biological signals and several sampling biases. The highest apparent diversity of extinct taxa occurs during the Miocene, with a drastic reduction during the Pliocene, reflecting a common trend in small 'herps' in general. We suggest that this pattern is partly influenced by a sampling bias, with continental Pliocene outcrops less sampled than the Miocene ones (for geological or anthropic reasons). Most of the Neogene and Quaternary taxa are known from isolated vertebrae, and the lack of articulated skeletons from these time bins constitutes a problem for the understanding of their taxonomic identity and the phylogenetic relationships among the taxa.

HOMOTHERIUM FROM THE LATE EARLY PLEISTOCENE OF PIRRO NORD (APULIA, SOUTHEASTERN ITALY)

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Keywords: *Felidae, Machairodontinae, Homotherium, Villafranchian, Pleistocene*

Homotherium was one of the most widely distributed felids, both geographically and chronologically. Records of this genus were found from the early Pliocene to the latest Late Pleistocene in Eurasia, Africa and America. Late Pleistocene Eurasian and American fossils, usually considered as representing two different species and well-known thanks to several complete specimens from Friesenhahn cave in Texas (USA), were recently ascribed to a single species thanks to ancient DNA evidence. On the contrary, Pliocene and Early Pleistocene *Homotherium* from Africa and Eurasia are ascribed to multiple species and remain poorly known, particularly their postcranial anatomy. In this regard, up to now only one complete skeleton from Senèze (France) and the collection of isolated finds from the Incarcal Complex (Iberia) characterize the early forms of *Homotherium*.

Here we describe *Homotherium* collection from a single fissure filling (DE11-1) from the Pirro Nord area in Gargano (southern Italy). It is one of the most diverse Old-World assemblage of *Homotherium* composed by an almost complete skeleton of an adult female, a partial skeleton of adult male, and remains of a juvenile and other 4 individuals, for a total number of 474 specimens. The adult female skeleton from Pirro Nord is a lioness-sized animal with a slender, long-legged appearance adapted to prey in open-environments, with powerful cervical area and reduced lumbar region. In the lumbar region, the female displays several pathologies on the neural arches. Even other specimens of the sample show other pathologies probably consequence of traumas in tibias, pelvis and metapodials.

ISOLATED THEROPOD TEETH FROM THE TENDAGURU FORMATION (UPPER JURASSIC, TANZANIA)

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Keywords: *Dinosauria, Theropoda, Mesozoic, Upper Jurassic, Africa*

The Oxfordian-Tithonian Tendaguru Formation (Tanzania) is still the most relevant reference for the study of Late Jurassic dinosaur faunas from Gondwana. This unit has yielded an abundant fossil record that includes sauropods, stegosaurs, ornithopods and theropods. The record of theropods consists mainly of fragmentary materials, including a large collection of isolated teeth. The description mainly of postcranial remains allowed the identification of a diverse fauna that includes at least four ceratosaurian and three tetanuran taxa, some of which also identified based on isolated teeth. However, the full diversity of tooth morphotypes represented in these levels had not been previously evaluated. A collection of 167 theropod teeth from the Tendaguru Formation was analyzed, using a combination of morphometric and cladistic tools. The identified tooth morphotypes are tentatively assigned to six taxa, including a non-abelisauroid ceratosaur, two indeterminate abelisauroids, a megalosaurid, an early branching allosauroid, and a carcharodontosaurid. No specimen could be clearly related to abelisaurids, which were previously identified based on postcranial materials. This clade might be represented by indeterminate abelisauroid teeth or by specimens identified as carcharodontosaurids, given the similarity of their tooth morphology. As with non-dental materials, the greatest abundance and diversity of tooth morphologies has been identified in the Middle and Upper Dinosaur Members. However, the distribution of the tooth morphotypes allowed to expand the record of megalosaurids to the Lower

Dinosaur Member, increasing the diversity of theropods in this basal unit of the Tengaduru Formation.

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THE BROMACKER LOCALITY: A REFERENCE SITE FOR PALAEOZOIC TETRAPOD ICHNOLOGY

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Keywords: *Permian, footprints, burrows, tracemakers, palaeoecology*

The Bromacker locality of central Germany (Tambach Formation, Cisuralian) is known since the late 19th century for its extraordinary fossil footprint content, especially with regards to abundance and preservation. The project “Opening science: new ways of knowledge transfer using the example of the research project Bromacker”, funded by the Federal Ministry of Research and Education, yields new preliminary results. Ichnotaxonomic studies evidence a more diverse ichnoassociation than previously thought, belonging to the *Dromopus* biochron. The occurrence of long trackways allows for studies on track taphonomy and on locomotion/posture of the trackmakers. Observed features, such as swimming traces, body/tail/digit drag traces and body/scaly skin impressions, are key for the inference of the trackmakers’ palaeoecology. The occurrence of complete, articulated autopodia at the same site allows for a thorough track-trackmaker correlation of the main producer groups. The correlation between footprints and autopodia evidences features in the skeletal record that are potentially useful for studies on phylogeny and biomechanics. The vertebrate footprint association was investigated through different census methods and our results indicate a dominance of diadectomorph tracks, which is

consistent with the proportions observed in the skeletal record of the same site. At least two distinct types of vertebrate burrows have been identified, and a study on the producers of these structures and their meaning under an evolutionary perspective has been undertaken. The relative abundance of tracks attributed to herbivores and of vertebrate burrows is currently investigated in the context of depositional environment, the evolution of terrestrial Cisuralian biota and climate change.

FILLING CRACKS TO IMPROVE THE CONSERVATION OF DINOSAUR EGGS FROM POYOS (UPPER CRETACEOUS. SPAIN)

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Keywords: *conservation, restoration, preparation, eggs, dinosaurs*

In the paleontological site of Poyos (Upper Cretaceous. Guadalajara, Central Spain), a large number of dinosaur eggs distributed along different stratigraphic levels has been recorded. The matrix surrounding and filling these eggs has between 34% and 76% of phyllosilicates, of which 10% are smectites, highly expansive clays that, in terms of conservation, are an important risk factor for deterioration).

The eggs are preserved in volume, showing a surface formed by a succession of shell fragments that the clay filler holds in position. However, this clay dehydrates after its extraction, losing volume and originating cracks that can break the structure that supports the egg, causing it to collapse. To avoid this, it is necessary to fill these cracks using materials compatible with the clays and analytically discernible (for example in radiological explorations).

For general consolidation of these eggs, it is used Paraloid B72 dissolved in acetone (sometimes by papering the surface with the adhesive embedded in Japanese paper). To prevent the treatment of the cracks from interfering with the general consolidation, it is filled with a water and alcohol soluble resin such as EVA Art and Polyvinyl alcohol, both of which have been tested. On the cracks, the consolidant was first applied without any type of thickener and once dry, the resin was introduced with glass microspheres which, due to their homogeneity and size, can be easily injected until the crack is filled. This treatment, together with the papering of the surface, improves conservation by eliminating areas of weakness.

NEW PRIMATE MATERIAL FROM THE MIDDLE EOCENE FOSSIL SITE OF CAENES (DUERO BASIN, SALAMANCA, SPAIN)

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Keywords: *Western Iberian Bioprovince, adapiform, omomyiform, Paleogene*

Caenes (MP15-16) was excavated in the 1980s-1990s, and yielded interesting primate remains still not studied in detail. This locality is found in the Western Iberian Bioprovince, a part of Iberia separated from the Pyrenean basins in some time intervals during the Eocene, that presents endemic faunas. Past revisions of the material showed that an *Anchomomys*-like primate was present in the locality, represented by two complete and one fragmentary upper molars, and two mandible fragments, one showing a complete P/4 and the other presenting an almost complete P/4, a partial M/1 and a complete M/2, and both with the rest of the alveoli from the lower C onwards. A new revision of the material recovered from this site has allowed us to identify more primate remains. On the one hand, a calcaneus that we attribute to the anchomomyin primate mentioned above, with an elongated distal part but smaller than the calcaneus of *A. frontanyensis*, the only anchomomyin calcaneus described so far. On the other hand, we have identified dental remains of a much smaller primate, represented by a mandible fragment with M/2 and M/3. Its morphology suggests that it is an omomyiform with *Pseudoloris* affinities, smaller than *P. pyrenaicus*, similar in size to *P. parvulus* and *P. cuestai*, presenting morphological differences with all of them. Further studies will elucidate the taxonomy of these primates, their phylogenetic affinities and the locomotor behavior interpreted from the anchomomyin calcaneus.

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THE ORIGIN OF AMNIOTA IN ITS PHYLOGENETIC CONTEXT

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Keywords: *Amniota, phylogeny, phylogenetics, scales, Tetrapoda*

Ever since the first phylogenetic analyses of early limbed vertebrates in the mid-1990s, there have been exactly two types of such analyses: (1) from the origin of limbs to that of Amniota, but barely reaching into Amniota; (2) covering amniote phylogeny and barely reaching beyond Amniota. This makes it impossible to research whether the diadectomorphs or certain “microsaurs” are amniotes. Moreover, research on amniote-internal problems like the positions of Varanopidae and the “parareptiles” may be misdirected if too distant outgroups are used (potentially leading to misrooted, distorted trees); which taxa are best suited as outgroups for amniote phylogeny depends on the abovementioned phylogenetic questions. I have updated and enlarged a dataset of early limbed vertebrates by adding amniotes and other taxa along with numerous characters, and doubled it to account for uncertainty over the “microsaurian” (etc.) tabular-or-supratemporal. Both matrices place Diadectomorpha and Varanopidae in Pan-Mammalia; the “parareptiles” and others are scattered. All “microsaurs” are found as stem-amphibians; moving any into Amniota requires about 30 extra steps. *Brouffia*, the only pan-amniote reported to retain dorsal dermal scales, appears to lie on the pan-amniote stem. Redescriptions of taxa and character complexes will be necessary, though not sufficient, to improve our understanding of amniote origins. My results also underscore the importance of “microsaurs” as close amniote relatives, and the closeness of the origins of Amniota and Lissamphibia. Extant amphibians may be better model organisms for amniotes like ourselves than used to be thought: phylogenetics using fossil data is important even for biomedical research.

NEW INSIGHTS INTO THE HIPPOPOTAMID (MAMMALIA, HIPPOPOTAMIDAE) FROM THE CASINO BASIN (TUSCANY, ITALY)

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Keywords: *Hippopotamidae, morphology, systematics, paleobiogeography, Mediterranean basin*

Fossil remains from the Casino basin (Tuscany) are known since the beginning of the 19th century thanks to the 1879 notes by D. Pantanelli. Among the others, the mammal assemblage includes *Mesopithecus pentelicus*, *Tapirus arvernensis*, *Propotamochoerus provincialis* and scarce and poorly preserved remains of a hippopotamid, consisting of a mandibular symphysis fragment, an apical fragment of a lower canine, some isolated lower incisors, a fragmented second lower premolar, and a second lower molar. These specimens were initially referred to *Hippopotamus hipponensis* (a pigmy species described by A. Gaudry in 1876 from the Early Pliocene locality of Pont-De-Duvivier, Algeria) and later ascribed to the new species *Hip. pantanellii* (now *Hexaprotodon? pantanellii*) by L. Joleaud in 1920. However, this attribution has been disputed during the past years. The hippopotamid remains from the Casino basin are here revised in order to clarify their systematic position and to infer paleobiogeographic and evolutionary patterns within the Mediterranean fossil record of Hippopotamidae. The canine displays a narrow longitudinal groove on the mesial side and the enamel is finely striated and crenulated. The lower molar lacks accessory cuspids and displays a well-developed trefoil wear pattern. The morphology of the remains collected from the Casino basin more closely resembles the African than the Asian hippopotamids' lineage. Hippopotamids' dispersal in Tuscany probably involved either the Iberian Peninsula or southern Italy, where the presence of *Archaeopotamus crusafonti* (Spain) and *Hex.? siculus* (Sicily) is well documented, in contrast to Eastern Europe where no Late Miocene site reports the occurrence of hippopotamids.

TETRACONODONTINE SUID REMAINS FROM CA L'ALMIRALL (MN6; VALLÈS-PENEDÈS BASIN, NE IBERIAN PENINSULA)

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Keywords: *Artiodactyla*, *Suidae*, *Tetraconodontinae*, *Miocene*, *Spain*

The suid dental remains from the late Aragonian (Middle Miocene) site of Ca l'Almirall located in the Vallès-Penedès Basin (NE Iberian Peninsula), are revised from a taxonomic and chronostratigraphic perspective by taking into account recent advances in tetraconodontine taxonomy. The Ca l'Almirall material, including a mandibular fragment and a few isolated upper and lower cheek teeth, are housed in the Institut Català de Paleontologia Miquel Crusafont in Sabadell, Spain. They were first attributed to *Hyotherium soemmeringi*, then to *Conohyus steinheimensis*, and most recently to *Versoporcus steinheimensis*. However, they were never described in detail and only the mandibular fragment had been figured thus far. Our taxonomic revision of the material indicates that, except for a listriodontine incisor fragment, most of the material belongs to the tetraconodontine genus *Versoporcus*, differing from both *Conohyus simorrensis* and *Parachelauastochoerus valentini* in premolar morphology. Mostly based on size, we attribute the Ca l'Almirall material to *Versoporcus grivensis* instead of *V. steinheimensis*. On biostratigraphic grounds, the site of Ca l'Almirall is tentatively correlated with the early MN6 (as conceived in Western Europe), with an estimated age of ~14.0–13.5 Ma that is roughly coeval with the oldest records of both species of *Versoporcus*. These species considerably overlap in chronostratigraphic range and have been considered synonyms by some authors, although based on size we provisionally support their distinction.

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CHARTING EVOLUTION, NEW METHODS TO MAP MORPHOLOGICAL CHANGE UPON THREE-DIMENSIONAL DIGITAL MODELS

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Keywords: *conv.map*, *rate.map*, *RRphylo*, *geometric morphometrics*, *digital models*

Three-dimensional computer-based technologies are increasingly becoming commonplace in the modern study of shape variation. Combining the fidelity of 3D rendering with innovative statistical tools, is now possible to visually inspect macroevolutionary patterns. Herein, we present two new applications of this kind, regarding the visualization of both morphological convergence and the variation in the rate of evolution directly on the phenotypes. The first application, named *conv.map* gives the possibility to visualize convergence by charting morphologically similar regions among pairs of analyzed species and to quantify the degree to which different regions of the phenotype contribute to overall convergence. The second application, named *rate.map* offers the possibility to chart phylogenetic ridge regression rate variation, directly onto the phenotype, giving first hand visual evidence of which parts of the phenotype changed more rapidly. Both algorithms dwell on landmark-based geometric morphometrics and are embedded in the R package 'RRphylo'. We tested *conv.map* on a renewed case of morphological convergence, the iterative evolution of the sabre-tooth morphotype, evolved independently among distinct mammalian clades from placentals to metatherians. The aim was to assess the cranial features that show the highest degree of convergence between the marsupial *Thylacosmilus* and the sabre-toothed cats. *rate.map* was applied to. To illustrate *rate.map*, we analyzed the evolution of facial skeleton in Hominoidea, including living and fossil taxa, to identify the regions of the face which evolved faster through time. The former application brings attention to the possession of expanded nuchal crest shared among sabertooths. The latter sheds light on the evolution of the canine fossa in *Homo sapiens*, and on the rapid evolution of the brow ridge.

PALAEOBIOLOGY OF *PANTHERA SPELAEA* (GOLDFUSS, 1810) AND IMPLICATIONS ON POCALA CAVE (TRIESTE, ITALY) PALAEOECOLOGY

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Keywords: *cave lion, morphometry, palaeoecology, taphonomy*

In Italy, cave lions (*Panthera spelaea*) are well represented by several fossil specimens but research mainly focused on their anatomy and taxonomy. In this study, lion remains from Pocala Cave (Trieste, Italy) preserved in the Museum of Geology and Paleontology of the University of Padova were redescribed. Morphometric analysis confirmed that these lions belong to the chrono-subspecies *Panthera spelaea spelaea*, most individuals are interpreted as adult males, and several young individuals are present. Taphonomic analysis shows low intensity water flow, few signs of scavenging, and cut-marks on a lioness jaw, probably of anthropogenic origin. Analysis of ⁸⁷Sr/⁸⁶Sr isotopes indicates that the same individual was not native of the Pocala Cave area. Those results confirm that exploitation of large carnivores was not unusual among Pleistocene humans, and provide an insight into the complex palaeoecology of Pocala Cave. The cave was used as a shelter by Pleistocene humans for collecting resources, and rarely by scavengers for consuming their preys. Furthermore, lions entered the cave to hunt cave bears during their hibernation, and Pocala Cave was probably used by lionesses as a refuge to give birth and take care of cubs, as suggested by the numerous remains of young individuals at different growth stages, providing the first possible evidence of a lion “den”.

