THE FOSSIL WEEK

ABSTRACT BOOK

5TH INTERNATIONAL PALAEONTOLOGICAL CONGRESS

From July 9th to 13th, 2018
France

S15 - Experimental approaches in palaeontology: new data from old fossils

Keynote

Oral communications

S15 // Keynote

Experimental analysis of how character loss biases interpretations of exceptionally preserved, soft bodied organisms

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In the exceptional deposits that preserve fossilized remains of soft tissues, it is tempting to think of the fossils themselves as essentially complete, and assume that we can reconstruct what they were like as animals by reading anatomy directly from the fossils. This would be a mistake: all fossil remains lie somewhere on a spectrum of decay, at one end of which is complete loss of all information (no fossil preserved). Exceptionally preserved remains lie towards the other end of the spectrum, but no fossils avoid decay completely, and the degree to which anatomical information is lost during decay and preservation can be hard to determine. For decades, taphonomic experiments have been used to investigate post-mortem processes and their role in exceptional preservation, but a wide range of known and unknown variables influences how soft tissue remains become fossilized - variables that at first sight might seem to limit the applicability of experiments to analysis of fossils. Focussing on character-based experimental decay I have worked with a small group of colleagues (particularly Sarah Gabbott, Duncan Murdock and Robert Sansom) to develop methods that allow clear analysis and quantitative testing of the repeatability and comparability of taphonomic experiments. Our approach allows factors that retard onset of decay to be differentiated from those that reduce the rate of character loss, and demonstrates that sequences of character loss are generally unaffected by the conditions in which carcasses decay. Empirically derived sequences can thus be applied to exceptionally preserved fossils to disentangle the relative importance of, and interactions between decay, maturation, and mineralization, and to inform our interpretations of fossil morphologies. Far from being of limited value, data from well-designed taphonomic experiments provide fundamental new insights into the processes and biases that have produced exceptionally preserved fossils, and the degree to which these processes distort our understanding of anatomy, function and ecology.

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S15 // Oral

Absolute and meso-wear in goats fed diets of different abrasiveness for half a year

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In herbivores' natural diets, the main abrasive factors contributing to tooth wear are phytoliths and grit. However, the different aspects in which they impact tooth wear and the timeframe a wear signature takes to develop, still remain unexplored.

The effect of intrinsic (phytoliths) and extrinsic (grit) abrasives was investigated on 28 adult female goats. The animals were kept in four groups, in a controlled feeding experiment over a six-month trial period. The four pelleted diets differed in their degree of abrasiveness (without phytoliths: lucerne L; phytoliths: grass G; increased phytoliths: grass/rice hulls GR; external abrasives: grass/rice hulls/sand GRS),and were supplemented with a necessary minimum of lucerne hay (lucerne group) or grass hay (the other groups). Tooth morphology was captured by medical CT scans at the beginning and end of the experiment. These scans, as well as the crania obtained postmortem, were scored using the mesowear method (cusp shape, occlusal relief). Comparisons between diet groups showed no significant effect after 0.5 years. However, when assessing the difference in mesowear signal between measures made at the start and end points of the experiment, significant effects emerged. In accordance with the theory of mesowear, the GR and GRS groups indicated significantly higher wear than the other diet groups. A feeding period longer than 0.5 years is deemed necessary for a mesowear signal to clearly develop in adult animals.

The accumulated 3D data was also used to gauge absolute wear of tooth crown material by quantifying volume loss. Significant differences in volume loss between the diets, consistent with abrasiveness, were made evident by 3D volume analysis of the upper left M2, with increased loss observed in the GR and GRS groups. Through these measurements, a simultaneous volume gain was noted, caused by root growth - despite the fact that all animals possessed permanent adult dentition. Overall, tooth volume loss was significant by the end of the experiment and a correlation was found between crown volume loss and root volume gain. This could imply the existence of a hitherto unknown feedback mechanism that attenuates wear caused by abrasive diets, even in animals with closed roots.

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Diagenetic alteration of dental surface textures by sediment transport: a tumbling experiment

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3D dental surface texture (3DST) is a powerful proxy for assessing tooth function and determining the mechanical properties of ingesta. Abrasion and/or attrition cause material loss and result in specific wear features on the enamel surface. Wear features at the μm-scale are related to feeding patterns and can be used to distinguish between soft or hard-object feeding in herbivores and faunivores.

However, taphonomic processes during burial, transport and fossilisation may alter original enamel surfaces and obscure ingesta-related 3DST. In this study, we performed tumbling experiments on teeth from three species of extant vertebrates with well-known feeding behaviours to evaluate the physical effects of fluvial transport on 3DST and to assess whether diet-related features are overprinted. Isolated teeth were tumbled in sediment-water (1:1.6) suspensions using different grain size fractions (63-125μm, 125-250μm, 250-500μm, 2-8mm) of siliciclastic Rhine river sediment. Teeth of the herbivorous rodent (*Otomys* sp.) and two large ungulates, a grazer (*Equus* sp.) and a browser (*Capreolus capreolus)*, were treated for time intervals ranging from 30 mins to 366 hrs. 3DST was measured on exactly the same occlusal enamel areas both prior to and after tumbling, using ISO-norm texture parameters.

