

PELYCOSAURIAN “LINEAGES”: A META-ANALYSIS OF THREE DECADES OF PHYLOGENETIC RESEARCH

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Pelycosaur-grade synapsids comprise the first major radiation of Synapsida, and their phylogenetic relationships have been the subject of over three decades of research in a cladistic framework. In this time three major “lineages” of shared character-taxon matrices have been created, each with distinct sets of characters and taxa which have been analyzed using different tree-construction methods. The majority of papers analyzing “pelycosaur” phylogeny belong to one of these research lineages. Papers rarely cross over to another lineage, but occasionally borrow a few characters from other research lineages. This bias in the sources of “pelycosaur” phylogenetic datasets means that there have been fewer truly independent tests of hypothesized relationships within the group than the number of published analyses would suggest, and that our understanding of “pelycosaur” phylogeny may be less certain than is sometimes portrayed. Here, we use a novel method to create a “pelycosaur” metatree to summarize our current understanding of the group’s phylogeny. We also perform a bipartite network analysis to describe relationships between individual datasets and to characterize distinct research lineages.

The topology of our metatree shows the most similarity to the results of the largest research lineage, reflecting the large contribution those papers made to the underlying dataset. We recover a monophyletic Caseasauria and Eupelycosauria. Relationships within eupelycosaur subclades also generally match previous hypotheses from the largest lineage. However, within Caseasauria, a monophyletic Eothyrididae falls within Caseidae, reflecting the influence of multiple dataset lineages on recent work on the group. The bipartite network analysis confirms the division of datasets into three main lineages. Moreover, the matrices in the older lineages are more conservative, with fewer character additions or deletions, whereas those in the newest lineage are more variable. Our results reveal how scientific practice has influenced our understanding of “pelycosaur” phylogeny, and suggest that the construction of additional, independent datasets will be an important step in further testing conventional wisdom and traditional phylogenetic hypotheses.

Technical Session XII (Friday, October 19, 2018, 2:30 PM)

FIRST 3D ENAMEL SURFACE TEXTURE ANALYSIS OF EXTANT REPTILES: ESTABLISHING A REFERENCE DATA SET FOR DIET RECONSTRUCTION OF EXTINCT SAUROPSIDS

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Teeth are usually the best-preserved fossil remains of vertebrates as dental enamel is the material most resistant against alteration. Dietary reconstruction based on tooth morphology and wear has always been a key component in palaeontological research. However, for 2D microwear and 3D microtexture analyses, reference datasets for extant species with known dietary habits are needed in order to establish feeding hypotheses for extinct taxa. To date, the majority of dental wear studies have focused on mammals, as these methods were initially applied to examine diet and ecology in primates, cetartio- and perissodactyls. Before the rise of mammals, the vast majority of Amniota did not show distinctive oral food processing through mastication, but rather employed a crop and swallow ingestion with short food-to-tooth contacts. Extant non-avian Sauropsida (“reptiles”) still rely on this simple food intake strategy, regardless of their dietary preferences. In order to establish 3D surface texture analysis for application to extant and extinct non-avian Sauropsida as well as other homodont tetrapod taxa (e.g., Synapsida), we have compiled a large dataset of 3D enamel surface textures of 234 teeth from 54 specimens belonging to 17 extant squamata taxa, representing eight different dietary traits. A combination of roughness (ISO 25178), flatness (ISO 12781), furrow, and scale- sensitive fractal analysis (SSFA) surface texture parameters significantly separate faunivores from herbivores and distinguish durophagous and frugivorous taxa. We found a broad overlap in textures between insectivores and omnivores, but these dietary groups are nonetheless separable by the height parameters Sp and Sz as well as in furrow parameter madf. The algae-eating marine iguana is well distinguished but nested within unspecialised herbivores, while bearded lizards, which feed primarily on eggs and hatchlings, form a distinctive group within the faunivore parameter space. Finally, we tested for variability in texture parameters within the same jaw and found them to be independent of tooth position. Our results indicate that short tooth-to-food contact in reptiles is sufficient to create characteristic wear patterns that allow for dietary discrimination, thus enabling us for the first time to pursue palaeodietary reconstruction through enamel surface texture analysis based on a modern reptilian reference dataset. This study further demonstrates the feasibility of using isolated teeth from reptilian and possibly other homodont taxa for dietary reconstruction.

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Romer Prize Session (Thursday, October 18, 2018, 10:15 AM)

THE INTERVERTEBRAL DISK GAVE REPTILES IMPROVED AXIAL MOBILITY—MORPHOLOGICAL, HISTOLOGICAL, AND PHYLOGENETIC EVIDENCE FOR INTERVERTEBRAL DISKS IN FOSSIL NON-MAMMALIAN AMNIOTES.

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Changes in the vertebral column are one of the major trends in the evolution of vertebrates. From the morphological perspective, the vertebral centra differ in the different clades of vertebrates. In amniotes, four different centrum shapes are typically recognized: amphicoelous, platycoelous, procoelous, and opisthocelous, with the latter two representing ball-and-socket joints. The notochord, which is an ancestral feature of all

vertebrates and present in amniote embryos, developmentally contributes to the adult vertebral column of mammals as the nucleus pulposus (NP) which is the internal part of the intervertebral disk of mammals (intervertebral disk proper), but not present in birds. The NP has large cartilage cells of notochordal origin and is surrounded by the annulus fibrosus which consists of fibrocartilage. The intervertebral disk is situated between the cartilaginous endplates of the vertebral centra and is encased by ligaments connecting the vertebrae.