**DINOSAUR TRACKS, SEDIMENTARY ENVIRONMENTS AND
PALAEOCLIMATE OF THE LATE CRETACEOUS EL MOLINO FORMATION IN
BOLIVIA (MAASTRICHTIAN, BOLIVIA; TORO TORO NATIONAL PARK)**

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Keywords: *El Molino Formation, Maastrichtian, Bolivia, dinosaur tracks, K/Pg boundary*

The El Molino Formation in the Toro Toro syncline (Department of Potosi, Bolivia) has long been known for its Cretaceous dinosaur tracks. The description of a trackway, *Ligabueichnium bolivianum*, attributed either to a ceratopsian or to an ankylosaur comes from the Toro Toro area.

The type trackway consists of undertracks with no anatomical details that can be seen under closer inspection. Five larger surfaces with trackways of theropods and sauropods have been figured in previous papers which are all situated close to the village center of Toro Toro. Recently, we assign the sauropod trackways to the ichnotaxon *Calorckosauripus lazari*, attributed to a non-derived titanosaur. Several sites, documented in 2019, are situated in the middle member of the El Molino Formation (Maastrichtian), and 15 different track levels have been recorded. The tracks occur as negative epichnia on fine-grained sandstones and limestones. In some sites, such as Las Golondrinas, positive hypichnia of theropods are present and sauropod footprints can be seen in cross-section. Today, more than 28 track-bearing areas are known inside and close to the National park Toro Toro, recording the presence of titanosaurid sauropods, different types of theropods, and ankylosaurs. The Toro Toro area is of key interest as it records dinosaur track levels that are close to the K/Pg boundary. The project's main focus is a multidisciplinary attempt to integrate stratigraphy, climate proxies (e.g., clay minerals, isotopes), sedimentary environments and ichnoassemblages in the context of the Latest Cretaceous in order to verify or falsify the rapid decline of dinosaur diversity.

NOTOCHORD PIT SIZE AS A POTENTIAL PROXY FOR EMBRYONIC STAGE IN ICHTHYOSAURS

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Keywords: *Ichthyosauria, embryonic stage, notochord pit, proxy*

Recently four different embryonic developmental stages have been proposed in the parvipelvic ichthyosaur *Stenopterygius* based on relative cranial ossification. *Stenopterygius* has the largest prenatal record of any ichthyosaur by far, including cranial and postcranial material in many embryos of gravid females. Other ichthyosaurs have a much more limited prenatal record, often lacking cranial material. This means that determining the prenatal stage in these embryos (relative to *Stenopterygius*) is difficult. The most common prenatal elements to preserve are vertebral centra. In *Stenopterygius* we noticed that the notochord pit is relatively larger in size in early development and smaller perinatally. Per embryonic stage preserved in *Stenopterygius*, we determined the relative notochord pit size of the vertebral centra. The relative notochord pit size ranged from ~ 50% in stage 1 to 40% in stage 2, 25% in stage 3, and 15% in stage 4. At every stage there were clear differences between the more anterior and more posterior vertebrae. However, preflexural vertebrae in every stage had roughly the same relative notochord pit size. We then examined gravid specimens of *Mixosaurus*, *Ichthyosaurus*, and *Leptonectes* with both cranial material and vertebral centra preserved. Comparable stages relative to *Stenopterygius* were hypothesized on the basis of cranial ossification. In all cases, the relative notochord pit size was similar to the size of hypothesized stage based on cranial ossification. This means that relative notochord pit size can be used as a proxy for embryonic stage in ichthyosaurs in the absence of cranial material.

THE MIDDLE EOCENE VERTEBRATES FROM PONTILS (EBRO BASIN, NE SPAIN)

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Keywords: *Bartonian, Robiacian, mammals, herpetofauna, ichthyofauna*

The Pontils locality (Ebro Basin, NE Spain) corresponds to a continental-to-marine sequence with several vertebrate-bearing levels. Previous works in this site documented the presence of scarce vertebrate remains, but only rodents were described in detail. Recent fieldwork carried out in this site has allowed recognizing seven levels yielding significant vertebrate remains. Among mammals, primates are particularly diverse and include abundant remains of a small, still undetermined omomyiform and scarce teeth of *Pseudoloris*, *Necrolemur* and an undetermined anchomomyin. Rodents are present in all the sampled levels and comprise additional material of

some species already described from this section (*Pseudoltinomys cosetanus*, *Sciuroides* cf. *romani*, *Paradelomys* sp.) and other forms unknown from this site until now (*Pseudoltinomys* sp., *Pairomys* cf. *ibericus*). Metatherian and eulipotyphlans are identified in several levels, although the material is scarce and fragmentary; similarly, chiropterans are only represented by two teeth from levels PO-22 and 33. Perissodactyls are diverse in PO-39 and include cf. *Palaeotherium* sp., cf. *Anchilophus* (*Paranchilophus*) sp., cf. *Anchilophus* (*Anchilophus*) sp. and “Pachynolophinae” indet., whereas artiodactyl remains have been found in PO-39 (Dacrytheriinae indet.) and PO-40 (Hyperdichobuninae indet.). Regarding the herpetofauna, amphibians are scarce, squamates are relatively diverse (including gekkotans, lacertids, iguanids, anguids and snakes), and crocodyliforms are represented by very abundant isolated teeth in nearly all levels. The ichthyofauna found in the upper levels (PO-39 and PO-40) includes chondrichthyans (three sharks and three rays) and actinopterygians. Summarizing, the assemblage from Pontils represents one of the most diverse Bartonian vertebrate faunas from the Iberian Peninsula.

ON THE AGE OF THE PONTILS FOSSIL SITE, AN EXCEPTIONAL CASE OF CORRELATION BETWEEN MARINE AND CONTINENTAL SCALES

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Keywords: *Middle Eocene, Bartonian, marine-continental correlation, vertebrates, foraminifera*

The fossil site of Pontils (Ebro Basin, NE Spain) is placed in a sequence that records the change from continental to marine conditions, thus representing an excellent opportunity for the correlation of biostratigraphic schemes based on marine and continental fossils. This locality has been known since the 1980s and was traditionally assigned to the Bartonian, on the basis of scarce mammal remains recovered from the lowest levels of the sections and, particularly, of marine fossils (foraminifera and nannoplankton) found in the overlaying marine sediments. However, some recent works have proposed an older, Lutetian age, for this site. Two field campaigns carried out by our team in the Pontils section have led to the recovery of abundant vertebrate remains from seven different levels, including chondrichthyans, actinopterygians, amphibians, crocodylians, squamates, metatherians, eulipotyphlans, chiropterans, rodents, artiodactyls, perissodactyls and primates, together with other non-vertebrate fossils. Among the latter, larger benthic foraminifera are particularly interesting, since the assemblage of *Nummulites garnieri sturi*, *N. garganicus*, and

Assilina (Operculina) schwageri allows assigning the site to the zone SBZ17 (Bartonian). Previous analyses of paleomagnetism determined that this site corresponds to a reversed-polarity interval, and therefore it can be confidently correlated to chron C18r (40-41 Ma). The rodent assemblage, including *Pseudoltinomys coetanus*, *Pseudoltinomys* sp., *Sciuroides* cf. *romani*, *Paradelomys* sp. and *Pairomys* cf. *ibericus*, also supports a Bartonian age for this site. Therefore, our results solve the debate about the age of the locality, which can be definitely assigned to the Bartonian.

HINTS OF INCREASED LONGEVITY IN EXTINCT INSULAR DWARF DEER

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Keywords: *bone histology, Candiacervus, Haversian bone, remodelling*

Dwarfed insular mammals evolve a suite of morphological and physiological adaptations triggered by a range of variables associated with geographical isolation. One of such variables is longevity which can extend in relation to body size reduction in ecological contexts of predator and competitor release, or reduced resource availability. Longevity in extreme cases of dwarfism can be reconstructed using palaeohistological approaches. Here, we studied the histology of seven rib fragments of the extraordinary, endemic dwarf deer *Candiacervus* (size 2) of Crete (Greece), dated to the Pleistocene. We tested whether its rib bone matrix shows evidence for extensive bone remodelling typically seen in larger and long-living mammals. We found that all ribs had well remodelled Haversian bone, which ranged from moderate to strong degrees of remodelling. Widespread Haversian bone with superimposed and remodelled secondary osteons implies experiences of several cortical bone resorption and re-deposition events. We also found some of the smaller rib cross-sections showed relatively higher osteon densities, along with instances of cortical bone porosity similar to that expected in elderly animals. These rib histology results agree with prior literature discussing longevity, and bone histology, in dwarf ruminants, and suggest this dwarf deer might have lived longer than what would be expected for its size. We highlight the usefulness of ribs when studying histology in palaeontological specimens.

LO HUECO QUARRY (UPPER CRETACEOUS. CUENCA, CENTRAL SPAIN), A PUZZLE OF ARTICULATED TITANOSAURIAN TAILS

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Keywords: *Titanosauria, Sauropoda, Phylogeny, Cretaceous*

Titanosaurian record from the Upper Cretaceous of Europe is abundant. This record is mainly represented by bones recovered from localities in which the degree of skeletal articulation or association is low, being difficult to establish the relationship between bones and where more than one titanosaur may be represented. Recently, partially articulated titanosaurian specimens have been found in the Ibero-Armorican domain, highlighting the fossil-site of Lo Hueco (Cuenca, Spain). Lo Hueco is a multitaxic bonebed with more than 10,000 collected fossils of which nearly half are titanosaurian remains. These specimens are key to understand the evolutionary history of European titanosaurs and to study their intraspecific variability and paleobiology, using a set of new methodologies. More than 10 individuals with fully to partially articulated or associated elements were found in this fossil-site, including several partial individuals preserving series of articulated caudal vertebrae. Analyses on these specimens are particularly important to understand positional, intra-, and interspecific morphological variability of caudal vertebrae, which can shed light to the systematics of European titanosaurs. Caudal vertebrae are source of several

morphological characters in datasets, and particularly diagnostic for titanosaurian subclades. Assessing positional variability can be relevant in the way we codify and score these morphological characters. To test this assumption, we provide a discussion on several caudal vertebrae anatomical characters such as the orientation of the neural spine, the ventral and longitudinal hollow of the centrum, the posterior condyle morphology, or the presence of postzygodiapophyseal lamina.

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CALCANEAL MORPHOLOGY IS A RELIABLE PROXY FOR THE LOCOMOTOR BEHAVIOUR OF EXTINCT PRIMATES

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Keywords: *Calcaneus, Functional Morphology, Locomotion, Primates, Paleogene*

The calcaneus plays a critical role in efficient foot movement required to navigate differing substrate conditions such as of the arboreal milieu. Therefore, we quantitatively studied the functional morphology of this bone in a large sample of extant primates using a novel 3D geometric morphometrics approach that combines anatomical landmarks along with curve and surface semilandmarks. To do so, we assessed the entire morphology of the bone as well as its different facets independently, such as the subtalar and transverse tarsal joints since they constitute functionally relevant regions within the foot. Allometric effects, phylogenetic signal and covariation between calcaneal shape and percentages of locomotor behaviour compiled from field studies were examined. Finally, representatives of the main Paleogene primate groups (plesiadapiforms, adapoids, omomyoids and stem anthropoids) were included in an exploratory analysis to assess their locomotor adaptations. Our results indicate significant allometry in the distal calcaneal region, with functionally informative departures from the allometric regression. Phylogenetic signal was found to be moderately low, thus hinting at an important functional signal. Calcaneal shape is strongly correlated with locomotor behaviour, either when the entire shape of the bone or its different facets are examined. This highlights the potential of this bone to extract reliable information regarding the locomotor behaviour of taxa for which only fragmentary remains are available. Lastly, the analysis including extinct species indicates that early primates displayed a wide range of calcaneal morphologies, suggesting that they engaged in a diverse array of locomotor behaviours early on in their evolutionary history.

PRIMARY OSTEOARTHRITIS RECORDS IN THE EXTINCT LAGOMORPH *PROLAGUS SARDUS* AND ITS LIFE HISTORY IMPLICATIONS

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Keywords: *eco-evolutionary adaptations, insular regimes, Lagomorpha, paleopathology, Sardinia*

The study of diseases, both human and nonhuman, in antiquity may discern novel biological details about extinct taxa. Current work in animal paleopathology has been limited to descriptions of exceptional abnormalities without quantitative reports at population level. In the present study, we examined 246 femora of *Prolagus sardus* (Ochotonidae, Lagomorpha) for evidence of primary osteoarthritis (pOA). The source of the specimens was from the renowned Dragonara cave, located in the north-western Sardinia, and dated back to the Late Pleistocene (22.390-21.910 ka cal BP). For each specimen, we established the age category and reconstructed the body mass, as well as evaluated hip and knee joints for pOA using high resolution radiographic and histological modalities. The prevalence of pOA in *P. Sardus* from Dragonara was 24.9%, particularly affecting hip joint, and its occurrence was associated with older age categories, but not with larger sizes. Morphologic features of thickened subchondral bones, irregular bone contours, partial collapse of the femoral neck and evidence of irregular bone composition, suggestive of adoptive modeling, were recognized in pOA-affected specimens. In femoral condyles, denser subchondral bone was suggestive of sclerosis. *Prolagus sardus* exhibited a pOA prevalence similar to that of domestic present-day rabbits, even

though it was a wild species and subjected to natural selection. A longer lifespan may be the main evolutionary trigger of the observed results, although other causes cannot be excluded. This study is framed within a comprehensive investigation which aims to unraveling the eco-evolutionary adaptations of extinct lagomorphs to insular regimes.

A NEW METHOD TO MODEL RARE SPECIES BY RELYING ON PHYLOGENY

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Keywords: SDMs, ENFA, mammals, climate change

Species distribution models (SDMs) are powerful tools with which to understand how environmental variation influences species geographical distribution. Although SDMs are widely used in ecology and applied conservation biology, they consistently lose accuracy precisely when they are needed the most, that is with rare species, originating the so-called rare-species modeling paradox. We overcome this issue presenting a new algorithm, ENphylo, developed for the R environment, which couples Environmental Niche Factor Analysis (ENFA) and phylogenetic imputation to model rare species. By using the fossil record of two large mammal species (*Rangifer tarandus*, a cold-adapted species, and *Sus scrofa*, a warm-adapted species) that lived during the late Pleistocene as the source data to sample from, we demonstrate ENphylo provides high predictive accuracy under different model evaluation metrics, when just 10 fossil occurrences are randomly drawn from their respective fossil records. ENphylo significantly outperforms ENFA and provides a fast and accurate solution to perform rare species distribution modeling, which will help predict their spatial distribution in the light of climate change, and to delineate how extinct species reacted to past climatic variation.

THE EARLY- MIDDLE PLEISTOCENE SORICIDAE (MAMMALIA) OF THE IBERIAN PENINSULA

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Keywords: *Post-Jaramillo, taxonomy, biometry, mandible, Europe.*

Soricids are small mammals that commonly appear in Pleistocene sites of the Iberian Peninsula. The soricids with a post-subchron-Jaramillo Early-Middle Pleistocene age currently cited in the Iberian Peninsula are: *Sorex minutus*, *Sorex* gr. *araneus-coronatus*, *Dolinasorex glyphodon*, *Neomys* cf. *fodiens* and *Crocidura russula*. Most of the records are indeterminate species due to the scant and fragmentary nature of the fossils. However, in other parts of Europe, there are up to ten different species of soricids in the same level.

The archaeo-paleontological locality of Gran Dolina (Burgos, Spain) is a cave infill dated to the post-Jaramillo Early-Middle Pleistocene where *D. glyphodon* was first discovered. We present a review and taxonomic attribution of the remaining soricid species from the whole stratigraphic sequence of Gran Dolina. Two-hundred fragmentary mandibles from levels TD4 to TD10 (recovered with washing-sieving methods during the 1991-2017 field campaigns), were photographed, described, measured and compared with data from other European localities. Nine taxa were identified in the Gran Dolina stratigraphic sequence: *S. minutus*, *Sorex* gr. *runtonensis-subaraneus*, *Sorex* (*Drepanosorex*) gr. *margaritodon-savini*, *D. glyphodon*, *Asoriculus*

gibberodon, *Neomys* cf. *newtoni* in the Early Pleistocene levels, and *S. minutus*, *S. gr. runtonensis-subaraneus*, *Neomys* cf. *fodiens*, *Neomyini* cf. *Macroneomys* and *C. kornfeldi* in the Middle Pleistocene levels. The biometric data shows extreme size values for the Gran Dolina taxa when compared to their counterparts in other regions of Europe, increasing the variability of these species.