The main goal was to assess if ingesta-related differences in 3DST of grazers and browser were preserved after the tumbling. Prior to tumbling, 12 texture parameters were significantly different between the two ungulates. After 16 hrs of tumbling, these 12 parameters remained significant and four additional parameters became significant. Subsequent tumbling for 336 hrs changed the significance-levels of some parameters: nine were still significant, including two new ones, while six lost their significance. Rodent teeth did not show any significant changes in 3DST. During tumbling, volume and flatness parameters remained relatively stable. Most significant alterations of the 3DST were found for the medium grain size fraction.

The 3DST of the tumbled teeth will be compared to those of fossil teeth from different fluviolacustrine depositional settings to assess if the experimental 3DST alteration resembles that caused by natural sediment transport.

Overall, our experiment provides promising insights into the stability of ingesta-related 3DST of mammal teeth during fluvial transport and helps to identify suitable 3DST parameters for dietary reconstruction in fossil vertebrates.

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The ruminant sorting mechanism: an innovative digestive strategy that washes off external abrasives before chewing

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In ruminants, the major contribution to particle size reduction of ingesta does not occur during ingestion but during rumination mastication. Historically, the less robust mandibles of ruminants (as compared to perissodactyls) and lower hypsodonty have been accounted for by a concept that material regurgitated from the rumen is softened, 'soaked', and therefore requires less masticatory force (and hence less robust mandibles) than freshly ingested material. Ingestive chewing in horses is very regular in the rhythmicity of its motions and resembles rumination chewing but not ingestive chewing in cattle and camels, raising the question why the latter do not apply this efficient chewing pattern already during ingestion. A convenient answer is that ruminating herbivores avoid wear-intensive chewing during ingestion and postpone it until after the ingesta has been exposed to forestomach fluids, which potentially wash off external abrasives (but cannot remove internal abrasives).

In a pilot study, we investigated the location of sand accumulation in the forestomach of goats fed a diet containing sand for several months before taking a full-body CT scan in the natural resting position, and before sampling different locations of the forestomach after slaughter. The results indicate that the dorsal rumen contents - from where material for rumination is recruited - was comparatively depleted of sand.

The resulting hypothesis is that a diet of a certain phytolith content should affect ruminants and non-ruminant herbivores alike; in contrast, a diet of a certain external abrasives content should affect ruminants less than nonruminant herbivores. Preliminary results from comparative feeding experiments with goats and rabbits support this hypothesis.

It should be further assessed whether environment reconstructions based on hypsodonty indices or tooth wear proxies become more accurate if this difference between ruminants and nonruminant herbivores is taken into consideration.

* Speaker

S15 // Oral

The present is the key to the past: assessing how extant marsupials track their environment to clarify mammalian responses to climate change

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Dental microwear texture analysis (DMTA) and stable isotope analysis have long been used to clarify the paleobiology and paleoecology of extinct animals. However, not all animals record their local environment similarly-with some tracking relative aridity and others tracking meteoric water via oxygen isotopes. Additionally, there has been significant debate regarding if DMTA records an animal's diet or local environment (e.g. grit on the landscape). As understanding dietary proxy data is critical to assessing faunal responses to climate change, the ecology of our ancestors, and a broad diversity of questions, it is necessary to assess if and how extant taxa track their local environment. Here, we use extant wild-caught marsupials to ”experimentally” test how these animals record their local temperature, precipitation, and/or relative aridity. We developed a DMTA and stable isotope baseline of extant possums, koalas, and macropods consuming a broad range of diets and/or occupying a broad geographic range, including: *Dorcopsulus vanheurni*, *Macropus fuliginosus*, *Macropus giganteus*, *Osphranter robustus*, *Osphranter rufus*, *Phascolarctos cinereus, Notamacropus rufogriseus*, *Petrogale lateralis*, *Setonix brachyurus*, *Trichosurus caninus*, *Trichosurus vulpecula*, and *Wallabia bicolor*. By examining a range of taxa from overlapping environments and across a range of habitats, we clarified that dental microwear is reflective of diet and less affected by environmental variables including evaporative conditions. Results demonstrate the ability of DMTA variables to differentiate between tough and hard food consumers, i.e. extant grazers and woody browsers, respectively. Additionally, koalas record a tough folivorous diet even when consuming leaves lacking phytoliths. When comparing *M. giganteus* and *M. fuliginosus* individuals that were killed during ”normal” conditions to those killed during extreme droughts, DMTA reveals dramatic dietary shifts in both taxa to include more woody material during periods of extreme aridity. Further, the majority of these marsupials track relative aridity via oxygen isotopes, providing confidence that fossil taxa within the same family can similarly track local climates through time. Collectively, these data reveal how mammals record a range of climates including extreme droughts, and help document the utility of DMTA for recording diet while stable oxygen isotopes in kangaroos, possums, and koalas all record evaporative conditions. The present is the key to the past: assessing how extant marsupials track their environment to clarify mammalian responses to climate change.

