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into a detailed computational mesh, accurately representing the major and minor airways of monitor lizards, Varanidae. The surface of the computational meshes expanded and contracted to simulate lung motion during ventilation and provided the boundary conditions for flow. During both phases of ventilation in the model, air moves caudally through the intrapulmonary bronchus and cranially through the secondary bronchi, moving between secondary bronchi through intracameral perforations.

#### A Tesla Valve in a Turtle Lung: Using Virtual Reality to Understand and to Communicate Complex Structure-Function Relationships

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The complexity of behavior of fluids within byzantine solid structures, such as the conducting airways of the respiratory system of vertebrates, presents a challenge that scientists have only recently been able to tackle; thanks primarily to advances in software and hardware engineering. We have used these advances in the processing and analvsis of radiological images, collected by either computed tomography or magnetic resonance imaging, to create mathematical models that faithfully represent pulmonary anatomy. These models allow us to analyze fluid flow, using the Navier-Stokes equation and open source computational fluid dynamics software (OpenFoam). Virtual Reality has proven an invaluable tool to both analyzing these results as well as communicating them effectively to non-specialists. Our investigations on patterns of airflow in the lungs of a semi-aquatic turtle, the red-eared slider, show that airflow patterns through this turtle lung are remarkably similar to the pattern of flow through a tesla valve. These surprising (and counter-intuitive) results are most powerfully communicated using Virtual Reality.

#### Where Does Footprint Morphology Come from? Developing Virtual Reality Visualizations for Exploring Dinosaur Track Formation

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Fossil tracks are purely sedimentary structures that preserve a substrate's flow around a moving foot. During the period of foot interaction, both the original surface and deeper layers are deformed. Fossil slabs can be exposed at bedding planes throughout this track volume. Variation in pedal anatomy, kinematics, and substrate properties are all known to influence track formation, but how do the features that make up footprint morphology arise? For extinct theropod dinosaurs, experiments with living birds offer valuable reference, yet substrate and foot opacity hinder direct observation of subsurface foot movement and sediment flow. We have developed Discrete Element Method (DEM) simulations based on guineafowl X-ray Reconstruction of Moving Morphology (XROMM) data and CT-scans of Early Jurassic fossil tracks. Foot motion data serve as inputs for dynamic DEM substrate simulations made up of millions of particles. DEM simulations of track formation are compared to the original fossil tracks, providing feedback for modifying the substrate parameters and foot motion. Splitting the substrate volume along "virtual bedding planes" exposes tracks as they emerge at any depth, elucidating how localized deformations associated with foot entry and exit generate specific features. To explore the dense volumes of 3D-data generated from these methods, we turned to an immersive virtual reality (VR) room, Brown's Yurt Ultimate Reality Theater (YURT). Our custom application creates interactive visualizations that allow us to synthesize substrate flow at the particle, particle cluster, surface, and volumetric scale. In the YURT, depth perception of the high-resolution particle volume frees up use of visual cues (e.g., colors, textures) to be used to display substrate flow patterns at any scale, while maintaining anatomical and sedimentological context—providing a dynamic perspective on the 3D-formation of dinosaur track morphology. Funded by US NSF.

#### Functional Morphology of the Reptile Heart

Wang T; Aarhus University, Aarhus, Denmark (tobias.wang@bios.au.dk) The heart of non-crocodilian reptiles (snakes, lizards and turtles) has two atria that fill an incompletely divided cardiac ventricle with oxygen-poor and oxygen-rich blood from the right and left sides, respectively. The degree of admixture of the two blood streams is reduced by several septa within the ventricle that divide the heart into three chambers (cavum venosum, cavum arteriosum and cavum pulmonale). Using CT and MRI we have described how the atrioventricular valves play an important role in directing the inflows of blood streams during cardiac filling (diastole), while the horizontal septum and particularly the muscular ridge separates flows during cardiac contraction (systole). There are large differences in the size of the muscular ridge amongst species that correlate with their ability to shunt blood flows between the systemic and pulmonary circulations, and some taxonomic groups, such as pythons and varanid lizards, have particularly large septa that provides for pressure separation between the left and right sides of the ventricle. I will discuss our frustrations in trying to pinpoint the evolutionary drivers for this trait, and I will discuss the difficulties of assigning functional roles to the cardiac shunt pattern.