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BITE TRACES, A POWERFUL TOOL IN PALAEOECOLOGY: THE CASE OF THE MIDDLE TRIASSIC LOWER KEUPER FOSSIL LAGERSTÄTTEN

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Keywords: *trace fossil, tetrapods, archosaur, feeding habits, Keuper*

Trace fossils, or ichnofossils, are important elements to understand the relationships and interactions of trace makers with the environment and/or with other organisms. In this regard, bite traces (commonly also known as “bite marks”) provide direct evidence on the feeding habits and potentially the ecological role of the bite maker, even in the cases in which it is not confidently identified. Bite traces are especially relevant for palaeoecological studies when coupled with other analyses, such as on taxonomy and taphonomy (including sedimentology). Here, we present a study on the bite traces present on tetrapod bones from the Lower Keuper fossil lagerstätten (Middle Triassic, S Germany). We identified nearly 200 bones and teeth with at least one bite trace (usually being more). We created a workflow for the documentation of bite traces, which includes: (1) morphological descriptions (ichnotaxonomy), (2) associations between bite trace morphotype, (3) location on the bones, (4) orientation of the traces on the bones. Such database allowed performing statistical analyses, creating “biting spaces” according to the bitten taxon, bone type and bone region. Derived interpretations on feeding behaviour were contrasted and confirmed with analyses on the tooth macroscopic wear and microanatomy of the bite maker, which was confidently identified coupling tooth and bite trace morphologies. In the Lower Keuper ecosystems, the pseudosuchian archosaur *Batrachotomus* was the top predator, showing scavenging, predatory and cannibalistic behaviours and mostly feeding on the giant temnospondyl

Mastodonsaurus. Comparisons with the bite trace record suggest a conserved feeding ecology among pseudosuchians, including present-day crocodylians.

PALAEOENVIRONMENTS AND TAPHONOMY OF THE KUPFERZELL VERTEBRATE LAGERSTÄTTE (MIDDLE TRIASSIC, S GERMANY)

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Keywords: *tetrapods, sedimentology, petrography, ecosystem, Keuper*

The Middle Triassic epoch witnessed a flourishing of ecosystems, with the radiation of several vertebrate lineages, eventually dominated by archosaurs. Fossil sites in terrestrial settings from this time interval, even if known from all continents, still hold unresolved questions regarding the evolution of faunas and their significance in the recovery during the aftermath of the end-Permian mass extinction and the evolution of some tetrapod groups. In order to fill this void of knowledge, we are carrying out studies on the sedimentology and taphonomy of the vertebrate fossil lagerstätten from the Lower Keuper (Ladinian, S Germany). In the present work, we focus on the singular Kupferzell locality, which delivered ~30,000 vertebrate remains in a 3-month-long salvage excavation in 1977 during road construction. We reconstructed the stratigraphic succession of the main excavation site with the aim of unravelling the palaeoenvironmental evolution of relatively complex ecosystems, which included different top predators. The bulk of the fossil material corresponds to two temnospondyl amphibians (*Gerrothorax*, ~70%; *Mastodonsaurus*, ~30%), with the archosaur *Batrachotomus*, ranging first among the other tetrapod remains, and a relatively high diversity of fishes. The sequence consists of: basal coaly mudstones, massive siltstones, green siliciclastic mudstones, yellow-brown carbonate claystones-marlstones, and massive dolostones. They represent the succession of relatively similar water bodies, some with characean meadows and ostracodes, from a lacustrine setting with recurrent marine influence. Drought periods marked the remodeling of environments and development of different faunal assemblages. The complexity

of vertebrate communities suggests recovery of ecosystems, with faunas adapted to changing environments.

A RE-EVALUATION OF THE NOTOSUCHIAN CROCODYLIFORM *EREMOSUCHUS ELKOHOLICUS* FROM THE EARLY EOCENE OF NORTH AFRICA AND THE PHYLOGENETIC RELATIONSHIPS OF SEBECOSUCHIANS

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Keywords: *Notosuchia*, *Sebecosuchia*, *Eremosuchus*, *Crocodylomorph*, *Systematics*

Notosuchian systematics have been highly debated in the past few decades, particularly regarding the placement of sebecid sebecosuchians, the only putative notosuchian taxa to have survived the Cretaceous/Paleogene mass extinction event, 66 Ma. Reconciliation of any conflicting views on notosuchian relationships through standardized approaches to character construction and improved taxon and character sampling is therefore required. Here, we redescribe the type material of *Eremosuchus elkoholicus*, a largely neglected species from the early Eocene of Algeria, as well as undescribed remains from the same locality that potentially represent a juvenile of this species. Both specimens are incorporated into one of the largest notosuchian-focused character-taxon matrices yet to be compiled, comprising 453 characters and 124 taxa. Particular focus is placed on increasing the sampling of sebecosuchians, especially the frequently neglected fragmentary remains from Europe and North Africa. Continuous characters relating to the mandible are implemented for the first time in a notosuchian-relevant dataset, increasing the sampling of mandibular characters by ~20%. All discrete mandibular characters are reassessed to improve consistency of scoring. Analyses are run under multiple weighting schemes including equal weighting and extended implied weighting. In all treatments, *Eremosuchus* is recovered within Sebecidae, as the sister taxon to *Lorosuchus nodosus*, from the Paleocene of Argentina. Given the sparsity of sebecosuchian remains in Northern Africa during this time interval, this taxon provides an important datapoint in elucidating the dispersal and radiation of the clade, which is particularly pertinent considering the ongoing fragmentation of Gondwana during the Late Cretaceous and Paleogene.

PHYLOGENETICAL ISSUES WITHIN THE SUPERFAMILY CTENODACTYLOIDEA

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Keywords: *Small mammals, Ctenodactylids, Oligocene, Miocene, parsimony*

During the last decades, there have been different phylogenetic approaches regarding the Ctenodactyloidea superfamily. Several molecular phylogenies pointed out the paraphyly of this group and propose the “Ctenohystrica” clade. Several morphological phylogenies have proposed different cladistic positions for the different genera included in this superfamily.

For the first time, we proposed the most complete morphological phylogeny referring to this superfamily, trying to clarify the position and relationships between and within the different genera. To do that, we performed a parsimony phylogenetic analysis with more than 40 species and 63 characters related to the dental and cranial remains. These remains comprise a sample that comes from five geographical regions (East Asia, Central Asia, Western Asia, Europe and Africa) and recorded from the Eocene to the Holocene.

Our results show ctenodactylids are recorded for the first time in East Asia during the Eocene and since that date, the species flourished and spread out through Western Asia, Europe and Africa and became one of the dominant rodents groups of the Oligocene. In relation to the morphological trends of this group, these species show an increase in the hypsodont pattern coinciding with a climatic change during the Oligocene-Miocene transition. Concerning the phylogenetic position of the species, we have clarified the relation between the European and African ctenodactylids and the relation between the extant ctenodactylids and extinct distylomyids.

ON THE DIAGNOSIS OF *IBEROSUCHUS MACRODON* (CROCODYLIFORMES, NOTOSUCHIA) FROM THE EOCENE OF PORTUGAL

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Keywords: *Notosuchia*, *Zipodont*, *Eocene*, *Europe*,

Laurasian notosuchians are a singularity within the record of crocodyliforms and, particularly, medium-large notosuchian zipodonts outside Gondwana are restricted to the Eocene of the Iberian Peninsula and Southern France. The best-known set of these notosuchians is composed by remains from the Eocene of Portugal, Spain and France that are usually related to the Portuguese form *Iberosuchus macrodon*, although they are not synchronous and have a relatively wide distribution in time (Lutetian to Bartonian)

Since the holotype of *Iberosuchus macrodon* is restricted to the anterior portion of a rostrum from the Eocene of Vale Furado (middle Eocene, Lutetian. Portugal) and no other material is known from the Portuguese record, the assignment of other specimens from Spain and Southern France, and thus the characterization of this crocodile from attributed material, should be taken with caution.

In fact, in the holotype of *Iberosuchus macrodon* only a series of characters that are common to many notosuchians (and particularly to the baurusuchids) are identified. The only recognized automorphic character on the rostrum of specimens attributed to *Iberosuchus* outside Portugal is a large premaxillo-maxillary palatal fenestra associated with a complex palatal fossa. This character could not be confirmed directly in the holotype of *Iberosuchus* because most of this structure is internal or hidden by a plaster filling placed during preparation.

A CT-Scan of the *Iberosuchus* holotype has been carried out to describe in detail its rostral anatomy, both to evaluate its diagnostic capacity, and to compare it with those of specimens from the Spanish record.

NEW MATERIAL OF THEROPODS (ABELISAUROIDEA?) FROM LO HUECO (LATE CRETACEOUS. CUENCA, CENTRAL SPAIN)

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Keywords: *Dinosauria, Theropoda, Mesozoic, Iberoarmorica,*

To date, theropod diversity from the Late Cretaceous of the Iberian Peninsula is still far from being well established, mainly because these dinosaurs are represented by very isolated remains. Up to now, the known diversity is composed of several taxa attributed to different groups of coelurosaurs and by medium-sized primitive forms whose characters are congruent with abelisauroid ceratosaurs. The Lo Hueco fossil-site (Campanian-Maastrichtian of Cuenca, central Spain) has provided an abundant record of titanosaur sauropods, crocodyliforms and testudines, in which the presence of ornithischian and theropod dinosaurs is scarcer. However, among the latter, teeth, and postcranial material of coelurosaurs are common in the fossil-site, but remains of non-coelurosaurian forms are rarer and so far, only a few teeth and one metatarsal have been previously described.

A discussion about a theropod posterior caudal vertebra from Lo Hueco is proposed. This vertebra presents some singular characters, some of them shared with members of Abelisauroidea. Centrum is amphicoelous and does not present transverse processes nor pleurocoels. The neural spine is extremely thin and, in lateral view, is relatively tall, triangular, and caudally positioned. Prezygapophyses are relatively short, postzygapophyses are very reduced and a shallow longitudinal groove is present along the ventral face of the centrum. This combination of features is compatible with those of some basal abelisauroids, providing new information for the discussion on the relationships of the non-coelurosaurian theropods from the Late Cretaceous of the south of the Ibero-Armorican domain.

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LIGHTS AND SHADOWS IN THE EVOLUTIONARY DYNAMICS OF THE PLEISTOCENE SARDINIAN MAMMOTH POPULATIONS

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Keywords: *Mammuthus lamarmorai*, *chronology*, *histology*, *population extirpation/extinction*.

The fossil record of the Sardinian proboscideans mainly consists of isolated remains found in sites ranging in age from the late Middle to the Late Pleistocene (an incomplete skeleton from Guardia Pisano, isolated remains from different localities, and some footprints from Funtana Morimenta) that have been ascribed to a single species of endemic, moderately reduced-in-size mammoth, *Mammuthus lamarmorai*. The paucity of remains, the different sizes of molariform teeth from different localities, the lack of dental remains at Guardia Pisano and the uncertainties about the chronology of some remains hamper any attempt to infer whether one or more species, originated by an anagenetic evolutionary process or by multiple arrivals from the mainland, inhabited the island. Therefore, the continental ancestor/ancestors of Sardinian mammoth populations, the time and number of dispersals of the ancestral taxon/taxa, the actual number of mammoth species that inhabited Sardinia, as well as the persistence through time of these populations still remain unsolved issues, due to the low number of findings and the imperfect chronological constraint of some remains.

This research aims to put out and discuss the main issues related to the actual number of mammoth species that inhabited Sardinia, the time and number of dispersals of the ancestral taxon/taxa, the morphological and dimensional differences shown by tooth remains, the dynamics of Sardinian mammoth populations and their persistence through time, and the possible causes of the populations' decline and disappearance, as well as preliminary data on the histological characteristics of a Sardinian mammoth long bone.

THE ENDEMIC GIRAFFID FROM THE *OREOPITHECUS*-FAUNAL ASSEMBLAGES OF THE TUSCO-SARDINIAN ARCHIPELAGO (LATE MIOCENE, ITALY)

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Keywords: *Giraffoidea, morphology, morphometry, phylogeny*

Over the past decades, numerous studies have been aiming to reconstruct the evolution of endemic mammals from the Late Neogene of the Tyrrhenian area in the Western Mediterranean Basin. Despite these efforts, however, no conclusive evidence has been provided yet to confidently address the debate about the origin of some of the species characterising the *Oreopithecus*-faunal assemblages of the Tusco-Sardinian archipelago. An emblematic case is the enigmatic giraffid-like *Umbrotherium azzarolii*. The occurrence of this mammal has been so far documented by the single type specimen from Casteani (V1 faunal assemblage) in Tuscany, and by the sample from the slightly younger locality of Fiume Santo (V2 faunal assemblage) in Sardinia. Despite the presence of teeth, an exhaustive diagnosis of *Umbrotherium* was not firmly established and its phylogenetic position remained unresolved. Albeit no new specimens, nor new localities yielding these taxa have been recently discovered, recent archival research at the Natural History Museum of Basel and the Department of Earth Sciences of the University of Florence (under the PalAss grant n. PA-SB202103) enabled to re-discover unpublished remains of giraffids, including an almost complete mandible, several isolated teeth and other cranial remains from the localities of Botro della Canonica and Serrazzano (Pisa). The new material shed lights on the morphological and morphometric variability of *Umbrotherium*, enabling a comparison between specimens collected from different Tusco-Sardinian Miocene localities spanning from V1 to V2 *Oreopithecus*-faunal zone. Phylogenetic affinities are investigated to detect a possible ancestor of this endemic taxon and reconstruct its dispersal route.

MORPHOLOGICAL CONVERGENCE IN THE HINDLIMB SKELETON WITHIN TITANOSAURIA

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Keywords: *Titanosauria, Geometric Morphometrics, Hindlimb, Phylomorphospaces.*

The hindlimb of Ibero-Armorican lithostrotian sauropods exhibits morphological similarities between the different proposed clades present in the Campanian-Maastrichtian. Comparison with other Late Cretaceous titanosaurs revealed that these similarities can be found between groups that are recovered apart in the phylogeny, with possible convergences in the shape of the elements of the forelimb and hindlimb zeugopodium. In this study, we analyzed the morphology of the main hindlimb elements (femur, tibia, fibula) in anatomical position via 3D-geometric morphometrics to assess the variability within Neosauropoda and to test if there is morphological convergence between different subclades. The hindlimb is also the main support for the sauropod body mass, therefore we tested if there was an allometric effect within phylogenetic context and explored the common allometric component. Our results indicate that there are wide morphological similarities between different Somphospondyli subclades after the acquisition of the wide gauge posture. Variation occurs mostly in the zeugopodium, as found in previous analyses based on the separated elements without more basal neosauropods. The occupation of the different areas of the morphospace is independent of the phylogeny. This morphological convergence may not be exclusively related to the evolutionary cascade towards gigantism, as there is a small, non-significant relationship between the shape and the hindlimb size in the analyzed sample.

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AN ICHTHYOSAUR BREEDING GROUND IN SOUTHERNMOST GONDWANA (TYNDALL GLACIER, SOUTHERN CHILE)

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Keywords: *Ichthyosaurs, Early Cretaceous, Chile, breeding, taphonomy*

Since 2004, paleontological expeditions have been conducted to the Tyndall Glacier in Torres del Paine National Park, Chilean Patagonia, resulting in the discovery of almost a hundred ichthyosaur skeletons to date. The ichthyosaurs are exposed in the rocks as a consequence of the ongoing melting of the glacier caused by climate change. Most of the ichthyosaurs in this locality are complete and articulated. Invertebrates such as ammonites and belemnites, as well as different types of fishes, have been found associated with the ichthyosaurs. According to a previously developed hypothesis, this area was used as a breeding ground for ichthyosaurs in southernmost Gondwana during the Early Cretaceous. To date, eight years since the hypothesis was published, we have yet to find marine reptiles other than ichthyosaurs, most finds corresponding to neonates and small juveniles. Pregnant females have also been recorded. These data, in addition to the abundance of food and the apparent absence of predators, allow us to support the idea of a breeding ground. The discovery of glendonites, correlated with cold to freezing water conditions, suggest that the site may have only been inhabited during summer months. Regarding taphonomy,

many of the skeletons have skulls that penetrate the sedimentary layers, indicating headfirst arrival at the seafloor. Several skulls show breakage consistent with high speed collision with the bottom. The frequency and depth of embedded skulls suggest relatively soft sediments at the sea floor.