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The positional repertoires of hominins: New insights from extant primates

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With regard to the diversity of positional (posturo-locomotor) capacities of extant non- human primates, it is very likely that our ancestors and extinct non-human primates were also able of various posturo-locomotor modes. Furthermore, the most obvious variations between extant primates are mainly in size and shape (i.e. morphotypes) that are shown to be strongly related to locomotor performances. In this context, understanding the diversity of the positional repertoires in extant species in relation to size, morphotype and environment may help to model evolutionary transitions in extinct species' positional repertoires. For this aim, we conduct experiments 1) in the frame of the *Motion Analysis of Primates* platform at the CNRS Primatology Station (Rousset, France) where we have a long experience of integrative studies (biomechanics, morphology and positional repertoire) of longitudinal samples of the olive baboon, *Papio anubis,* and 2) in Zoological parks on the morphometrics of different gibbon species, *Nomascus gabriellae* and *N. siki,* in the zoos of Besançon and Mulhouse and on bonobos, *Pan paniscus,* in the zoo of Planckendael. By collecting radiographs, making external measurements (segment lengths and diameters) and quantifying posturo-locomotor behaviours, we increase our understanding of the relationships between bones, body mass distribution and positional behaviours. By using a developmental perspective, our results suggest strong relationships between limb mass proximal migration and the variations in the proportion of climbing behaviours. We also found a marker, in the skeletal proportions of the foot, for the proportion of grasping behaviours in baboons. Based on these results and on the functional relationships between body mass distribution and posturo-locomotor repertoires found in the literature, we propose a meta-analysis of the changes in morphotypes in Catarrhini species. This multivariate analysis allows us to predict the emergence of new positional repertoires, including its diversity, in relation to morphotypes and bone size during the evolution of primates, including hominins.

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Inhibitory cascade and serial segmentation in teeth, limbs and body segments: from trilobites to hominids

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Many animal bodies display serial structures made up of repeating segments of similar size and shape, including teeth, limb/finger bones/segments and body segments. Gradations in size and shape are often apparent in these series, forming a 'morphogenetic gradient'. One model for the developmental control of the size of adjacent segments is the inhibitory cascade. This model was first established in mouse molars, showing that teeth form a linear pattern in size along the tooth row, but the slope of this linear pattern varies among species. The inhibitory cascade has considerable power in explaining tooth size development and evolution in humans and fossil hominins, allowing us to predict the sizes of undiscovered teeth based on this developmental pattern. The inhibitory cascade has also been inferred to influence the size of other segmented structures in the vertebrate body, including phalanges, limbs and somites/vertebrae. Given the apparent widespread presence in vertebrates, we hypothesised that the inhibitory cascade mechanism influences non-vertebrate appendage and body structures. A key example is the basal arthropod group trilobites, which have serial segments in the thorax. From measurements of segment sizes in trilobites, we show that the inhibitory cascade strongly controls relative segment size in the pygidium in 51 out of 53 species, and also explains thorax segment size in adults of 69 out of 99 species of trilobites. Our results suggest that the developmental mechanism of the inhibitory cascade was present early in arthropod evolution, and is likely influential throughout the animal kingdom.

* Speaker

Cracking the link between brain and skull in Archosauria: evolutionary and developmental perspectives

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The brain has a primacy in both neural control and early cranial development. Extant birds underwent through a dramatic enlargement of the brain in comparison to other reptiles. This process caused important changes to the bird skull, in particular the skull roof. However, a link between the brain regions and the skull roof elements was never formally addressed. Moreover, disagreement regarding the homology of the skull roof elements in birds with other reptiles arose in literature, due to the lack of a comprehensive approach tangling their evolution and development.

3D morphometric analysis recovers stem diapsids, stem archosaurs and early dinosaurs tightly clustered. Birds and *Archaeopteryx* are divergent. Correlation tests between the boundary of brain regions and the suture between frontal and parietal were statistically significant, suggesting a deep evolutionary link between brain regions and skull roof elements.

We implemented our evolutionary scenario with developmental data. Developmental series of *Alligator* and *Gallus* were assembled. CT scan, immunofluorescence and confocal imaging were combined to track mesenchymal condensation and ossification patterns of the skull roof along the development of the brain and its regionalization pattern. Mesenchymal cells condense early in organogenesis between the forebrain and midbrain and midbrain and hindbrain. However, it is only after establishment of the facial region and its chondrogenesis that the mesenchymal condensations of the primordial skull roof start to express Collagen I. We found no support for Sox9 and Collagen II expression in these mesenchymal condensations. Birds show a delayed patterning of the skull in comparison to reptiles. We suggest this is due to the positive allometry of the bird brain, contrary to the negative trajectory observed in reptiles. Early ossification centers for frontal and parietal appear with a one-to-one relationship with forebrain and midbrain respectively. This integration between brain regions and skull roof elements slightly decouple later in ontogeny.

In conclusion, the skull tracks the development and evolution of the brain. Non-coelurosaurian taxa show a conservative skull roof and brain morphology, whereas a strong paedomorphic signal and hyperenchephalization are found in Eumaniraptora. Skull roof elements are extremely conservative and there is little evidence for a wholesale restructuring of skull roof composition in birds as suggested by recent studies.

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S15 // Oral

Can studies on the interplay between the musculo-skeletal system and performance shed light on the paleoecology of extinct species?