#### Evolution, Development, and Regulation of Ruminant Headgear – Organizers: Katherine Brakora, Gertrud Rößner, Andrew Lee

## Disentangling Early Antler Diversity: Is There a Causal Link with Extrinsic (Climate-Related) Factors?

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Antlers are the only branched, bony appendages of apophyseal nature among mammalian headgear that can be regularly shed and rebuilt in an annual cycle. Annual cycles are controlled intrinsically by fluctuating hormone levels. At higher latitudes, this cycle is seasonally synchronized depending on extrinsic photoperiodicity, suggesting the influence of climate-related factors in their evolution. A single developmental and

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evolutionary origin has been assumed, and is considered a synapomorphy for Cervidae. Moreover, given their complexity and the physiological effort of the regeneration process, it has been argued that deciduous antlers could have been developed from previous non-deciduous antlers. Several types of branched frontal headgear (probably of apophyseal nature) were exhibited by early Miocene pecorans in the "Old World" and in North America. Differences in ontogenetical development, histological features, surface texture, and ramification mechanisms suggest that these appendages could be non-homologous, and thereby subject to independent evolution. In fact, they emerged at the same time as other headgear in several pecoran lineages, triggered by global climatic changes. As in modern antlers, four of these appendage types underwent spontaneous autotomy (or self-amputation). However, only three show evidence of complete regeneration. In these appendage types, a true coronet (indicative of regenerated antlers) is not developed, and there are differences in mineralization processes and histology, which suggest that their growth cycle was aperiodic. Antlers with true coronet and similar seasonal cycle were first recorded later, in middle Miocene sites of Eurasia. Although the meaning and origin of such innovative features is still not fully understood, it should be born in mind that these evolutionary changes were concomitant with the Middle Miocene Climatic Transition event, suggesting that the annual cycle was an evolutionary response to a new step in increased seasonality.

# Headgear and Sexual Selection in the Fossil Record: Implications for Paleoecology

Bibi F; Museum für Naturkunde, Berlin, Germany (faysal.bibi@mfn.berlin) Fossil vertebrates are often identified on the basis of diagnostic anatomical features of the skull that are shaped by environmental and dietary needs. Skeletal ornamentation that is under heavy sexual selection - such as headgear - provides an additional window onto the evolutionary history of a clade. Given different underlying selective pressures, headgear is expected to evolve faster (through random drift or female choice) and to be a more labile and sensitive indicator of population isolation than other parts of the skeleton, which are under intense anatomical and environmental constraints (e.g., cranial, dental, postcranial elements). For example, in the case of population divergence, changes in dental morphology are expected only if habitat divergence has also taken place. Changes in headgear, however, can arise rapidly following genetic divergence, even if environments and habitats remain constant. At any point in time then, headgear morphology should represent phylogeographic relationships at a finer scale than do other elements of the skeleton. This is the case in extant and fossil ruminants, in which headgear often varies significantly across the geographic and temporal range of a clade while the remainder of skeleton remains largely conserved or identical. The recognition of headgear as a rapid and sensitive marker of biotic isolation suggests that different components of the skeleton can be used to differentiate the contribution of different selective pressures on phenotype evolution. This requires a concerted study of variation and disparity in headgear, in the same way these are generally

quantified in the remainder of the skeleton. Metric, geometric morphometric, and trait-based approaches are all possible. An example is given from the African late Miocene to Pleistocene bovid fossil record, in which the rates of morphological diversification in horns and teeth are decoupled.

# Making Points: Past, Present, and Future Studies into the Origins of Ruminant Cranial Appendages

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Ruminant cranial appendages are a major feature of mammalian morphological diversity. These include four structurally distinct types of "headgear" in living ruminants (antlers, horns, ossicones, and pronghorns). Despite their familiarity, it is unknown if the different headgear types evolved in parallel or if they share deep homologies in their genetic and developmental architecture despite important anatomical differences. First, we summarize the main types of headgear and the living and fossil taxa that possess them. Then we review key discoveries in the 20th century that set the stage for current research, from Mendelian genetics and tissue transplantation experiments in domestic species to phylogenetic studies that produced diverse topologies and hypotheses of ruminant evolution. Many crucial guestions remain in our understanding of headgear. What is the relationship between genotypes, molecular expression patterns, histogenesis, and phenotypes, especially in ossicones and pronghorns? How do these traits and processes vary between the sexes and across populations, species, and major clades? And how can we use a greater knowledge of development and variation in living species to most productively analyze and interpret the headgear of extinct species, and vice versa? Deeper, more integrative knowledge of headgear biology may suggest novel applications in biodiversity conservation and management, herd improvement, veterinary medicine, and models of human disease, and simultaneously help resolve ruminant phylogenetics, clarifying an important story in mammalian evolution. With greater collaboration by researchers across taxa, fields, and methods of study, we have the potential to gain powerful insights into one of the most recognizable and important groups of vertebrates.

#### Multiple Physiological Constraints Affect the Antler Growth, Morphology and Evolution

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Sexual selection has been widely accepted as the main force driving the evolution of animal weapons, including antlers, as suggested by both intra- and inter-specific studies. However, the genetic potential acquired during evolution is never reached in wild animals, but only under captivity with intensive care and nutrition. Thus, we have been trying to find evolutionary patterns in a sexual secondary trait grown