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LATEST EARLY PLEISTOCENE *DAMA*-LIKE CERVID REMAINS FROM CAL GUARDIOLA AND THE TANGLE OF VILLAFRANCHIAN CERVID TAXONOMY

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Keywords: *Villafranchian, Early Pleistocene, Cal Guardiola*

The taxonomy and phylogeny of the small to mid-sized Plio-Pleistocene cervids of Europe, commonly known as *Dama*-like deer, have been a matter of vast dispute, as specimens referred to this group have been attributed to multiple genera such as: *Dama*, *Pseudodama*, *Axis*, *Euraxis*, *Rusa* and *Metacervocerus*. Here we present a preliminary study of 305 cervid remains from the site of Cal Guardiola (CGR), consisting of 157 craniodental and 148 postcranial elements. The site of CGR, along with the nearby site of Vallparadís Estació (EVT), are correlated along the Vallparadís Section, cropping out in the western bank of the Torrent de Vallparadís (Terrassa, Vallès Penedès Basin, Iberian Peninsula). The CGR section consists of two units separated by an erosional surface, and it hosts seven fossiliferous layers spanning in age from 1.2 to 0.86 Ma. Both quantitative and qualitative morphological comparisons of the studied cervid material from CGR allow us to attribute it to the Plio-Pleistocene *Dama*-like group of deer. The antler morphology from the CGR cervid, in particular, resembles those from Capena, Pietrafitta, Redicicoli and Collecorti (Italy), Le Vallonet (France) and Untermassfeld (Germany) which have been attributed to a variety of taxa that we can group in two clusters/taxa/species: *Pseudodama farnetensis* and *Pseudodama vallonetensis*. Our results support an attribution of the CGR specimens to *Pseudodama vallonetensis*. The present study helps clarifying/to clarify the taxonomic status of European Plio-Pleistocene *Dama*-like deer as well as to re-evaluate the geographical and chronological distribution of this group in the Mediterranean area.

LIMB DEVELOPMENT IN EARLY TETRAPODS: INSIGHTS FROM MACROEVOLUTIONARY PATTERNS OF LIMB PROPORTIONS

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Keywords: *Lissamphibia, pre-axial polarity, skeletogenesis*

Limb skeletogenesis in living anurans and amniotes is characterized by a proximo-distal progression and a post-axial polarity in digit development. In contrast, in salamanders, distal mesopodial elements form early and digits follow a preaxial-polarity. The salamander mode of limb development has been also documented in Paleozoic temnospondyls (i.e., the putative stem-group of lissamphibians) based on exquisitely preserved early ontogenetic series. However, it is still unclear which of the two developmental modes is ancestral for Tetrapoda. Given the lack of fossilized early stages of Paleozoic groups other than temnospondyls, other approaches are needed to address this issue. Interestingly, amniote limb proportions follow a very conservative pattern (i.e., occupy a restricted region of the theoretical limb morphospace) that is predicted from activation-inhibition dynamics during limb proximo-distal patterning. Taking this into account, we quantified limb proportions in salamanders, anurans, and Palaeozoic tetrapods to test whether they depart from what is documented in amniotes and, in turn, to explore whether limb proportions might be informative of limb developmental polarity in fossils. We found that, matching the pre and post-axial modes, anurans overlap in the limb morphospace with amniotes, whereas salamanders and temnospondyls share a different region. Surprisingly, all the Paleozoic taxa sampled, including stem tetrapods and putative stem amniotes, clearly overlap in the morphospace with salamanders and temnospondyls. These results suggest, in agreement with recent evo-devo studies, that the limb developmental mode of salamanders might be plesiomorphic for Tetrapoda and that post-axial polarity might have evolved independently in Anura and within Amniota.

A NEW MEMBER OF ERYMNOCHELYINI (TESTUDINES, PLEURODIRA) FROM THE EARLY PLIOCENE OF CENTRAL AFRICA

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Keywords: *Podocnemididae, Erymnochelyinae, Sinda-Mohari region, Democratic Republic of Congo, early Zanclean*

The pleurodiran turtle *Erymnochelys madagascariensis* (the ‘Madagascan big-headed turtle’) is the only representative of Erymnochelyini (Pelomedusoides, Podocnemididae) that is part of the current biodiversity. *Erymnochelys* was traditionally used as a wastebasket taxon, but the extant species from Madagascar is currently considered as the only valid representative of the genus. In the early 1990s, the remains of several groups of turtles were reported in some Early Pliocene (Zanclean) outcrops of the Sinda beds, in the Sinda-Mohari region of the Democratic Republic of Congo. Among them, several postcranial elements were attributed to *Erymnochelys* sp. Unpublished cranial remains from that locality, exclusively corresponding to the anterior area of the skull, were subsequently cited in papers published over the subsequent two decades. These specimens were recognized, without justification, as compatible with the extant *Erymnochelys madagascariensis*. Knowledge about the extinct representatives of the Erymnochelyini lineage has increased remarkably in recent years. In fact, most of them correspond to genera defined in the 21st century. In this sense, the attribution of the taxon from the Sinda-Mohari region to the genus *Erymnochelys* has been recently indicated, without justification, as incorrect. The study of abundant and well-preserved cranial material from this Pliocene locality, not only corresponding to the anterior region of the skull but also to elements that make it possible to know most of the cranial anatomy, allows me to justify its attribution to a new taxon. It corresponds to the only extinct member of Erymnochelyini represented in the Neogene record by more than one skull.

CRANIAL ANATOMY OF THE IBERIAN CENOMANIAN BOTHREMYDID TURTLE *ALGORACHELUS PEREGRINA*

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Keywords: *Pleurodira, Bothremyidae, Skull, Late Cretaceous, Spanish record.*

The European bothremydid turtle *Algorachelus peregrina* (Bothremydini) is one of the oldest representatives of the crown Pleurodira known in Laurasia. The species has been identified in several Iberian Cenomanian outcrops, both in Portugal and in Spain. A partial shell of a single individual has been found in most of these sites. By contrast, hundreds of remains, attributable to dozens of individuals, have been identified at its type locality: the uppermost middle or lowermost upper Cenomanian site of Algora (Guadalajara Province, Central Spain). In fact, Algora have provided the largest concentration of vertebrate macroremains for the Cenomanian of southwestern Europe so far known, this turtle being the most abundant taxon there. Numerous plates of *Algorachelus peregrina* from Algora have been analyzed so far, in addition to several complete or almost complete shells, not only providing detailed information about its shell anatomy, but also about its intraspecific variability. Several appendicular elements are also known. However, the cranial information so far available are exclusively based on a partial skull. A complete and very well-preserved skull from Algora is here presented. Both the previously known partial skull and the new complete one have been scanned. The three-dimensional reconstruction of each skull, as well as that of each of the bones that compose them, has been carried out. Thus, the detailed anatomy of the skull of *Algorachelus peregrina* can be characterized. This allows us to noticeably improve the encoding of the species in the data matrices and, therefore, to provide new information about its phylogenetic position.

THE HOLOTYPE OF *HYLAEOCHELYS KAPPA* IS NO LONGER THE ONLY KNOWN SPECIMEN FOR THIS TURTLE GENUS IN THE JURASSIC RECORD

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Keywords: Late Jurassic, Lusitanian Basin, Portugal, Testudinata, Thalassocheilydia.

Turtle remains are very abundant in the Upper Jurassic (Oxfordian to Tithonian) record of the Lusitanian Basin (West-Central Portugal). The best represented lineage, especially considering its diversity, is that of the aquatic turtles Thalassocheilydia. Thus, several members of the coastal marine clade Plesiocheilyidae have been identified there, through relatively numerous finds since the 19th century. However, a member of Thalassocheilydia not attributable to Plesiocheilyidae was recently identified in the Lusitanian Basin. It corresponds to a representative of *Hylaeochelys*. Previously, the presence of this freshwater genus had been exclusively confirmed for the British Lower Cretaceous record. In fact, *Hylaeochelys* corresponds to the only representative of Thalassocheilydia found in post-Jurassic levels. *Hylaeochelys* is known in the Portuguese record by a single specimen, corresponding to a partial articulated shell. It displays several character states that allowed its attribution to a different species: *Hylaeochelys kappa*. Therefore, knowledge about the *Hylaeochelys* taxon represented in the Jurassic levels is currently very limited. New data are provided here by the study of two new specimens of this genus from the Upper Jurassic levels of the Lusitanian Basin. Each of them comes from a different locality that are not the type locality of *Hylaeochelys kappa*. One of these individuals corresponds to a partial articulated shell, which preserves some regions not represented in the holotype of that species. The other is a disarticulated partial shell, which provides data on the variability of the genus in Portugal.

GIANT SHADOWS IN LATE TRIASSIC SEAS: HISTOLOGICAL ANALYSIS ON PUTATIVE AND GENUINE GIANT ICHTHYOSAURS BONES

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Keywords: *histology, ichthyosaurs, Rhaetian, Shastasaurus sikanniensis, Parallel-Woven complex*

Large to very large unidentified fossil bone shafts from European Late Triassic deposits have been puzzling the paleontological community since the second half of the 19th century. Over the centuries, differing hypothesis have been proposed regarding the nature of these fossils: amphibian, ichthyosaurian and dinosaurian/archosaurian. In this study a comprehensive histological description and comparative analysis was conducted to test what we coin as the “*Huene-Lomax hypothesis*”; i.e. an ichthyosaurian affinities for large bone fragments of uncertain origin recovered from different Rhaetian fossil localities across Europe. Resulting histological comparison of the material in exam, including the Norian holotype of *Shastasaurus sikanniensis*, found a common combination of unusual histological features (e.g. Parallel-Woven complex rich in Interstitial Structural Fibers and preferential secondary remodeling through “*double-zoned*” osteons) shared with bonafide giant ichthyosaurs. Our study is therefore unable to find histological evidence to reject the *Huene-Lomax hypothesis*, further supporting the widespread presence of large sized ichthyosaurs at the Tr-Jr boundary. Finally, the aforementioned shared histological features, suggests the presence of a yet-to-discover biological or phylogenetic signal possibly related to the acquisition of large sizes in gravity-free aquatic environment or to specific niches occupation in late Triassic ichthyosaurs.

FEET REFINE THE ECOLOGY OF EARLY THEROPOD FLYERS

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Keywords: *early flyers, theropods, ecology, feet, soft tissue*

The feet of modern birds are closely correlated to their ecology. Their toe pads, foot scales, joints and claws reflect their cursoriality, feeding mode and grasping ability. To reveal these ecological characteristics from the feet of early theropod flyers, we present equivalent fossil evidence in the form of soft tissues surrounding the bones. The ecology of the earliest theropod flyers has been studied using their anatomy, diet and locomotor capabilities as well as the environments and climates they lived in. Our results are interpreted in the context of these existing lines of evidence. The earliest theropod flyers including *Anchiornis* and *Archaeopteryx* from the Middle-Late Jurassic had feet indicating a more ground-dwelling lifestyle. In the Early Cretaceous aerial lifestyles diversified, including generalists such as *Confuciusornis* and specialists such as the climbing *Fortunquavis*. Some early birds had complex ecologies that were seemingly unique among modern birds e.g., the Berlin *Archaeopteryx* and the Early Cretaceous *Sapeornis*. Unexpectedly, the non-avian flyer *Microraptor* was recovered with a more specialised raptorial lifestyle featuring

hawk-like characteristics rare among theropod flyers of the time. This suggests that non-avian flyers like *Microraptor* were specialists, similar to certain birds in modern ecosystems.

PALEONEUROANATOMY OF THE CENOMANIAN CROCODYLOMORPH, *PORTUGALOSUCHUS*

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Keywords: *Crocodylomorpha, Eusuchia, neurosensorial capabilities, Late Cretaceous, Portugal*

Thanks to CT technology, advances in paleoneuroanatomy have grown remarkably since the beginning of the 21st century. In this context, we present the first neuroanatomical study of *Portugalosuchus azenhae* from the Cenomanian of Portugal. This eusuchian crocodylomorph was originally described as a putative Crocodylia and one of the oldest representatives of this clade. Based on new data obtained from micro-CT images, and in order to test this hypothesis, this study aims to improve the original description of this taxon and update the scarce neuroanatomical knowledge of eusuchians and crocodylians from this time interval. The resulting 3D model allowed a detailed description of its very well-preserved neurocranium that helped to correct and complete some of the original observations. These new anatomical data were included in one of the most recent morphology-based phylogenies. The position of *Portugalosuchus* differs slightly from the original publication since it is now located as a thoracosaurid within Gavialoidea, but still as a crocodylian. It was also possible to reconstruct the cavities of the olfactory region, nasopharyngeal ducts, brain, nerves, carotid arteries, blood vessels, paratympanic sinus system, and inner ear which allowed an estimation of its neurosensorial capabilities. By comparison with other crocodylomorphs, these analyses showed that *Portugalosuchus* displayed olfactive acuity, sight, hearing, and cognitive skills within the range of that observed in other basal eusuchians and

crocodylians. Despite all this, in order to better constrain these results, additional phylogenetic analyses, including this new morphological character coding, together with DNA data should be performed.

DENTAL VARIATION IN *HYPNOMYS MAHONENSIS* BATE, 1918 (GLIRIDAE, RODENTIA, MAMMALIA) FROM THE NEWLY REDISCOVERED TYPE-LOCALITY

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Keywords. *Insular Evolution, Menorca's third stage of fauna, Pleistocene, Chronospecies, Independent phylogenetic lineage.*

Punta Esquitxador 17 is a small coastal site of karstic origin, formed by very hard red silt, rich in remains of small vertebrates. This is the same site from which Dorothea M. A. Bate recovered and described, in 1918, *Hypnomys mahonensis*. The limited number of specimens of the type series (a left maxilla, a right mandible and an M1) has, historically, limited the adequate knowledge of this species. The recovery of new remains has allowed us to describe the different dental morphotypes characteristic of *H. mahonensis* and their comparison with other species of the genus. Overall, *H. mahonensis* has simpler tooth patterns than *Hypnomys morpheus*, with isolated ridges in upper M1. Moreover, *H. mahonensis* displays a small transverse ridge connecting the anteroloph and protoloph. This is a derived feature absent in *H. morpheus*. Two hypotheses have been put forward to explain the origin of *H. mahonensis*: 1) is considered the final representative of a phyletic lineage originating in Menorca; 2) *H. mahonensis* evolved from the arrival to Menorca of a late representative of the existing phylogenetic line in Mallorca (*H. morpheus*). This study also made possible to confirm the taxonomic validity of *H. mahonensis* and its geographical and temporal distribution.

NEW THEROPOD REMAINS FROM THE LATE JURASSIC CAÑADÓN CALCÁREO FORMATION OF CHUBUT, ARGENTINA

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Keywords: *Late Jurassic, South America, Theropoda, Coelurosauria*

Late Jurassic theropod dinosaurs from the former continents of Gondwana are still very poorly known. From South America, only two taxa have been named so far, the poorly known early branching tetanuran *Pandoravenator*, and the enigmatic *Chilesaurus*. Whereas *Pandoravenator* is so far only known from the very fragmentary holotype, which does not allow to establish its phylogenetic position confidently, *Chilesaurus* shows a unique combination of characters that has even led to suggestions that this taxon is not a theropod at all. Recent fieldwork in the Oxfordian-Kimmeridgian Cañadón Calcáreo Formation of Chubut, Argentina, have led to the discovery of several new theropod specimens. One represents a second specimen of *Pandoravenator*, and provides additional evidence on the anatomy of this taxon, including the first cranial remains. This new material helps to establish *Pandoravenator* as an early branching coelurosaur, representing the first representative of this clade known from the Jurassic of the southern hemisphere. A new taxon of small theropod dinosaur is represented by at least three partial, articulated skeletons, which together represent most parts of its anatomy. The pelvis resembles that of *Chilesaurus* in being opisthopubic, with a relatively low, simple ilium. Likewise, the fore- and hindlimbs also resemble those of *Chilesaurus*, although the foot is more typical theropodan in that the first metatarsal does not reach the ankle joint. The skull is unusual in being rather short and broad, with an extremely short snout and an apparently herbivorous dentition, whereas the cervical vertebrae closely resemble those of elaphrosaurine noasaurids.

BALEEN WHALES IN MATERA BASIN: PALEOENVIRONMENTAL AND BIOSTRATIGRAPHIC RECONSTRUCTION AS REVEALED BY COCCOLITH ASSEMBLAGES

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Keywords: *Baleen whales, calcareous nannoplankton, Matera Basin, Central Mediterranean*

Blue whales (*Balaenoptera musculus*) are the largest living mammals and the largest known animals ever appeared on the Earth to date. *Balaenoptera musculus* plays a pivotal role in modern ocean ecology as it is a major consumer. On the other hand, ecological and oceanographic feedback processes may influence baleen whales size, thriving and migration paths. Recently, a Mysticete partial skeleton (sharing multiple traits with extant *Balaenoptera musculus*) was retrieved near Matera, buried into the early Pliocene to middle Pleistocene foredeep deposits of the Bradanic Trough, southern Italy. The fossil was previously dated at 1.5 – 1.3 Ma.