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The reconstruction of the palaeobiology (ecology, behaviour and lifestyle) of an extinct species is a difficult exercise. Unfortunately, a fossil is rarely well-preserved; and thus teeth, bones, or parts of bones are the main material with which palaeontologists work due to the fact that soft tissues rarely fossilized. As such palaeontologists need to understand the adaptive nature of the morphology of the skeleton in extant species and its relation to locomotion, or behaviour while accounting for effects of shared ancestry. Palaeobiological reconstructions assume that the morphology of a species reflects its ecological adaptation(s). Bones allow movement and, whilst supporting loads, also need to respond and resist to muscular forces. As bones are shaped by force and motion, their morphology is likely to be intimately related to the movements executed. Thus, to understand the adaptive nature of the morphology of the skeleton it is essential to study the relationships between bones and muscles in living species and their relation to ecology and behaviour while taking into account potential effects of shared ancestry. In this presentation, we show how the study of the musculo-skeletal system of the cranium in relation to bite force performance allows for integrative inferences of performance and diet in extinct species of strepsirrhine primates. To do so, we use a data set of 21 living species of strepsirrhines for which data were collected on the shape of the bones of the masticatory system (cranium and mandible), the architecture of the masticatory muscles, as well as *in vivo* data on isometric bite force. Our results show that the masticatory muscles have a significant impact on cranial shape in comparison to mandibular shape. In contrast, bite force strongly impacts mandibular shape but not cranial shape. Thus, we focus on the cranial shape to reconstruct the myology of extinct species, whereas we use mandibular shape to reconstruct the bite force. These quantitative inferences on extinct species allow us to shed light on the evolution of diet in extinct species.

* Speaker

IPC5

S15 // Oral

Macrowear and tooth enamel mechanical properties

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Dental macrowear occurs when the amount of enamel removed is evident to the naked eye. The degree of macrowear can be scored and used to identify population differences related to diet. Though excessive macrowear can compromise the utility of a tooth, many mammalian species rely on a degree of enamel wear to maintain tooth functionality. Thus, the factors affecting macrowear hold important information about dietary adaptation. The loads required to cause wear are described mathematically as a function of the mechanical properties of enamel. Here, we review research exploring the link between macrowear and mechanical properties, and implicate the angle between enamel prisms and the occlusal surface as an important factor in wear-resistance. This angle changes as macrowear accrues, which affects the mechanical properties and has implications for further wear-resistance. To explore changes in wear-resistance with macrowear, we test the hypothesis that mechanical properties at the occlusal surface will change as crown height is reduced. We use nanoindentation to map the mechanical properties and microstructure of enamel in a baboon molar as its cusp height is reduced. Our results show how mechanical properties differ with degree of wear, and add to our understanding of their role in resisting macrowear.

[*] Speaker

Wrinkling of the occlusal enamel surface in Anthropoidea: insights from virtual modelling and dental topographical analysis

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During the course of evolution, various primate clades (Pitheciidae, Pongidae, Hominidae and the extinct Omomyidae) have acquired complex occlusal surfaces displaying dental wrinkles, located in the molar central basins and on cuspal inner slopes, in addition to the main cusps and crests. Early dental morphologists defined wrinkles as generated by localized thickening of the enamel (sometime referred as crenations), with than a lack of concordance between the enamel-dentine junction (EDJ) surface and occlusal enamel surface (OES) for the expression of these localized features. Hence crenations differ from features which are reflected by the surface of the dentine like folds and true cusps.

Among fossil and extant primates, taxa convergently show various degree of 'wrinkling' of their occlusal enamel surfaces suggesting potential functional values for this feature. Wrinkled basins are hypothesized to be involved in trapping/stabilizing the food item, in increasing dental longevity in relation, for instance, with wear resistance and/or stress dispersal during crushing, or in draining fluids away during food comminution by producing a network of narrow valleys. This make crenations especially interesting in terms of dental evolution. It also highlights the need to investigate the relationship between wrinkling and enamel thickness variation in primates.

Here we aim to quantitatively characterize wrinkle development in anthropoid's occlusal basin using dental topography approaches. Besides, the relative implication of enamel thickness variations in influencing the wrinkling expression (as crenations) is investigated.

We performed a quantitative study of OES in anthropoid upper molars, which were investigated using microCT and 3D surface analysis. Dental topographical variables (eg orientation, curvature, ambient occlusion) were computed for each mesh's occlusal surface and wrinkles were detected using combinations of these variables. Furthermore, the 3D enamel thickness (3DET) was computed for each molar as the minimum normal Euclidean distance from each OES polygon to the first EDJ polygon intersected.

Our method allows a better understanding of the wrinkling expression and its quantification on molar occlusal surfaces. Our approach will allow to test the functional hypotheses related to wrinkling in extant primates, and to interpret their convergent emergences in distinct primate lineages, including early Hominines like *A. afarensis* and *P. boisei*.

[*] Speaker

Functional locomotor morphology of Lophiodontidae (Perissodactyla: Tapiromorpha) with comparisons to potential modern analogues