Here, we attempt at reconstructing the ecosystem in which this huge mammal died, and was successively buried, using coccoliths. These have been widely used for biostratigraphic purposes in the central Mediterranean, with several recognizable event. Analysis of the calcareous nannoplankton fraction throughout the sedimentary succession of the Matera Basin may be useful to corroborate radiometric age data. Besides, coccolithophore association analysis can yield a broad range of information about the paleoecological/paleoceanographic environment in which this Pleistocene analogue of modern days blue whale dwelled. The aim of this work is to shed light on the timing of the onset of whale gigantism in the Mediterranean and its relationships with paleoecological and paleoceanographic changes in the study area.

BODY SIZE IN THE INSULAR MURID *MIKROTIA* FROM GARGANO (LATE MIOCENE, ITALY)

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Keywords: insular evolution, body mass, Gargano, Mikrotia, gigantism

Body size is one of the main determining factors in a mammal's life strategy. Nowhere is this clearer than on islands, where mammals tend to change in body size compared to their mainland ancestors. This study focuses on such an island mammal, the giant rat *Mikrotia* (Muridae) of the Gargano palaeoisland of the Italian Peninsula. While the cranial and dental elements of *Mikrotia* have been studied elaborately, the postcranial skeleton was largely unexplored. In order to determine the body weight and locomotory habits of *Mikrotia*, we studied limb bone features and calculated indices of three species of *Mikrotia* from San Giovannino, one of the youngest fissures of the palaeoisland. Our results were then compared to those of extant rodents with known body masses and locomotion. The distal joint widths of femur and humerus are the most accurate for estimating weight, the femur length tends to overestimate body mass. Based on the distal joints, we estimate the body mass of the smallest *Mikrotia* species at 140 g, for the middle-sized species at 630 g and for the largest species at 1700 g. Body mass estimates based on limb bones of *Mikrotia* are much higher than those from earlier studies based on the lower incisor.

THE FIRST SIVATHERIINE (ARTIODACTYLA, GIRAFFIDAE) FROM THE MIDDLE MIOCENE OF PORTUGAL

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Keywords: *Samotheriinae, Sivatheriinae, Giraffidae, Miocene, Portugal*

The revision of the giraffid material stored at the Museu Geológico (Lisbon, Portugal) using current analytical tools and methods leads us to the first identification in Portugal of a member of the Samotheriinae-Sivatheriinae clade. The material consists of a metacarpal from Casais da Formiga, Azambuja (MG 5733, later Middle Miocene, MN 7: 13-12.5 Ma). Although previously tentatively assigned to *Palaeotragus* sp. due to size, several morphological features point to the specimen belonging to the widely distributed Samotheriinae-Sivatheriinae clade, whose earliest member recorded in the Iberian Peninsula is the Vallesian *Decennatherium* (MN 9-10). Giraffid metapodials have a high diagnostic value, and according to its morphology MG 5733 is most similar to *Decennatherium* (especially the proximal epiphysis and palmar diaphysis), which was present during the Vallesian (MN 9-10) in the Calatayud-Teruel, Duero, and Tagus basins. It is especially similar to *D. pachecoi* (MNCN-42769) from Los Valles de Fuentidueña, with the only relevant difference being a more dorsoventrally compressed proximal epiphysis in MG 5733. When compared to *Palaeotragus*, the condyles in *P. rouenii* are less developed and distally the diaphysis does not widen. The central trough is also deeper in *P. rouenii* and the proximal articular surface is on the same plane. A PCA analysis reveals this specimen as metrically falling between the ranges of variability of *Decennatherium pachecoi* and *Palaeotragus rouenii*. This is the first report of Sivatheriinae in Portugal.

STABLE ISOTOPE RECORD OF *TRICERATOPS* FROM A MASS ACCUMULATION (LANCE FORMATION, WYOMING, USA) PROVIDES INSIGHTS INTO *TRICERATOPS* BEHAVIOUR AND ECOLOGY

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Keywords: *Stable isotopes, seasonality, isoscapes, niche partitioning, bonebed*

Our understanding of Late Cretaceous dinosaur ecosystems from North America has considerably improved through stable isotope analyses on fossil bones and teeth. Oxygen and carbon isotopic compositions of structurally-bound carbonate in fossil teeth are commonly used to detect (temporal) variations in ingested water and food sources, which are in turn related to shifts in environmental and climatic conditions. So far, these reconstructions are based on spatiotemporally diverse datasets. Here, we present oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotopic records from a large well-constrained monospecific *Triceratops* bonebed from the Lance Formation (Wyoming, USA), allowing to elucidate the palaeoecology of these large herbivores in detail, as well as their habitat use, diet and possible migration. Depending on tooth size, three to eight incremental samples were taken from seven *Triceratops* teeth, revealing relatively low intra-tooth $\delta^{18}\text{O}$ variation (average 1.3 ‰), comparable to contemporaneous hadrosaurs and modern mammals. Ambient water temperature reconstructions based on associated gar scale $\delta^{18}\text{O}$ follow modern freshwater fish and comply with earlier temperature-proxies for the Late Cretaceous. Average $\delta^{13}\text{C}$ values (-5.2 ‰) are higher than in modern C3 plant grazers, but support the previously stated hypothesis of different metabolic fractionation in herbivorous dinosaurs. The combined $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ *Triceratops* isotope signatures indicate a living environment intermediate between inland forests

and coastal floodplains, which was previously believed to strictly adhere to hadrosaur and ceratopsian niche partitioning, respectively. Our dataset provides an accurate palaeoecological reconstruction for *Triceratops*, and highlights the need for spatiotemporally well-constrained fossil remains in isotope analyses and large-scale isoscape reconstructions.

A BASAL ANKYLOPOLLEXIAN DINOSAUR FROM THE LATE JURASSIC OF PORTUGAL AND ITS IMPLICATIONS FOR IGUANODONTIAN DIVERSITY

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Keywords: *Ornithopoda, systematics, phylogenetic analysis, Europe*

Historically, Portugal has been a hot spot for Late Jurassic dinosaur diversity and several institutions have been conducting fossil collections over the past few decades. Here we re-describe known specimens of basal ankylopollexian iguanodontians hosted at the Sociedade de História Natural (SHN) and Museu da Lourinhã (ML), and present novel interpretations. The material has been recovered from the Upper Jurassic Lourinhã Formation from various localities and has been figured and described already in peer-reviewed publications or other academic works. The specimens include: SHN.(JJS).015, associated scapula, humerus, femur and calcaneum; ML 434 isolated femur (previously regarded as *Draconyx loureiroi*); SHN.073 isolated femur; ML 2055 associated femur and partial tibia. These specimens share a bowed femoral shaft, high crest on the cranial surface of the shaft and pendant 4th trochanter of the femur with an extensive lamina projecting dorsally, and the difference in size suggests they represent different ontogenetic stages of the same species. With the abovementioned features, SHN.(JJS).015 presents a combination of characters which distinguish it from *Draconyx loureiroi* and other Late Jurassic ankylopollexians, such as: straight scapular blade, glenoid and deltoid fossa not strongly

separated. We modified published data matrices to explore the systematic affinities of this specimen. Employing maximum parsimony, we recover SHN.(JJS).015 at the base of Ankylopollexia. These results increase the diversity of Late Jurassic iguanodontians present in the Late Jurassic of Portugal, possibly reporting the first ontogenetic series for ankylopollexians in Europe. Further investigation on histology is needed to elucidate growth patterns in this clade.

3D LIFE RECONSTRUCTION OF THE INTRASPECIFIC VARIABILITY IN THE FOSSIL GIRAFFID *DECENNATHERIUM REX* RÍOS, SÁNCHEZ AND MORALES 2017 (LATE MIOCENE, IBERIAN PENINSULA)

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Keywords: 3D-reconstruction, ZBRUSH, Giraffidae, Late Miocene, intraspecific variability

The recovery of hundreds of skeletal remains of the extinct giraffid *Decennatherium rex* Ríos, Sánchez and Morales, 2017 from the Late Miocene deposits of the site Batallones-4 and Batallones-10 (MN 10, Cerro de los Batallones, Madrid Basin) sheds light on the complex intraspecific variability of the fossil giraffid. Here we reconstruct for the first time a hypothetical herd including all the morphological variability recovered in the Batallones sample. Using Zbrush, which allows for digital 3D modelling, sculpture and painting we were able to show through a paleoartistic approach the wide range of ontogenetic and sexual variability present in this taxon. The results include an accurate representation of its paleohabitat and cranial and postcranial morphological variability with several scenes including females, juveniles and older males. Fur colour was inferred using knowledge of the ecosystem and actualism principles.

THE LARGE, THE SMALL AND THE UNUSUAL – A NEW, MULTISPECIFIC TANYSTROPHEID ASSEMBLAGE FROM SOUTHERN POLAND

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Keywords: Lower Keuper, Tanystropheus, Triassic, Ladinian, Archosauromorpha

Many long-necked non-archosauriform archosauromorphs are grouped in the family Tanystropheidae. In the Triassic this group diversified and achieved evolutionary success, occupying disparate ecological niches over a wide geographical range. The main factor thwarting the progress of research on some of the tanystropheids, is the state of preservation of their remains. These fossils are predominantly found 1) three-dimensionally preserved, but isolated and in limited numbers or 2) articulated and largely complete, but flattened.

In this study, we report new three-dimensionally preserved material, including numerous remains of the largest *Tanystropheus* individuals and other articulated specimens; cervical vertebrae of a much smaller *Tanystropheus*, as well as a vertebra of another, yet unidentified, tanystropheid. The specimens have been acquired from the Miedary site in Upper Silesia (Poland). It is the only existing large-scale outcrop of the Lower Keuper sediments in the eastern part of the Germanic Basin. Faunistically, it shares many similarities with other Ladinian sites, especially those located in Germany. This resemblance is supported by the presence of tanystropheids. Co-occurrence of multiple tanystropheid taxa in a single locality has been reported from the Monte San Giorgio area (Italy/Switzerland), the Xingyi Fauna (China) and possibly Vellberg (Germany) and Maktesh Ramon (Israel) sites. The Miedary site exposes a unique chance to explore that phenomenon and uncover the anatomical factors responsible for the evolutionary success of tanystropheids.

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A NEW DIGITAL TOOL FOR STUDYING SMALL TETRAPOD FOOTPRINTS

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Keywords: *photogrammetry, 3D optical scanners, footprints, Permian, DEM*

Since the early 2000s, digital photogrammetry has become increasingly popular in ichnology. Such approach has enabled the digitisation of footprints and the objectivisation of data collected in the field. In particular, the opportunity to analyse the footprints through colour-coded images represents a powerful tool to highlight the morphological characters preserved in the tracks. This approach has been used in the recent study of almost all medium- and large-sized tetrapod footprints. In contrast, photogrammetry or other 3D application for centimetric and millimetric footprints is sparse and limited. In this contribution, we introduce the use of optical scanners with blue light technology in ichnology. This tool allows high-resolution scans with the production of closed double precision polygonal mesh. It also offers multiple advantages in addition to the very high-resolution model, with a significant reduction in data acquisition and processing time compared to photogrammetry.

Here we present preliminary results of the application of this new technology to several very small Permian footprints from the Museum of Nature South Tyrol (Bolzano, Italy) collection. Three-dimensional data were acquired using both scanners and traditional photogrammetry and the results were compared highlighting the huge resolution improvement obtained using scanners. We developed a new extensive workflow compatible with file type generated by the scanner's proprietary software to produce colour-coded image (e.g., Digital Elevation Model). The obtained

digital elevation models, allow to ensure a new level of detail in the interpretation of these small footprints, which have so far only been studied with bare eye.

A BETA TAXONOMY APPROACH TO LATE JURASSIC AND EARLY CRETACEOUS DINOSAUR ASSEMBLAGES

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Keywords: *Paleobiogeography, Mesozoic, Similarity index, Cluster analysis, Principal Coordinate Analysis*

Although dinosaurs achieved worldwide distribution during the Mesozoic Era, their biogeographic distribution patterns are subject of high debate. A major geological influence on dinosaur distribution is the progressive separation between Gondwanan and Laurasian landmasses, leading to a faunal segregation by mid/Late Cretaceous. To elucidate the *tempo* and *modo* of such segregation, we adopted a Beta Taxonomy approach by comparing the similarity of dinosaur occurrences of various geological formations around the globe. Jaccard, Dice, and Simpson similarity indices were employed for the following time-bins: Kimmeridgian-Tithonian, Berriasian-Valanginian, Barremian, and Aptian-Cenomanian. Based on each of these indices, we performed: 1) a set of cluster analyses (UPGMA, neighbor joining, K-means), 2) Principal Coordinate Analysis, and 3) Correspondence Analysis. Results derived from the Jaccard index presented the highest statistical support, appearing to be more robust when compared to the other two indices. Absence of faunal segregation between Laurasia/Gondwana was identified during Kimmeridgian-Tithonian interval, although we found evidence of Asiatic provincialism. This distribution remains unchanged during Berriasian-Valanginian, even though sampling bias in this interval partially affected our results. Similarly, Barremian sampling bias hampered the possibility to discriminate Laurasian and

Gondwanan faunas, despite having higher statistical support in our analyses than the other time-bins. Finally, the Aptian-Cenomanian interval presented a clear faunal segregation between Laurasia and Gondwana, suggesting that a major faunal re-organization occurred no later than the Barremian. Further investigation, using clade-specific historical biogeography techniques, is required to clarify whether dispersal or vicariance events shaped this faunistic re-arrangement.

SPHEROLITH VARIABILITY OF MEGALOOOLITHID AND FUSIOOLITHID DINOSAUR EGGSHELLS

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Keywords: *Campanian-Maastrichtian, Titanosauria, oological record, eggshell units*

The oofamilies Megaloolithidae and Fusioolithidae have a rich fossil record composed of clutches, eggs and eggshells, most of which come from the Campanian-Maastrichtian of South America, Europe and Asia, and have been attributed to sauropods as their producers. Overall, Megaloolithidae and Fusioolithidae present similar eggshell macro and microstructure features and are mainly differentiated by the degree of fusion of their eggshell units (spheroliths). Many of these ootaxa present a relatively wide range of variability in thickness and/or ornamentation. These features are linked to the height, width, and thus the shape of the spheroliths that form the eggshell. Therefore, the morphological variability of spheroliths of megaloolithid and fusioolithid specimens has been assessed. The length and width, along with the morphology of the accretion lines of each spherolith of each sample, has been registered and analysed to search for differences between ootaxa. The height of the spheroliths between the analysed ootaxa ranges from 0.9 to 2.9mm, whereas the width ranges from 0.1 to 1.1mm. Generally, the range of variability in width is greater than that of spherolith height within each ootaxon, with few exceptions. These results have been compared with dinosaur eggshells from the Poyos fossil site (Upper Cretaceous, Villalba de la Sierra Formation, Guadalajara, Spain). The morphotypes from Poyos have the lowest values for both spherolith height and spherolith width among the analysed ootaxa.

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2D OPC: A NEW METHOD TO DESCRIBE DENTAL COMPLEXITY OF HERBIVORE MAMMALS

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Keywords: *dental topology, enamel orientation, dental complexity, enamel thickness*

Dental morphology is a major aspect of ecological and evolutionary studies of both extant and fossil mammalian species. Previously two-dimensional (2D) methods quantified the resistance of enamel through the cutting area as the ratio between enamel length and tooth area. Other approach uses the fractal index as an estimate of enamel folding. However, these variables give no information about local variations of important enamel structures within a tooth. In recent years, a series of novel methods have been proposed to analyze three-dimensional (3D) dental models. However, 3D data poses its own limitations: the initiatives to make it widely accessible and freely available are still limited and 3D scanned data needs computationally expensive pre-processing and costly software to optimize raw mesh/voxel information. On the other hand, 2D images are broadly prevalent in the literature as a main source of information for systematic studies, is available for nearly every species, and requires little preprocessing. With this in mind, we created a novel workflow using 2D image analysis techniques with unprecedented resolution over individual tooth's structures by combining multiple methodological tools included in the image analysis software 'Fiji'. A general case study is proposed using two independent clades within the Family Rhinocerotidae containing species regarded as hypsodont. To test the robustness of this tool under different practical scenarios, additional samples have been evaluated. These include differences in image size, rotation, or differences in dental wear.

THE ACEDERAL CAVE: A NEW QUATERNARY LOCALITY WITH FOSSIL LYNXES IN ARAGÓN (NORTHEASTERN SPAIN)

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Keywords: *Lynx pardinus*, cave site, Pleistocene, Holocene, Iberian Peninsula

The Iberian lynx (*Lynx pardinus*) is an endemic wild cat, now restricted to the South of the Iberian Peninsula, and the most threatened carnivore in Europe. The Acederal cave, located in the municipality of Aldehuela de Liestos (Zaragoza, Aragón, Spain), has been found to contain an important accumulation of lynx remains (at least two almost-complete skulls and abundant postcranial remains), preliminary assigned to *Lynx pardinus*. The cavity has a moderate inwards development, and, at the bottom of a 26-m-deep sinkhole, there is an area where bones of large mammals, that appear half-buried in the clay infill, were accumulated. Despite a precise chronological framework is not yet available, the facies, the conservation state, and the faunal association (including *Equus* sp., Cervidae indet., Caprinae indet., *Felis* sp., *Martes* sp., *Vulpes*

vulpes, *Oryctolagus cuniculus*, *Rhinolophus* sp. and Corvidae indet.) would be consistent with a Late glacial to early Holocene accumulation, but a more recent chronology cannot be ruled out. The lynx fossil record in the Quaternary of Aragón is limited to the sites of La Puebla de Valverde (Lower Pleistocene, Villafranchian) and the Cueva de Chaves (Upper Pleistocene, Magdalenian). Albeit the study of the site is still at an early stage (further studies are scheduled, including ancient DNA analysis and direct datings), this locality has the potential to contribute to the phylogeographical knowledge of this species in a significant way.

REDESCRIPTION OF THE NEOTYPE OF *PLATEOSAURUS* AS FOUNDATION FOR FUTURE STUDIES

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Keywords: *Plateosaurus*, *Basal Sauropodomorpha*, *Triassic*, *taxonomy*, *Intraspecific variability*

The taxonomy of *Plateosaurus*, the fifth dinosaur genus named, has always been majorly problematic. In the early 1900's more than 20 species were erected within three different genera that are currently all synonymised with *Plateosaurus trossingensis*. However, there is an enormous amount of morphological variability within the *P. trossingensis* specimens in the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS) in Germany, as well as with specimens from the same locality in other collections and from other localities. In the most recent literature, it has been proposed that the variability is consequential of developmental plasticity, however the explanation is evidently multifaceted, with further investigation of material from all horizons and localities essential to resolve this question. In 2019, SMNS 13200 was designated as the neotype of *Plateosaurus* after the holotype was deemed undiagnostic – however, no modern description of a relatively complete, mature specimen of *P. trossingensis* is currently available. The most recent description was made by von Huene in 1926, written in German. Here we redescribe the neotype of *Plateosaurus trossingensis* and present an updated phylogeny. The results will form the basis of several other associated projects currently underway, such as a large-scale 3D geometric morphometric study of *Plateosaurus* material from across all known localities and collections, description of pathologies, both in the neotype and other undescribed specimens, as well as fieldwork at the historical Trossingen site to collect more stratigraphic and sedimentological data and to excavate additional *Plateosaurus* specimens from the underrepresented beds.

INFERENCE OF SAUROPOD POPULATION ECOLOGY FROM TRACKWAYS? – ASSESSMENT OF THE SWISS JURA TRACK SITES

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Keywords: *sauropod, demography, Jura, ichnology, ontogeny*

Studying population ecology in the vertebrate fossil record is a difficult task because of drawbacks such as taphonomic biases. Fossil tracks, conversely, are the *in situ* evidence left by animals to provide data for the likely natural grouping and relative abundance. This raises the question: can we infer potential changes in populations repeatedly traversing an area, through time, from their trackway record alone? This question seems impossible to answer in the affirmative as continental ichnology is fraught with inherent complexities (e.g., small surface areas and time-restricted track sites, preservation bias, etc.). Uniquely, the Swiss Jura track sites can provide insight into sauropod populations from their trackways. This is because of the nature of the track sites, their distribution in space and time, the easy stratigraphic correlation between sites, and the repetitive use of the track site areas. We document temporal patterns in abundance and distribution of sauropod trackways and by inference sauropod dinosaurs using the Jura coastal platform in the Late Kimmeridgian. We deduce population sizes, grouped walking directions, and the presence of juveniles, subadults, and adults. Overall, the Swiss Jura coastal platform acts as a means to estimate population sizes, stage classes, and gregarious movement of sauropod herds through time. Moreover, the rare occurrence of tracks attributed to juveniles at different stratigraphic heights (i.e., different times), and at different sites, provides an exceptional glimpse into the sauropod populations. Although preliminary, this approach brings into question seasonal habitat use, nesting behavior, dispersal, parental care, and predation in the Jura area.

MESOZOIC HEAVY MEAL: TELEOSAUROID REMAINS IN A REGURGITALITE FROM THE UPPER JURASSIC OF NORTHEASTERN ITALY

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Keywords: *Regurgitalite, SEM-EDS analysis; Upper Jurassic, Teleosauridae.*

The Upper Jurassic record of marine reptiles from the western Tethys is poorly documented, together with information on their trophic interactions. A fragmentary set of small crocodylomorph bones from the Rosso Ammonitico Veronese Fm. (RAV) of Ponte Serra (northeastern Italy) was officially described in 2021. The age of the specimen was restricted to the late Kimmeridgian-earliest Tithonian thanks to calcareous nannofossil analysis. The fossil is tentatively assigned to the teleosauroid subfamily Aeolodontinae based on the presence and morphology (size, thickness and ornamentation) of osteoderms, its stratigraphic position, and pelagic nature of the RAV deposit. The peculiar clustering of axial, pelvic and dermoskeletal elements suggests its interpretation as a bromalite, a fossilized item that was processed by the digestive system of a predator or scavenger. This hypothesis is supported by UV fluorescence, SEM microstructural analysis of the bone and EDS geochemical analysis of the surrounding matrix. Limited bone etching and a dearth of background phosphorus in the surrounding matrix further distinguish the specimen as a regurgitalite, an egested fossilized mass that experienced limited gastric processing by the producer. Data on phosphorous weight percentage from this specimen closely match the array of other regurgitalites, while substantially deviating from the geochemical composition of coprolites. The specimen represents the first occurrence of Aeolodontinae in Italy as well as its most southward record in the western Tethys ocean. The fossil marks the first record of a marine

crocodylomorph preserved in a regurgitalite, bringing new insights into the taphonomy and paleoecology of the Upper Jurassic mesopelagic realm.

REDISCOVERED THALATTOSUCHIAN AND ICHTHYOPTERYGIAN MATERIAL FROM THE MIDDLE-UPPER JURASSIC OF NORTHERN ITALY

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Keywords: *Rosso Ammonitico Veronese, Middle-Upper Jurassic, Metriorhynchoidea, Ichthyosauria*

The mesopelagic depositional setting of the Rosso Ammonitico Veronese of northeastern Italy (RAV, Bajocian-Tithonian) is known since the XVIII century for the very rare, fragmentary, and badly preserved record of metriorhynchids, ichthyosaurs and pliosaurs. Preliminary information is presented here for two “new” specimens from the Altopiano d’Asiago area rediscovered during collections survey. The first, briefly reported in a museum short note, was discovered in the ‘80s and housed in the collection of Museum of Geology and Paleontology of Padova. After a quick evaluation the specimen is assigned to Metriorhynchoidea thanks to unequivocal large impressions of the prefrontals in the matrix. The specimen is represented by impressions and fragments of middle and posterior portions of the skull together with mandibular rami, one tooth, cervical vertebrae and ribs on a slab of limestone from the RAV lower member (Bajocian-Bathonian). The second specimen was found in a RAV boulder used in a dam in the ‘90s and later housed in Chioggia Civic Museum; shortly after restoration the specimen was interpreted as an ichthyosaur. The specimen is represented by mandibular elements in ventral view, posterior portions of the skull and some semi articulated vertebrae. A rich invertebrate fossil fauna is also found associated with the skeleton. The boulder appears to come from the upper member of the RAV (Kimmeridgian-Tithonian). While the poor preservation challenges any specific taxonomic attribution, the two specimens enrich the record of marine vertebrates from the RAV Fm., bringing valuable paleoecological and taphonomical insight on this pelagic depositional environment.

FUNCTIONAL MORPHOMETRY OF MAMMALIAN LIMB BONES: CARNIVORES AND UNGULATES COMPARED THROUGHOUT THE CENOZOIC

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Keywords: *adaptative radiation, disparity, locomotion, long bones ratio, mammals*

Mammals show a broad range of long bones morphologies linked to their ecological diversity. Even though mammalian morphologies were well established near the beginning of the Cenozoic, modern taxa exhibit different adaptations within and between clades. For example, Artiodactyla and Perissodactyla have both evolved elongated limbs in proportion to their large body mass. In contrast, predatory Carnivora do not show particularly large body sizes and their limb proportions can vary a lot between taxa due to specific hunting behaviours. The hypothesis of coordinated diversification events between these clades has rarely been tested, and it is still not clear why and when predators and prey evolved specific locomotory adaptations. Here, we assessed morphological variation of limb proportions in a rich sample of extant and fossil Carnivora, Artiodactyla, and Perissodactyla in order to examine hypothesized associations with ecological adaptations and diversification through time. The phylogenetic relationships among species were incorporated into the analysis to allow the use of comparative methods. Results show that limb bone proportions change in relation to life habit with amphibious species having relatively shorter limbs than ground-dwellers. Also, major climatic events clearly appeared to have had a temporal impact on patterns of morphological diversification, expressed as disparity, in several clades and ecological groups. Ground-dwelling Carnivora and Artiodactyla showed increased morphological disparity during the coldest Cenozoic phases. Our analysis provided evidence that patterns of disparity were often synchronous among large mammalian clades although we did not find evidence that a predator-prey “arms race” was responsible for these changes.

DENTAL MESOWEAR ANALYSIS AND MASS ESTIMATION OF *GAZELLA BOUVRAINAE* (MAMMALIA, BOVIDAE)

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Keywords: *Artiodactyla*, *dietary partitioning*, *palaeoecology*, *Early Pleistocene*, *Villafranchian*

Gazella bouvrinae Kostopoulos & Athanassiou, 1997, is an Early Pleistocene gazelle species, typical of the Middle Villafranchian faunas of Greece. This taxon is absent from Western Europe, but constitutes a rather common find in Greece, being the most common species of the genus *Gazella*. The material used for this study includes numerous relatively well-preserved dental elements from three Lower Pleistocene Greek mainland localities, Karnezeika, Sésklo and Gerakarou, as well as post-cranial elements from Karnezeika. Phylogenetically, *G. bouvrinae* is closely related to contemporaneous Asian gazelle taxa, while its palaeoecological profile is yet not fully investigated. The main aim of this study is to partially fill this gap by analysing its dental wear pattern, utilizing the extended mesowear technique. Moreover, we attempt to estimate its average body mass, based on the metric characters of the radius and the femur. Mesowear analysis of *G. bouvrinae* molars showed a mixed to browsing diet, similar to most extant gazelles and the partly contemporary, European species *G. borbonica* Depèret, 1884. As far as its body mass is concerned, it has been estimated to 19–20 kg, comparable with the extant Thompson's gazelle, *Eudorcas thompsonii* (Günther, 1884).

A NEW EARLY MIOCENE ELASMOTHERIINE FROM SWITZERLAND: PHYLOGENETIC AND PALAEOBIOGEOGRAPHICAL INSIGHTS

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Keywords: *Perissodactyla*, *Rhinocerotidae*, *Phylogeny*, *Palaeobiogeography*, *Miocene*

The study of fossil remains from Benken (early Miocene; Zurich Canton, Switzerland) unveils an unexpected rhinocerotid taxonomic richness, with seven species identified. They are most likely originating from two distinct levels referable to the MN4, with 6 and 3 species recorded, respectively. Interestingly, two skulls and several isolated remains (permanent and decidual teeth, postcrania) are referable to *Victoriaceros*, which supports the first occurrence of the genus outside of Africa. These new remains support a new species. The main diagnostic characters are a skull with a concave dorsal profile, a sole nasal horn, and a U-shaped nasal notch. The third upper molar (M3) has pinched hypocone and a strongly-developed antecrochet. A parsimony analysis, including 36 taxa and 282 morpho-anatomical characters allows for retrieving the monophyly of *Victoriaceros*, as a sister group to the *Elasmotheriina sensu stricto*. From a palaeobiogeographical perspective and thanks to ancestral character reconstruction, the topology retrieved reveals that the *Victoriaceros* clade likely diversified in Africa. This is compatible with the first spread of Eurasian rhinos toward Africa during the earliest Miocene. The unexpected presence of a new species of *Victoriaceros* in Benken both considerably expands the palaeobiogeographical range of the genus and documents the oldest occurrence of rhinocerotids of African ancestry in Eurasia.

BOVID DIVERSITY AT THE LATE MIOCENE FAUNA OF PIKERMI (ATTICA, GREECE) AS REVEALED BY NEW EXCAVATION DATA

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Keywords: *Bovidae, Diversity, Systematics, Late Miocene, Pikermi*

Bovids emerged during the Neogene and continued to disperse and radiate almost on a global scale, constantly adapting to ongoing ecological conditions. A significant diversity of bovid species has been revealed at Pikermi -one of the richest fossil-bearing localities of the late Miocene of Europe, which has been extensively excavated and studied since the 19th century. Since 2008, a series of recent and stratigraphically calibrated excavations (NKUA-SARG Project 70/3/12977) has taken place, primarily at the new sites PV1 (“PV”=“Pikermi Valley”) and PV3 (which correlates with the historical excavations). The abundant bovid material that has been extracted carries much potential to provide a thorough assessment of the locality’s bovid systematics, paleoecology and biostratigraphy. The studied specimens consist of numerous craniodental elements, representing eight different bovid species: *Tragoportax amalthea*, *Miotragocerus valenciennesi*, *Gazella capricornis*, *Oioceros rothii*, *Palaeoreas lindermayeri*, *Palaeoryx pallasii*, *Protragelaphus skouzesi* and *Sporadotragus* sp. Preliminary examination of the material provides several new insights. Among them is the presence of a *Sporadotragus* species, which does not correspond to *Sporadotragus parvidens* known hitherto from the historical excavations. Further, the absence of *Protoryx carolinae* and *Prostrepsicerus rotundicornis* thus far from the studied sample is also notable, since they are considered to be typical species of the Pikermian fauna. The strong occurrence of *Protragelaphus skouzesi* at the new sites is also noteworthy. Additionally, the cranial dimensions of *Palaeoreas lindermayeri* specimens seem to exhibit inter-site differences. All these points may indicate variations (with a possible temporal component) in the bovid diversity among the different sites at Pikermi.

NEW INFORMATION ON THE ARCHOSAURS FROM THE LATE TRIASSIC FISSURE FILLS LOCALITY OF PANT-Y-FFYNNON, WALES

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Keywords: *Triassic, Archosauria, CT-scanning, Phylogeny, Morphology*

The Late Triassic to Early Jurassic fissure fill localities of the Bristol Channel area preserve a diverse fauna of mostly small-bodied vertebrates, which has provided important insights into the early evolution of major tetrapod groups such as mammaliaforms, rhynchocephalians, crocodylomorphs, and dinosaurs. The Late Triassic site at Pant-y-ffynnon yields a particularly rich, but poorly understood assemblage of archosaurs, including the recently named theropod dinosaur *Pendraig milnerae*, the cursorial crocodylomorph *Terrestrisuchus gracilis*, the small sauropodomorph *Pantyraco caducus*, and the enigmatic pseudosuchian *Aenigmataspina pantyffnonensis*. Ongoing research has revealed several new insights into this fauna. *Pendraig* is identified as a small-sized non-coelophysid coelophysoid dinosaur. A revision of *Aenigmataspina*, characterised by unique, bifurcating osteoderms and conspicuously T-shaped neural spines on the cervical and anterior dorsal vertebrae, recovers this genus as the sister taxon of Erpetosuchidae + Aetosauriformes in a new phylogenetic analysis. Finally, CT-scanning has elucidated the braincase anatomy of *Terrestrisuchus gracilis*, highlighting several features likely plesiomorphic to Crocodylomorpha, such as a quadrate that is not fused to the braincase. Together, these studies reveal the significance of the fissure fills fauna from the Bristol Channel? Of Pant-y-ffynnon? for our understanding of early archosaur evolution and diversity.