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The Lophiodontidae are an endemic Eocene family of odd-toed ungulates (Perissodactyla: Tapiromorpha). A number of studies have been conducted into the biology and ecology of lophiodontids, drawing comparisons to tapirs based upon dental morphology and jaw mechanics. Here, we explore another aspect of lophiodontid biology – locomotion – to ascertain whether modern tapirs represent a viable analogue for lophiodontid locomotor morphology and behaviour. We laser scanned 65 forelimb bones from three species of lophiodontids, with additional specimens examined from published articles. A 3D geometric morphometric analysis was used to compare lophiodontid bone shape to modern tapir and contemporaneous perissodactyl forelimb bones. Measurements pertaining to biological or mechanical outcomes were also taken from scans (e.g. body mass measures, lever-arm ratios, long-bone ratios). Principal components analyses and neighbour-joining trees were used to visually compare morphological variation, with significant differences assessed using perMANOVAs, ANOVAs and Tukey WSD post-hoc tests. Mass estimates from humeral measurements suggest lophiodontids in this study approximate modern New-World tapirs in average body mass (155-240kg). Results from shape analysis of the humerus suggest that interspecific variation within the genus *Tapirus* is greater than differences between lophiodontids and tapirs; however, manus bones demonstrate significant differences. Lophiodontid unciform and metacarpals exhibit flattened distal joint surfaces; this disperses compressive forces across the joint facet, indicative of greater loading. In contrast to shape analyses, lever-arm ratios for upper arm muscles show similarities between lophiodontids and modern New-World tapirs. Long-bone ratios (proxy for locomotor style) demonstrate similar forelimb proportions in modern tapirs and *Paralophiodon* when compared to contemporary Eocene perissodactyls. Our morphological analyses suggest lophiodontids were not capable of moving as swiftly as modern tapirs; greater loading over the manus was most probably as a result of increased mass in the shoulder and cranial regions in lophiodontids. With the data available, we believe that modern New-World tapirs adapted for greater loading over the manus (e.g. *Tapirus bairdii)* represent the most viable locomotor analogue for lophiodontids.

* Speaker

Wear at different levels of resolution in rabbits fed diets of different abrasiveness

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To assess the effects of internal and external abrasives on tooth wear, we performed a controlled feeding experiment in rabbits fed diets of varying phytolith content and with addition of sand as an external abrasive. 16 rabbits were kept individually, each fed four pelleted diets of varying abrasiveness (no phytoliths: lucerne L; phytoliths: grass G; more phytoliths: grass and rice hulls GR; external abrasives: grass, rice hulls and sand GRS) for 2 week-periods at random order. Wear was quantified as absolute p3 length using burr marks, relative cheek tooth length (in proportion to length on lucerne) measured from CT scans, and at the end of the experiment on macerated skulls as mesowear and 3D surface texture analysis.

The 2-week-periods proved sufficient to show a significant difference of tooth wear. The wear effect was more prominent on maxillary than mandibular teeth. The relative length of the upper cheek teeth showed an additional effect of the tooth position on wear pattern. In GRS the upper third premolar had the largest decline in relative tooth length compared to others in the same tooth row. The hypselodont teeth compensated for wear by increasing growth in response to it.

The different wear patterns of the upper and lower cheek teeth were also discernible in the mesowear scores. The upper cheek teeth had more rounded cusps and a flatter occlusal relief. The impact of diet abrasiveness on the mesowear signal was only clearly visible for the most abrasive diet due to the limited sample size. However, for the second upper molar and the first lower premolar a trend of the mesowear score inverse proportional to the diet abrasiveness could be shown.

Complementing the previous findings, the 3D surface texture analysis identified increasing roughness and larger volume in surface texture features with increasing abrasiveness of the diet (L less than G less than GR less than GRS). Surface textures of antagonistic upper and lower teeth were significantly different in the L, G, and GR diets, with rougher and more voluminous textures for the upper teeth, contradicting the concept that gravity makes lower molars more susceptible to impact from abrasives, but supporting the concept of upper and lower molars as an inverted pestle-and-mortar system.

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S15 // Oral

Tooth wear, diet and ecology : From French country-side sheep to extinct antelopes from the Omo valley, Ethiopia

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The Shungura Formation, Lower Omo Valley, Ethiopia have yielded major Plio-Pleistocene paleontological and archeological contents. This formation is subdivided into 12 geological members dated by radiochronological and magnetostratigraphy methods. Next to biogeochemistry, dental microwear textural analysis constitutes an alternative approach to explore feeding ecology and thus evolutionary hypotheses thanks to this accurate chronostratigraphic framework. However, recent studies have challenged our understanding in tooth wear and have hypothesized that dental microwear textures might not reflect differences in diet but in dust or grit contents. Such assumptions may have severe consequences as our present objective is to investigate ecological segregation between taxa of bovids and to track changes in food resources in a context of environmental changes (increase of aridity).

To assess the contributions of biotic and abiotic factors in tooth wear, we conducted a controlled food testing on 180 sheep fed on different dust-free and dust laden fodders. These fodders were composed of either herbaceous dicots (clover) with and without seeds, or on herbaceous monocots (ray grass or a multi-specific assemblage of grasses), modeling the different ecodietary spaces from browsers to grazers known in the wild game.

Then, we re-interpret the dental microwear textures we gathered from 141 fossil antelopes belonging to Reduncini, Aepycerotini, and Tragelaphini, all coming from the geological members E and F over a time interval between 2.4 and 2.27 Ma. From Member E to F members, there are significant variations towards more grazing habits for reduncines and more browsing preferences for tragelaphines, a pattern that cannot be explained by differences in dust but by differences in food resources. We here conclude that these two taxa of bovids occupied more contrasted habitats. Besides, aepycerotines do not show any significant changes in diet over time attesting that as their modern relatives, they were mixed feeders, both engaged in browsing and grazing.