COMPARATIVE ANATOMY OF THE PASSERINE CARPOMETACARPUS SUPPORTS THE PRESENCE OF CROWN SUBOSCINES IN THE OLIGOCENE OF EUROPE

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Keywords: *Passeriformes, phylogenetics, oscines, suboscines, carpometacarpus*

Among crown birds, the major clade Passeriformes (passerines) exhibits unparalleled diversity, comprising over 6,000 living species and accounting for over 60% of extant bird species. However, the early evolutionary history of this key living group remains enigmatic due to a relative lack of research attention on passerine comparative morphology. This has hampered attempts to interpret the clade's fossil record, obscuring patterns of morphological evolution across one of the most diverse clades of extant vertebrates. Numerous potentially important crown passeriform fossils, including some of the oldest crown passerines, have proven challenging to place in a precise phylogenetic context. This is due in part to a paucity of phylogenetically informative characters from across the passerine skeleton, as well as inadequate characterisation of variation in key skeletal elements that preserve readily in the fossil record. Here, we begin to address this gap in our understanding of passerine evolution by presenting a comparative framework for a morphologically variable, functionally important, and frequently-fossilised skeletal component of the wing: the carpometacarpus. We sampled >70% of extant family-level passerine clades (132 extant species) as well as several fossils from the Oligocene of Europe, and scored them for 54 phylogenetically informative carpometacarpus characters optimised on a recently published phylogenomic scaffold. We document a considerable amount of previously undescribed morphological variation among passerine carpometacarpi, and, despite widespread homoplasy,

our results support the presence of representatives of both crown group oscines and crown group suboscines in Europe during the Oligocene.

DIVERSIFICATION “EARLY BURSTS” AND SMALLER TAXA DON’T DIVERSIFY QUICKER DURING THE RISE OF ARCHOSAURS

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Keywords: *radiation, Archosauromorpha, body size, PyRate, diversification dynamics*

The archosauromorph radiation, beginning after the End-Permian extinctions and progressing during the Triassic, was a spectacular evolutionary radiation that ultimately begat the dinosaurs and pterosaurs, which would dominate the Mesozoic land and skies, and even the stunning diversity of modern birds. However, phylogenetic relationships underlying the Triassic radiation are –like of many fossil clades– greatly uncertain, relying as they do on morphology from an incomplete fossil record. Thus, methods of estimating diversity dynamics that rely on phylogeny should best be compared and complemented with phylogenetic topology-free methods for a better understanding of this radiation. Here, we employ, for the first time in this group, the occurrence-based Bayesian approach PyRate to estimate extinction and origination rates for archosauromorphs from the late Permian to Early Jurassic. We use chronostratigraphic uncertainty for most species rather than actual occurrences, due to abundant true singletons and test for correlations of diversification rate with body size using femoral length as proxy. We find a latest Permian diversification peak, meaning that the initial radiation was coeval with major extinctions, and possibly evidencing morphologically cryptic early diversification. Subsequently, net diversification rates gradually decline, reaching zero in the early Norian, potentially indicating niche-filling. Individual clades show similar patterns of initially high diversification dropping off through time, indicating “early bursts” of diversification following development of ecomorphological novelty. We find no significant correlation of diversification with body size, but the relationships are

generally positive, contradicting hypotheses that larger-bodied clades are more prone to extinction or less likely to diversify.

THE RECORD OF *ALEPHIS TIGNERESI* FROM CAMP DELS NINOTS (LATE PLIOCENE, IBERIAN PENINSULA)

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Keywords: *Pliocene, Camp dels Ninots, Alephis, Bovids, Late Ruscinian*

Camp dels Ninots (Caldes de Malavella, NE Spain) is one of the most remarkable Konservat-Lagerstätte of the European Pliocene. The site is located in la Selva depression, within the Catalan Volcanic Complex. The intense volcanic activity that characterized this area during the Pliocene led to the creation of the Camp dels Ninots maar lake (CN), and the related fossiliferous site chronologically constrained at ~3.1-3 Ma (MN15–16 transition, late Ruscinian). The particular anoxic condition of the lake bottom waters allowed the preservation of a rich vertebrate assemblage with several skeletons in anatomical connection including: bony fishes, amphibians, reptiles and mammals. The latter group is particularly interesting for the presence of large ungulates such as the bovid *Alephis tignerese*, the rhinoceros *Stephanorhinus* cf. *jeanvireti* and the tapir *Tapirus arvernensis*. Here we present the preliminary study performed on the *Alephis* records which stands out as one of the most abundant collections of Late Pliocene bovid in Europe. This genus, closely related with the basal bovine *Parabos*, populated the Mediterranean area until the earliest stages of Ruscinian. The relatively low-crowned teeth and the extremely slender limbs, evidence how this animal was adapted to thrive in humid, closed habitats, as the one inferred for CN site. The progressive harshening of the climatic conditions and the shrinking of the forested areas, started at the end of Pliocene, ultimately led to the extinction of these animals; replaced by *Leptobos* as the main representative of the large bovine guild in the Early Pleistocene of Europe.

MIDDLE MIOCENE METATHERIANS FROM JUAN GUERRA (SAN MARTIN, PERU) EXPAND THE RECORD OF SMALL MAMMALS IN THE PROTO AMAZONIA

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Keywords: *Paucituberculata*, *Didelphimorphia*, *Laventan*, *Paleobiogeography*, *Pebas Mega-Wetland System*.

Currently, marsupials (modern members of Metatheria), are widely distributed in tropical and subtropical areas of South America, but poorly represented in their fossil record. Except for the species-rich fossiliferous localities of La Venta (Colombia), additional Miocene metatherians from tropical-equatorial South America are sparsely reported in Bolivia, Brazil, Peru, and Venezuela. Here, we introduce new metatherian remains recovered in the late middle Miocene TAR-31 locality, Peru, assigned to the early Laventan South American Land Mammal Age (~13 Ma) by mammalian biostratigraphy. U-Pb analysis made on detrital zircon grains from TAR-31 gave a maximum depositional age of 17.4 ± 0.12 Ma. Three metatherian taxa are recognized at TAR-31: the didelphid *Thylamys* cf. *T. colombianus*, plus the paucituberculatans *Palaeothenes* sp. (palaeothenid) and the new abderitid *Pitheculites ipururensis* nov. sp. This assemblage, along with a cebid primate at TAR-31, suggests predominantly humid and warm tropical conditions, with the occurrence of both forests and drier habitats in the surroundings. Comparisons with other Miocene metatherian assemblages at low and mid latitudes of South America clearly confirm closest relationships between TAR-31 and La Venta (previously observed on monkeys and rodents), as well as, to a lesser extent, with Acre River local fauna and Madre de Dios (MD-67) and in Brazil and Peru, respectively. The current results further the hypothesis of Western Amazonia as a single and consistent biogeographical region for land mammals over middle Miocene times, at the western edge of the Pebas Mega-Wetland System, and highlight the role of the Amazonian region concerning marsupial Neogene radiation.

NEOTAPHONOMICAL OBSERVATION OF A BONE BED FORMATION IN A RIVER BED

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Keywords: *neotaphonomy, bone bed, accumulation, river, actualism*

The timing of bone bed formation is a subject of sedimentological/taphonomic studies. Although there are mathematical models that allow estimations of the rate of formation of such fossil assemblages, modern-day (actualistic) observations are the most reliable. In late 2021, as a result of the cessation of mining activities of a mine in southern Poland, three rivers, previously supplied with water from the drainage of mining excavations, began to disappear. A drying stream bed of one revealed an accumulation of forest mammal remains. The initial section of the river was regulated by a steep concrete channel created in the late 1950s, making an obstacle for animals trying to cross it. As a result, for 70 years large forest mammals died in the canal, and their bones, transported by water, were deposited on the first meander after the decrease in the river's flow energy. In ascertaining the area occupied by and thickness of the bone bed, as well as the time span during which it was formed, this site is an excellent testing ground for neotaphonomical studies concerned with vertebrate assemblages formed as a result of fluvial accumulation. Using a FARO's LiDAR scanner we documented the entire bone bed. We made small trenches to evaluate its thickness, studied the orientation of the bones in the accumulation and determined its taxonomic composition. We believe our research will contribute to understanding the timing of non-catastrophic bone bed formation in fluvial settings.

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MALIGNANT NEOPLASM IN *METOPOSAURUS* VERTEBRA

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Keywords: *Triassic, cancer, paleopathology, osteosarcoma, Metoposaurus*

Each case of cancer in the fossil record is interesting for general biology as well as oncology, providing – from an evolutionary perspective – precious information on somatic vulnerability to neoplasms in extinct animals. On the other hand, the documentation of skeletal pathologies in amphibians is scarce, both in herpetological and paleontological literature. Here we demonstrate the first case of the development of advanced spinal osteosarcoma in the temnospondyl *Metoposaurus krasiejowensis* from the Late Triassic of Poland. Massive, irregular outgrowths on the post-cervical/anterio-dorsal vertebra (intercentrum) of the metoposaur spread in multiple directions, with the lateral domination. The location of the bone mass surrounding the affected vertebra and clear boundary between normal and altered bone suggest that the neoplasm originated from the outer layer of the periosteum. It is consistent with one of the most common primary neoplasms affecting the musculoskeletal system called osteosarcoma. The neoplasm started on the cortical surface of the bone, affected the entire periosteal domain and penetrated inside the vertebral intercentrum towards the endosteal domain, indicating parostotic variant of osteosarcoma. Spinal osteosarcomas are rare and aggressive neoplasms in humans, making up only 0.6-3.2% of all osteosarcomas. Their appearance in *Metoposaurus* a distant relative of modern amphibians imply that at large, extinct genera were more vulnerable to cancer than much smaller, recent species, believed to be cancer-resistant.

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DO CONICAL AND SABERTOOTHED CATS REPRESENT AN EXCEPTION TO CRANIOFACIAL EVOLUTIONARY ALLOMETRY?

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Keywords: *Evolutionary allometry, Macroevolution, Carnivora, CREA hypothesis, Sabertoothed cats*

CREA (CRaniofacial Evolutionary Allometry) is an evolutionary trend proposing that, among closely related species, the smaller-sized of the group would appear paedomorphic with proportionally smaller rostra and larger braincases. We use a phylogenetically broad cranial dataset (51 species), 3D geometric morphometrics, and phylogenetic comparative methods to assess the validity and strength of CREA in the most species-rich groups of extinct and living felids. In particular, we aim to explore whether sabertoothed cats, thanks to their unusual rostral morphology, constitute an exception to CREA, even testing the impact of taxonomic rank, phylogeny, and mode of evolution on this evolutionary trend. Our results unambiguously provide support to the validity of CREA within Felidae as a whole and within the small and medium-sized

felines. By contrast, Machairodontinae fail to support CREA. The adoption of different landmark configurations, phylogenetic hypotheses, and corrections for phylogenetic effect have a limited impact on CREA pattern recognition within felids. Our findings suggest that Machairodontinae constitute one of the first well-supported exceptions to this biological rule currently known. We hypothesize the acquisition of specific cranial features resulting from extreme ecological specialisation - such as sabertoothed upper canines - to represent a preferential way to escape from common evolutionary patterns of morphological variation such as CREA.

LONG BONE HISTOLOGY OF AETOSAURS AND PHYTOSAURS FROM KRASIEJÓW (NORIAN) REVEALS STRONG ENVIRONMENTAL INFLUENCE ON THE GROWTH PATTERN

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Keywords: *Parasuchus*, *Stagonolepis*, *Late Triassic*, *humerali*, *femora*

Palaeohistology is a good source of information regarding the animals age, metabolism or mode of life. The Norian Krasiejów locality offers an unique possibility to study multiple skeletal elements of amphibians and reptiles. We tested the influence of external conditions on the growth pattern of taxa originating from the same locality but belonging to different phylogenetic groups vs. the same taxa but from geographically distinct localities. We studied the growth pattern of the phytosaur *Parasuchus* cf. *arenaceus* and the aetosaur *Stagonolepis olenkae* femora and humeri. For comparison, we sampled a phytosaur *Nicrosaurus* sp. femur from the Norian Heselach (S Germany) locality. All samples show a lamellar-zonal bone, consisting mostly of low-organized parallel-fibred tissue, and showing a low to moderate vascular density. Beside the *Stagonolepis* femora, all bones are stratified with zones and annuli. None of the Krasiejów taxa preserve lines of arrested growth (LAGs) and only the *Nicrosaurus* femur displays one LAG. Instead, the Krasiejów taxa show the deposition of rest lines and sub-cycles throughout the cortex. A change in tissue from fast-growing inner cortex to slower-growing outer cortex was previously described for numerous phytosaurs and aetosaurs from North and South America, however, it was not observed in the taxa studied herein. *Parasuchus* and *Stagonolepis*, despite their occupation of different habitats and not being phylogenetically closely related, show a very similar growth pattern, which varies from their close relatives originating outside Krasiejów. This implies, that the local environmental conditions strongly influenced their growth pattern, and potentially overprinted their genetic precondition.

TROPHIC NETWORK RECONSTRUCTION AND ANALYSIS OF THE DIFFERENT FOSSILIFEROUS LAYERS OF THE MIDDLE TRIASSIC MONTE SAN GIORGIO WORLD HERITAGE (SWITZERLAND/ITALY)

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Keywords: *trophic networks, ecological interactions, Middle Triassic, marine fauna.*

Since its discovery, the Middle Triassic Monte San Giorgio (MSG) lagerstätte near Meride (Canton Ticino, Switzerland) has revealed an enormous quantity of exceptionally preserved fossils. Distinct changes in faunal composition have been identified in the MSG lagerstätte, illustrating significant ecological changes of this extinct ecosystem over a time-lapse of 3 Ma. However, there has never been a detailed study on the network of trophic interactions among the organisms of the MSG Faunas. Here we present the most complete database on MSG fossils with specimens from museums in Zurich and Lugano in Switzerland and Milano in Italy. These initial results will be expanded to reconstruct a succession of 8 trophic networks for 8 distinct fossil layers of the MSG lagerstätte. We are using well-documented feeding behaviours and interactions of several hundreds of different taxa collected and a new Rstudio package called PFIM (Paleo Food Web Inference Model). The aim of this project is twofold. Firstly, our study will shed a new light on the ecological changes of a Middle Triassic marine fauna set between two of the deadliest mass extinction events in Earth history. Secondly, we will add a new element to the growing list of fossil faunas studied for trophic network reconstruction. This will open new research opportunities for the understanding of extinct ecosystem complexities and organizations and how these evolve through deep time.

PALEOECOLOGICAL CHARACTERISTICS OF *PLATYOPOSAURUS* (AMPHIBIA, TEMNOSPONDYLI) FROM THE MIDDLE PERMIAN OF EASTERN EUROPE

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Keywords: *Archegosauridae, temnospondyls, paleoecology, Middle Permian, East European Platform*

Archegosaurid temnospondyls of the genus *Platyoposaurus* were large (total reconstructed skull length up to 0.7 m; body length about 3.5 m) gavial-like amphibians that were widely distributed in the Middle Permian throughout today's Eastern Europe. The genus *Platyoposaurus* includes four described species (*P. rickardi*, *P. stuckenbergi*, *P. watsoni*, *P. vjuschkovi*), now confidently identified from 18 localities. The paleoecological characteristics of *Platyoposaurus* were identified and refined based on morphological, paleohistological, coprological, lithological facies, and taphonomic analyses. Through this study it was possible to establish that *Platyoposaurus* were actively swimming and specialized piscivorous predators, with a more likely semi-aquatic type of ecological adaptation. *Platyoposaurus* habitats included rivers, lakes and lagoons, in which respect it resembled *Archegosaurus*, and may indicate a considerable environmental plasticity of members of Archegosauridae generally. For comparison, the fossils of other archegosaurids have been found in the following types of deposits: *Archegosaurus* in lacustrine and fluvial, *Bashkirosaurus* in fluvial, *Collidosuchus* in fluvial, *Prionosuchus* in lacustrine. For *Platyoposaurus* a change of paleobiotopes in the process of individual development with relatively passive hydrodynamics (lakes and lagoons) to rivers with more active hydrodynamics while maintaining their former habitats was established, as evidenced by the discovered morphological transformations of skeleton elements. *Platyoposaurus* actively competed for food resources with Melosauridae in those paleobiotopes in which they could live together. Thus the use of different methods in the study showed the effectiveness of complex approach for more accurate determination of paleoecological characteristics and in particular the type of ecological adaptation.