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Finite Element Analysis of durophagous crab predation

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The shells of bivalves protect these organisms from their environment. One of the most dangerous aspect of their life are encounter with predators. Especially crushing (durophagous) predators pose considerable threat to the mostly immobile mollusks. Amongst putative defensive adaptation in bivalves, shell shape has often been hypothesized to strengthen the valves during a predatory attack, but not much data is available to corroborate this claim. Using Finite Element Analysis we model the crushing attack of Florida stone crab on a hard clam, a soft clam, and a blue mussel. Nanoindentation tests provide material properties of the different shells, and feeding experiments inform the location of contact areas between shell and crab claw, and direction of applied force. Our results show a close relationship between shell material and the way valve symmetry distributes the loads applied by the crushing attack. The hard clam disperse the loads of a crushing attack evenly across its heavy, brittle shell. These valves experience the lowest stresses out of all the models. The soft clam model documents that these bivalves respond to the more localized stresses with deformation rather than dispersion. The blue mussel geometries show that loads are distributed in an alternating stress distribution pattern. Dispersing stress to inside or outside of the shell allows them to absorb more energy than the more brittle shells.

* Speaker

S15 // Oral

Dental growth and development in Turolian hipparionine species: comparison with extant Equus and life history inferences

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Dental histology has proved to be a valuable tool for reconstructing life histories, since dental formation times and growth rates are closely related to the animal's pace of life. The timing of the first molar eruption, for instance, correlates well with the age at weaning, while the eruption of the third molar marks attainment of skeletal maturity. Current advances in dental histology of extant equids have shed light on the pattern of growth of their hypsodont teeth, providing a solid framework for studying fossil taxa. The high diversity of the Old World *Hipparion s.l.* lineage during the late Miocene constitutes a perfect opportunity to test for differences in life history strategies related to size changes. Here, we aim to infer the life history traits of three different-sized hipparionines from the Spanish Turolian through dental histology. To achieve this objective, we analyzed the enamel growth of the lower first-second and third molars of *Hipparion concudense* (95 kg), *Hipparion gromovae* (59 kg) and *Hipparion periafricanum* (23 kg) from two Spanish fossil sites, Concud (MN12) and Rambla de Valdecebro II (MN13). Moreover, we reconstructed the enamel growth pattern of the first and third lower molar of the extant species *Equus quagga* (245 kg) for comparative purposes. In this extant equid the growth trajectory is described by a first high-speed growth phase followed by an asymptotically decreasing rate until root formation. This process spans for almost 2 years in first molars and 5 years in third molars. *Hipparion* teeth, however, grow at slower rates and during a shorter time, but following a similar growth trajectory. Considering the important differences in hypsodonty between *Equus* and *Hipparion,* the higher enamel growth rates found in *E. quagga* suggest the need to form higher-crowned teeth. The studied hipparions, however, present similar hypsodonty indexes and little difference in tooth formation, which points to a similar pace of life for all the species analyzed. Considering the coupling between size and life history, we infer a slower pace of life for the small species as formation times and extension rates are similar to those found in the larger taxon.

* Speaker

Can seasonal climatic contrast in ancient tropical contexts be estimated from growth of tropical ectotherm vertebrates as controlled by environmental drivers? An experimental study

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During the Neogene, the intensity of the contrast between wet and dry seasons may constitute a main component of climatic variations in continental areas. Our project aims the use of the growth rates that are recorded in skeletal elements of fossil ectotherm vertebrates to depict local seasonality and its change through time. Effectively the growth cycles of the ectotherms are partly controlled by environmental conditions. However, seasonal factors that may modulate growth are multiple and it is necessary to process calibrated study to interpret consistently change in bone growth rates measured in fossil remains. Our dispositive includes an experimentation in controlled conditions. Three species that are frequently yielded by Neogene outcrops from Africa were used: the fishes *Polypterus senegalus*, *Auchenoglanis occidentalis* and the turtle *Pelusios castaneus*. Specimens were bought in an animal farm and the experiment got ethical agreement (n◦ 86050). We aimed to evaluate the relative influence of three environmental parameters known to modulate growth rates and growth rhythm in ectotherms: food abundance, temperature and photoperiod. In replicated tanks, 3 groups of specimens were submitted to seasonal variations of these parameters following the variation intensities and durations observed in tropical environments of Africa, while a 4th group was reared in constant conditions. Every change applied on parameter values to simulate seasonal fluctuations was associated with the injection of a calcium-binding fluorescent dye. Temperature of the water was measured daily and somatic growth of each specimen was measured each week. At the end of the experimentation, specimens were euthanized and their otoliths and bones were sampled and prepared (thin section) for growth pattern analyses regarding the controlled framework. As a first result, we observed that inner natural rhythm has operated at least in the fishes, independently of the conditions applied. Then, food abundance appeared as the only parameter to have pulled a significant growth difference compared to control groups. Depending on the fish social status, the growth was more or less rapid, but the rhythm was similar in all tanks under similar conditions. Finally, we also observed that depending on the taxa, reduction of the food doses did not affect growth in the same respect.

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S15 // Oral

How ecologically sensitive is texture analysis of tooth microwear? Testing hypotheses of niche partitioning in sympatric species

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Recent work shows that tooth microwear analysis can be applied further back in time and deeper into the phylogenetic history of vertebrate clades than previously thought (e.g. niche partitioning in early Jurassic insectivorous mammals; Gill *et al.,* 2014, *Nature)*. Furthermore, quantitative approaches to analysis based on parameterization of surface texture are increasing the robustness and repeatability of this widely used dietary proxy. Discriminating between taxa *within* dietary guilds has the potential to significantly increase our ability to determine resource use and partitioning in fossil vertebrates, but how sensitive is the technique? Can microwear texture analysis detect differences between sympatric species which exhibit niche partitioning with significant dietary overlap? To address these questions we combined detailed dietary analysis with tooth microwear texture analysis of sympatric populations of shrew species (*Neomys fodiens*, *Neomys anomalus*, *Sorex araneus*, *Sorex minutus)* from Bialowieza Forest, Poland. Dietary analysis reveals that these populations exhibit varying degrees of niche partitioning with greatest overlap between the *Neomys* species*. Sorex araneus* also exhibits some niche overlap with *N. anomalus,* while *S. minutus* is the most specialised. Multivariate analysis based only on tooth microwear textures recovers the same pattern of niche partitioning, demonstrating that validated microwear texture analysis can provide very subtle dietary discrimination in fossil insectivores. Application of these results to a combined dataset of extinct and extant taxa has some surprising implications.

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S15 // Oral

Wear your diet on your teeth: Dental Microwear Texture Analysis as a proxy for estimating the diet of extinct South American caviomorph rodents

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Modern caviomorphs or South American hystricognathous rodents exhibit a great taxonomical and ecological diversity,with a broad spectrum of dietary habits, ranging from frugivorous to grass eaters. Their oldest record dates back to the late middle Eocene from Peruvian Amazonia. Continuous paleontological field efforts have substantially increased the fossil record of early caviomorphs, testifying of a complex early evolutionary history. The late Oligocene locality of Salla (Bolivia) has yielded a diverse assemblage of caviomorphs, including taxa representing the four extant superfamilies. The systematics of the Salla rodents is now better established, but little is known regarding their ecology and ecological interactions.

Here, we reconstructed the diet of the Salla rodents in performing a Dental Microwear Texture Analysis (DMTA) on the enamel tooth surface. Microwear analyses are proxies providing an insight not on the ability but directly on the use of teeth. The DMTA describes and analyzes automatically surface textures with a high degree of precision. We firstly analyzed the microwear texture of 79 wild specimens of extant caviomorphs showing different feeding habits that we compared with those of 241 fossil specimens from Salla. For each specimen of modern and fossil species, we performed a scan on a high resolution silicon mold of the molar occlusal surface with an optical surface profilometer (2). We then applied a scale-sensitive fractal analysis with Toothfrax and Sfrax softwares to describe the microwear textures through four variables: Asfc (complexity), epLsar (anisotropy), HAsfc (heterogeneity of the complexity), and TFV (textural fill volume).

Feeding habits among extant caviomorph species provide distinct microwear textural signals for each studied variable. However, diet distinctions for the extinct Salla species are not as marked as in extant species. Dental microwear textures vary significantly among Salla species primarily on the complexity and textural fill volume. But only main tendencies regarding the paleoecology and niche partitioning can be advocated for the Salla rodent community.

Based on complexity, *Incamys*, *Sallamys*, *Migraveramus* and *Cephalomys* appear to have been generalist frugivorous (as the modern *Dasyprocta)*, and *Eoviscaccia* might have fed on tougher items such as leaves (as the modern *Phyllomys)*. In contrast, *Protosteiromys* and *Branisamys* seemingly included blander young leaves in their diet (as the modern *Coendou)*.

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S15 // Oral

Everything matters: molar surface texture in goats fed diets of different abrasiveness

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A previous feeding experiment with sheep suggested that dust added to a diet of natural forage at a quantity of approximately 1% of dry matter had little effect on molar surface texture. Here, we maintained 28 adult female goats in four groups, fed pelleted diets of lucerne (L, without phytoliths), grass (G, phytoliths), grass/rice hulls (GR, increased phytoliths) and grass/rice hulls/sand (GRS, external abrasives at 5% of the pellet ingredients), supplemented with a necessary minimum of lucerne hay (lucerne group) or grass hay (the other groups). After 0.5 years, the animals were slaughtered and 3D surface texture analysis applied to the upper and lower second molar.

Increasing dietary abrasion in the diet (L less than G less than GR less than GRS) led to gradually increasing roughness and larger volume in surface texture features. Highest void volumes (largest pits) were found in the GRS group. This is consistent with texture results from rabbits fed the same pelleted diets. We conclude that the same diet forms similar surface textures even in two very different mammal species. Further it indicates a general diet-dependent principle of surface texture formation.

In the direct comparison of upper and lower molars, the sand diet had a significantly more pronounced effect on the upper molar, having more voluminous valleys and larger texture direction values. This contradicts the concept that gravity making lower molars more susceptible to impact from external abrasives, but supports the concept of upper and lower molars as an inverted pestle-and-mortar system.

The results indicate that external abrasives (of the size and concentration of the present experiment) do have a 3D texture effect in goats that could be relevant for dietary/environmental reconstructions based on this method.

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IPC 5

Low prevalence of molar crushing behavior in tufted capuchin monkeys, and its consequences for the investigation of seed predation in extinct mammals

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From squirrels to peccaries, seed predators are found in several mammalian orders. To access protected seeds, seed eating mammals can use their teeth in two types of ingestive i.e., non chewing behaviors. The first one involves the use of anterior teeth i.e., incisors and canines to open and remove seed shells, while the second involves the use of post canine teeth i.e, premolars and molars, to crush seed shells and get access to their content. Both can result in dental adaptations, some of which could be used to infer seed predation ability in extinct mammals. Most of the literature on adaptations to seed predation focuses on molars, which is based on the basic assumption that seed predators either (i) commonly chew hard, stress-limited food or (ii) use molar crushing to ingest food items protected by a hard shell. Both assumptions have been tested in a seed predator primate notorious for using both anterior and post-canine teeth, the tufted capuchin monkey *Sapajus apella*. The first assumption was tested by comparing hardness scores of seeds and seed shells reported in the literature. To test the second assumption, captive specimens (N=13) from Guangzhou Zoo were observed during feeding trials. Monkeys were fed with seeds characterized by either soft shell (peanut) or hard shell (walnut), and ingestive actions were scored using ethograms.