PAPIONIN AFFINITIES IN THE ENDOCRANIAL ANATOMY OF *CERCOPITHECOIDES WILLIAMSII* CALVARIA KA195

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Keywords: *Cercopithecoidea*, *Plio-Pleistocene*, *Cradle of Humankind*, *Inner ear*, *Endocast*

Cercopithecoids are relatively common in the fossil Plio-Pleistocene record of Africa and are found in most South African hominin-bearing localities. Due to their usefulness in paleoenvironmental reconstruction and biostratigraphy, many research efforts have been dedicated to them. However, the taxonomic attribution of several specimens remains problematic. For example, the KA195 calvaria from Kromdraai was initially designated as the holotype of the papionin *Parapapio coronatus* and subsequently assigned to the colobine *Cercopithecoides williamsii*. Subsequent studies have reported similarities with either *Cercopithecoides kimeui*, a very large extinct colobine from East Africa, or *Theropithecus*. To investigate the taxonomic affinities of KA195, we analyzed its endocast and inner ear morphology, both known as good proxies for phylogenetic relatedness. Then, we compared this specimen to a sample of Plio-Pleistocene and extant cercopithecoids. In addition to cranial capacity and sulcal pattern assessment, endocast and bony labyrinth morphology were inspected using a deformation-based 3DGM approach, allowing direct

comparison between continuous surfaces. Results show that the morphoarchitecture of the endocast, and the shape of the semicircular canals contrast with those of fossil colobines and highlight similarities with papionins, especially *Theropithecus*. Yet, despite the similarities, a reassignment of KA195 to *Theropithecus* would be premature without an inspection of the endocranial morphology of *C. kimeui*, currently unavailable. Additional 3DGM analyses, including the external cranial morphology, are required and should assess if the morphological affinities with *Theropithecus* are be homoplastic, potentially related to the increased terrestriality inferred for fossil colobines and/or to their large body mass.

SKELETAL STRESS IN 3D SIMULATIONS OF HIGH-SPEED LOCOMOTION IN LARGE THEROPODS

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Keywords: *biomechanics, multibody dynamics, locomotion, Theropoda, Tyrannosauridae*

Non-avian dinosaurs experienced uniquely high skeletal loads due to their large body sizes. Megatheropods (>1000 kg) may have been particularly limited by stress, because their bodies were supported by two legs. Multibody dynamic physics simulations represent an ideal method to test this phenomenon. However, previous studies have simulated maximal speed of *Tyrannosaurus rex* while limiting movements to the midsagittal plane. This constrains a 3D model to move in 2D, which can be physically interpreted as walking between two walls – a necessary simplification due to computational costs. This earlier work suggested that speeds exceeding 5.5 m s⁻¹ (at 7207 kg body mass) may have resulted in skeletal injuries. We have built on this work, by combining it with a novel, computationally efficient optimization method (direct collocation). This sophisticated workflow enables us to simulate full-3D periodic movements of *Tyrannosaurus*. Our model has 23 degrees of freedom (versus 11 in previous models), and weighs 8158 kg. Despite being nearly 1000 kg heavier, our 3D simulations display substantially lower femoral peak-stresses than found in 2D. Furthermore, because our model included the gastralia, knee penetration into the belly segment was only preventable in 3D. These findings suggest that this added model complexity may have relevant biological interpretations: megatheropods may have been capable of stress-avoidant locomotion at higher speeds. We are currently developing a model of an emu (*Dromaius novaehollandiae*) to validate these new

predictions. Our results demonstrate the power of applying novel computational methods to the fossil record.

VIRTUAL ENDOCASTS OF THE BRAIN AND INNER EAR OF LEPTICTIS (LEPTICTIDA: MAMMALIA)

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Keywords: *Eutheria, Brain, Inner ear, Avizo, Computed Tomography*

The genus *Leptictis* is an enigmatic small-sized insectivorous mammal from the middle Eocene to late Oligocene of North America. This taxon has been challenging to place in the mammal tree, being considered basal to Placentalia, or closely related to specific mammalian crown groups. Endocranial data provide a wealth of phylogenetic, neurosensory, and behavioural information. Published studies on the natural brain endocasts of *Leptictis* were limited to anatomical descriptions, and the proportion of different brain regions could not be measured to inform us about the behaviours and senses of this extinct mammal. For this study, we scanned and segmented the brain and inner ear endocasts for two specimens of *Leptictis* from the AMNH collections in the USA. Our results show that *Leptictis* had an EQ range of 0.43 – 0.69, similar to contemporaneous rodents such as *Paramys* and *Ischyromys*. The olfactory bulbs represented 9.1% of the total endocast volume, which is in the range of *Hyopsodus*, indicating that *Leptictis* likely relied heavily on olfaction to find its prey. The petrosal lobules were small, representing 1.1% of the total endocast volume similar to the fossorial rodent *Pseudotomus*. The neocortical surface area is relatively small compared to contemporaneous crown placental mammals (12.2% of the total surface area), which is similar to the condition seen in the stem taxon *Hyopsodus*. *Leptictis* was relatively agile, with an agility score of 4.04. A mosaic of plesiomorphic and derived traits support the hypothesis that *Leptictis* was likely a stem placental mammal closely related to crown groups.

FLY PUPARIA IN A MAMMOTH SKULL FROM THE NETHERLANDS: IMPLICATIONS FOR MAMMOTH TAPHONOMY

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Keywords: *blowflies, mammoth, Weichselian, preservation, taphonomy*

A fragmented mammoth skull of Weichselian age, recovered at a dredging site at Lent in the Netherlands, has been found to contain fly puparia. The puparia belong to necrophagous flies, which lay their eggs in carcasses. These fly puparia can inform on the palaeoenvironment and offer insights into the preservation and taphonomy of fossil mammoth material from Lent. The uncovered skull contained puparia from a single blowfly species: *Protophormia terraenovae*. The presence of a single species allowed for a tentative estimation of the season of death, namely spring. This is because in warmer seasons the presence of more blowfly species is common. The minimum temperature for colonisation of a carcass by *P. terraenovae* is 9 °C. This would rule out winter for colonisation, but not necessarily for the death of the mammoth, as colonisation could occur after rapid thawing. The colonisation of the carcass by blowflies not only informs on the taphonomy of the mammoth, the presence of blowfly puparia in the mammoth remains also further constrains the age estimate of this individual mammoth fossil. Temperature reconstructions of Weichselian summers do not frequently show excursions above 9 °C, which only occur in the beginning of the Weichselian or during interstadials. The mammoth thus must have lived, and more importantly died, during one of the somewhat warmer periods of the Weichselian.

NETWORK MODELING AND CAPTURE-MARK-RECAPTURE METHODS FOR THE IDENTIFICATION OF SPECIES FACTORIES

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Keywords: *Species factories, NOW database, Capture-Mark-Recapture, Network modelling*

Species factories are defined as times and places in the fossil record where and when an exceptionally large number of new species occur. While several tailored solutions for the mammalian record have been proposed, how to identify species factories computationally in a standardized way is still an open question. To quantify what is exceptional, we first need to quantify what is regular. One of the main challenges in this identification process is to account for sampling unevenness, which depends on several methodological decisions, including the scale of the analysis (aggregation radius).

Here we use Capture-Mark-Recapture methods (CMR) with spatial aggregation guided by network modelling, to estimate the sampling probabilities for the species in the NOW database. Since the mammalian record is sparse and most localities include only a few species, we couple CMR with tailored spatial aggregation approaches to estimate the sampling probabilities. We then use these sampling probabilities to quantify background speciation rates and assess what rates are abnormal. We represented aggregated fossil data as a bipartite network and used community detection to evaluate how the choice of an aggregation radius impacts the modular structure. While estimating sampling probabilities allows the adjustment for sampling unevenness so that the difference in findings can be compared across locations and cannot be due to differences in sampling. We have identified as species factories the locations with origination rate in the highest 5% per time unit. To characterize those locations we looked for paleoecological patterns in these places that may be lacking elsewhere.

THE LATE CAMPANIAN MICROVERTEBRATE ASSEMBLAGE FROM PETREȘTI (TRANSYLVANIAN BASIN, ROMANIA), A NEW WINDOW INTO THE EVOLUTION OF EUROPEAN CRETACEOUS INSULAR FAUNAS

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Keywords: *Late Cretaceous, Romania, microvertebrate bonebed, island faunas*

The latest Cretaceous continental vertebrate faunas of Romania are well known for their unique features, derived from prolonged evolution in isolation on an insular landmass, the so-called 'Hațeg Island'. The discovery of new vertebrate assemblages, of Campanian–Maastrichtian age, at Petrești, in the SW Transylvanian Basin, offers the opportunity to take a look at the composition of insular vertebrate faunas of the region at an older age than other better known records of the Hațeg Basin. On-going research on the palynomorph, calcareous nannoplankton, and foraminifera assemblages of the Petrești section more confidently support a late Campanian age (Upper Cretaceous) for the fossiliferous bonebed that yielded the largest part of the vertebrate remains. Continued screen-washing of the bonebed sediment from the grey deposits from the base of the Sebeș Formation, overlying the marine-transitional Bozeș Formation, have yielded numerous microvertebrate remains, belonging to: lepisosteid fish; albanerpetontid and anuran amphibians; crocodyliforms (teeth of various morphologies); rhabdodontid, ankylosaurid, and theropod

dinosaurs; and multituberculate mammals. This contribution presents the new microvertebrate material found at Petrești, adding up to the previous, shorter taxonomic list, and compares the new additions to the later, Maastrichtian faunas of Transylvania, aiming to better understand their evolution within their insular environment.

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A NEW VERTEBRATE ASSEMBLAGE FROM THE LATE PLIOCENE OF MĂRU (DACIAN BASIN, SOUTHERN ROMANIA)

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Keywords: *late Pliocene, Romania, freshwater fish, rodents*

Pliocene vertebrate assemblages from the Dacian Basin (southern Romania) are poorly known, and generally represented by isolated large mammal remains. So far, non-mammalian material was reported from Podari (freshwater fishes), Berești, and Mălușteni. The latter two localities yielded reptile and fish remains collected and only preliminarily described the 1930s.

Recent investigations in the north-western Dacian Basin led to the discovery of new outcrops in Măru (Gorj County). Mollusc-bearing mudstones were screen-washed, producing rare rodent molars, and numerous teeth and postcranial bones of freshwater fish. The rodent material is tentatively assigned to the arvicolid *Mimomys hajnackensis*, indicative for biozone MN16a (early late Pliocene). The fish specimens are assigned to *Leuciscus* sp., *Rutilus* sp., *Scardinius* sp., *Chondrostoma* sp., *Abramis* sp., *Barbus* sp., *Carassius* sp., *Tinca* sp., another indeterminate cyprinid, *Silurus* sp., *Esox* sp., and an indeterminate percid. The taxonomic composition of the fish community indicates a lacustrine environment. The fossil assemblage from Măru adds important information on the composition of late Pliocene freshwater fish assemblages of the Dacian Basin, previously known only from Podari (*Tinca* sp., *Scardinius* sp., *Esox* sp., *Silurus* sp.), and provides new data that will be useful in further assessment of connections to neighbouring basins comprising similar assemblages.

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SHAKE A LEG: VARIABILITY ON PELVIC MUSCULATURE OF THE TITANOSAURS FROM LO HUECO (LATE CRETACEOUS, SPAIN)

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Keywords: *Titanosauria, Sauropoda, Muscle Reconstruction, Extant Phylogenetic Bracketing, Late Cretaceous*

Titanosaurs from Lo Hueco fossil-site are among the better preserved and articulated specimens of the Late Cretaceous of Europe. Preliminary analyses on these titanosaurian specimens have revealed a high degree of disparity in the caudal axial skeleton, with up to four different morphotypes in the assemblage. Most of these partial skeletons preserve articulated or closely associated caudal series and pelvic girdles, making them prime specimens to evaluate their locomotor capabilities.

Several pelvic girdles and associated femora, tibiae and fibulae were scanned using stereophotogrammetry. These elements were virtually assembled in osteological neutral pose. We used the extant phylogenetic bracket to map the attachments of pelvic musculature in the girdle, limb (when preserved) and their corresponding caudal series of each of the four putative titanosaurian morphotypes. Then, we compared the proportions and development of the different

osteological correlates, as well as disposition of muscle lines of action, to assess potential locomotor capabilities in each morphotype.

Main differences among the morphotypes were found in the proportions and orientation of the ilium preacetabular lobe (origin sites for *M. iliotibialis*, *M. iliotrochantericus caudalis* and *M. iliofemoralis externus*). These differences imply changes in the lines of action of these muscles and their volumes. This showcases different capabilities in femoral protraction, abduction and hip flexion that could be related with minor variations in pelvic width and femoral morphology among the different morphotypes. This suggests that the four putative titanosaurian morphotypes had different ecomorphologies and might have occupied different niches.

QUANTIFYING BONE SURFACE ROUGHNESS IN *BRANTA CANADENSIS* USING 3D DIGITAL MICROSCOPY: IMPLICATIONS FOR TEXTURAL AGEING OF EXTANT AND EXTINCT SPECIES

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Keywords: *Textural ageing, surface texture, digital microscopy, skeletal ontogeny, histology*

Ontogenetic ageing is applied in the fields of taxonomy, morphology, ecology, archaeozoology and palaeontology and plays a crucial role when studying the osteology and ontogeny of species. Textural analysis is a non-destructive ontogenetic ageing method that uses bone surface textures to determine the relative age of skeletal remains. Variations in bone surface textures between individuals result from a decrease in penetrating blood vessels through the bone surface during the growth of an animal. Textural ageing patterns have been observed independently in numerous species (e.g., *Branta canadensis*, *Ardea cinerea*, *Pygoscelis antarctica* and centrosaurine dinosaurs), but previous research has exclusively investigated textural ageing patterns through qualitative, subjective, and unsystematic visual inspection.

Here, we apply 3D digital microscopy (Keyence VHX-6000) to quantify bone surface roughness and investigate textural ageing patterns conforming the roughness parameters ISO-25178 (3D areal surface texture) and ISO-4287 (2D line roughness). Measuring the skeletal remains of extant bird taxa was prioritised over the skeletal remains of fossil taxa, due to potential interference from taphonomic signals. Therefore, *Branta canadensis* longbones were analysed. 2D line roughness analyses on *Branta canadensis* long bones were able to retrieve numerical surface roughness parameters conforming to the bone texture patterns observed during visual inspection. Similarly, *Triceratops* fossil remains of varying states of preservation returned comparable parameters. Future research will focus on osteohistological analyses to link the observed patterns in textural ageing and aims to better constrain taphonomic effects in the analysis of fossil material.

GLOBAL PHYLOGENY OF DIPLOCYNODONTINAE AND ITS IMPLICATIONS FOR CROCODYLIAN EVOLUTION

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Diplocynodontinae represents the only crocodylian lineage that survived the Eocene-Oligocene transition in Europe and is known for its long endemic evolution in the continent. Current phylogenies place Diplocynodontinae as an early diverging member of Alligatoroidea, a group that otherwise originated in North America during the Late Cretaceous. This phylogenetic position is incongruent with the spatiotemporal distribution of fossils and leaves the origin of Diplocynodontinae enigmatic. In this study, we critically reassess the evolutionary relationships of Diplocynodontinae through first-hand revision of key taxa and homologies placing, according to previous phylogenies, the group into Alligatoroidea. We find that several synapomorphies supporting the alligatoroid position represent irreproducible or poorly defined character states. Parsimony analyses of a revised dataset results in several most parsimonious trees with an alternative position for Diplocynodontinae, along the stem lineage of crown-group crocodylians. The traditional basal alligatoroid position is persisting in the remaining trees but the synapomorphies supporting this placement are poorly known for outgroup taxa. A stem-crocodylian position for Diplocynodontinae is more congruent with stratigraphy and European vertebrate paleobiogeographical patterns, and would clarify the origin of the clade as a result of an

early Paleogene dispersal from North America. Furthermore, phylogenetic patterns of extinction across the Eocene-Oligocene transition likely need to be reconsidered together with our current hypotheses of early alligatoroid morphology.

THE DINOSAUR ICHNOLOGICAL RECORD OF NORTHERN CHILE: A REVIEW AND ITS POTENTIAL DEVELOPMENT

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Chile's ichnological record has great potential but, apart from a few mentions in the literature, its study has been neglected. Rich track bearing levels, between Late Jurassic (Oxfordian) to Early Cretaceous in age, are known especially, but not only, from the Tarapacá to Atacama regions in northern Chile. These track-bearing sequences were deposited in various depositional environments (e.g., littoral, fluvial, etc.) providing an excellent base for detailed studies of the relationship between ichnofauna and their palaeoenvironment. Fossil tracksites on the western margin of Gondwana at these palaeolatitudes have not been fully investigated. However, they represent a unique record and the finding new tracksites will increase our knowledge on dinosaur diversity correlated to the different palaeoenvironments.

In addition to the many known tracksites (e.g. Quebrada Chacarilla, Quebrada Arca, Quebrada La Descubridora), especially in the Tarapacá, Antofagasta and Atacama regions, the potential for new relevant discoveries is very high. This is because of several not-yet-validated reports of dinosaur footprints from those regions and a large number of potential outcrops in barely explored areas, no doubt vastly outnumbering known sites. This potential is going to be exploited in the near future through a Ph.D. project. Stay tuned for more new and exciting news.