The first assumption was rejected, as seed shells were significantly harder with most seed classified as non challenging. Regarding the second assumption, molar shell crushing was observed for both soft and hard seed shells. However, monkeys performed significantly less molar crushing when opening hard shells, relying more on their anterior teeth. This low prevalence of molar shell crushing might be due to the difference in food size. Regardless, this study does not support either of the two basic assumptions, meaning that seed predators could rely less on their molars and more on their incisors or canines to ingest protected seeds.

The classification of several extinct mammals as 'seed predators' is further examined at the light of these results. Different conclusions could be drawn in some occurrences. It is therefore recommended to (a) assess the prevalence of molar crushing in other mammalian orders and (b) when it is possible, consider the whole denture when inferring adaptation to seed predation in fossils.

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S15 // Oral

Developing a systematic approach to virtual three-dimensional avian bone histology

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Bone histology in fossil vertebrates is critical to palaeobiology as it enables reconstructions of developmental age, life history, and growth rate, as well as biomechanics. Histological studies on birds have transformed our understanding of avian evolution but the production of thin sections for histology is destructive and time consuming, typically resulting in a single plane cut from a small region of interest. Furthermore, the resulting sections are two-dimensional (2D), not representing structures in their genuine three-dimensional (3D) context.

In order to mitigate some of the difficulties inherent with the use of (2D) thin sections, a non-invasive and fully 3D imaging approach can be adopted using high-resolution X-ray-based computed tomography (CT). CT is becoming increasingly widespread throughout palaeontology, from scanning whole skulls to interrogating small regions at the cellular level. Nevertheless, limited systematic work has so far been carried out to characterise bone microstructure in extant birds in 3D, a crucial prerequisite before extrapolation to fossils.

We imaged cortical bone from the midshaft of the femur, tibiotarsus, and humerus, encompassing a complete growth series of modern domestic ducks (*Anas platyrhynchos)* using highresolution synchrotron-based CT at the TOMCAT beamline of the Swiss Light Source (X-ray energy 21 keV, voxel size 1.6 μm, exposure time 180 ms, 1501 projections). We scanned 21 naturally deceased individuals: a range of juveniles (less than 6 months), and three adults (two years).

After segmentation of intracortical porosity by absolute thresholding, 2D and 3D visualisation revealed cortical microstructural changes during development, including bone volume fraction, heterogeneity in canal diameter across the cortex, and differences in canal orientation and delayed mineralisation in the humerus compared to the leg bones. Variation between bones reflects limb use: ducks are precocial and run immediately after hatching, but fly later in life. Our results corroborate published observations in 2D sections, but critically add further information in the true 3D measurement of canal networks and osteocyte lacunae, impossible from 2D sections. The next steps of this work will be to quantify the observed variations in bone microstructure through the life course, and across different extant species to characterise the influences of life history, bone mechanics, and phylogeny on 3D microstructure.

[*] Speaker

Dental 3D surface texture in guinea pigs fed fresh or dried forages reflects phytolith content and plant material properties

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Although it is still debated whether phytoliths can abrade dental tissue, recent experimental work has repeatedly shown that this can occur, even though native phytoliths are softer than dental enamel. The resulting hypothesis is that phytolith content should be reflected in dental wear features, which allows for subtle discrimination of feeding traits along the browser-mixed feeder-grazer continuum. It has, however, been noted that phytolith characteristics depend on the extraction method, with native phytoliths showing lower indentation hardness than phytoliths extracted by dry ashing. We thus propose that the state of the plant tissue, fresh or dry, will have an effect on dental abrasion.

To assess this, we performed a controlled feeding experiment with 36 adult guinea pigs, fed exclusively with three different natural forages: lucerne (no phytoliths; low silica content of 0.0- 0.4% DW), timothy grass (phytoliths, moderate silica content of 0.8% DW), and bamboo (more phytoliths, high silica content of 8.3% DW). Each forage was either fed in fresh or - harvested from the same batch/field - dried state (6 groups of 6 animals each). After three weeks, the animals were euthanized, and 3D surface texture analysis (3DST) was performed on the upper fourth premolar.

Generally, enamel surface roughness and volume increased with higher phytolith/silica content of the feed (lucerne lower than grass lower than bamboo), confirming that 3DST reflects the amount of phytoliths in the diet. Additionally, fresh and dry forages caused distinct dental surface texture signals, with fresh grass and dry grass displaying the most pronounced differences in wear patterns. Surface textures of animals feeding on fresh grass were often similar to those on fresh or dry lucerne, supporting previous reports that ’fresh grass grazers’ have a less abrasion dominated wear pattern than ’dry grass grazers’.

Our results confirm that different types of forage can cause distinct 3D surface texture patterns, but also indicate that besides phytolith content, other material properties such as moisture content can significantly affect plant fodder abrasiveness; even to such an extent that wear patterns characteristic for dietary traits (i.e. browser versus grazer) become indistinguishable.

Thus, feeding on fresh or dry grass matters and needs to be taken into account for dietary reconstructions.

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