Conventional wisdom holds that reptiles cannot have an intervertebral disk. However, based on histology and morphology, we posit that the intervertebral disk proper is not a mammalian autapomorphy and show that an intervertebral disk is present in many fossil and a few recent reptile clades. On the one hand, we found soft tissue preservation in the intervertebral spaces in the articulated anterior dorsal vertebral column of a Jurassic ichthyosaur which clearly shows the presence of intervertebral disks. There appears to be a large NP with notochordal cells surrounded by the annulus fibrosus. On the other hand, we observed different cartilage cell types that indicate the presence of intervertebral disks in sauropterygians, choristoderes, basal archosauromorphs, and dinosaurs. Furthermore, our hypothesis is supported by vertebral centrum morphology because in platycoelous vertebrae lacking an NP, intervertebral movement would be restricted to translation, resulting in a stiff vertebral column.

We offer an evolutionary scenario, wherein the plesiomorphic amphicoelous vertebra, the notochord becomes constricted, forming a spherical accumulation of notochordal cells, the NP. The evolution of the NP was thus prerequisite for the evolution of the platycoelous centrum, which in turn was prerequisite for the evolution of a synovial intervertebral joint in pro- and opisthocelous vertebrae. These results take us closer to understanding the evolution and development of the amniote vertebral column.

Technical Session XVIII (Saturday, October 20, 2018, 3:30 PM)

A TIME-CALIBRATED PHYLOGENY OF NORTH AMERICAN ARVICOLINE RODENTS: INSIGHTS INTO DIVERSIFICATION AND TAXONOMY

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The study of fossil arvicoline rodents has largely been immune to modern phylogenetic methods because, more often than not, all we have are isolated molars with few preserved apomorphic characters. This, combined with species richness and homoplasy caused paleontologists to rely on “expertograms” as a source for phylogenetic hypotheses, rather than modern analytical approaches. Molecular data provide a powerful tool for assessing phylogenetics of arvicoline rodents. I generated a phylogenetic hypothesis based on molecular data from GenBank that includes all 36 extant North American species of arvicolines. I present the first time-calibrated phylogeny of North American arvicoline rodents using Bayesian methods.

A robust phylogeny with time calibration allows me to test hypotheses concerning the timing of the diversification of clades. I exemplify this with the clade *Microtus*. My time-calibrated phylogeny suggests that the crown clade of North American endemic *Microtus* diversified at least 2.5 Ma. The oldest occurrence of *Microtus* in the North American fossil record is based on a lower first molar with three closed triangles (*Allophaiomys*) from the Nash Fauna at 2.1 Ma. The maximum documented age of *Microtus sensu stricto* (five closed triangles on lower m1) is at 1.2 Ma. My data suggests that *Allophaiomys pliocaenicus* may be a member of the crown clade, which would provide a close correspondence between the fossil record and the time-calibrated molecular phylogeny. The alternative is that we are missing a fossil record of approximately a million years. Broader implications for this include confirmation that the dominant in-group molar morphology of five closed triangles evolved after the diversification of the clade and implies that the taxonomic recognition of *Microtus pliocaenicus* is warranted.

Podium Symposium (Friday, October 19, 2018, 8:30 AM)

FLESHING OUT THE PAST BY ENHANCING RADIOGRAPHIC CONTRAST IN THE PRESENT: SPICECT, DICECT, AND VASCULAR INJECTION OF EXTANT DIAPIIDS TO BETTER UNDERSTAND DINOSAUR BIOLOGY

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Fossil vertebrates tend to preserve just the hard parts like bones and teeth. Time has stripped the biology from the fossils, challenging our ability to understand the function, physiology, and behavior of extinct organisms. As a result, paleontologists have long sought to reconstruct the soft-tissue attributes of extinct species. Studying the soft tissues of the extant outgroups that phylogenetically bracket the extinct taxa has provided a window into the past, with successes being achieved using dissection and other traditional techniques. However, the jump to 3D modeling and simulation-based hypothesis testing requires anatomical detail that standard x-ray computed tomography (CT scanning) cannot fully provide due to a lack of soft-tissue contrast. The goal of this presentation is to present our team’s efforts to enhance soft-tissue contrast in CT of extant diapsids as a means to reconstruct soft-tissues in fossils. The use of contrast media such as iodine and barium that absorb x-rays dramatically increases anatomical resolution. Our team has been using diffusible iodine-based contrast-enhanced computed tomography (diceCT) to stain and visualize a diversity of soft-tissue systems (e.g., muscles, nerves, brain, epithelia, glands) in the heads of extant diapsids. We also recently developed a more rapid iodine-based technique called spiceCT that involves selectively perfusing (the “sp”) in spiceCT specimens by injecting iodine into the vascular system, yielding excellent results in hours rather than the days, weeks, or months required for diffusion-based techniques like diceCT. Likewise we have developed a barium-based technique called differential-contrast dual-vascular injection (DCDVI) to explore arterial and venous circulation. These techniques have allowed us to clarify the relationships between soft and hard tissues using µCT and diagnostic (hospital) CT, providing better osteological correlates for restoring soft-tissue attributes of fossils. Examples include studies of the evolution of: (1) the brain and neural tissue that provide insight into sensorineural evolution (diceCT); (2) the eyeball and orbital soft tissues that test hypotheses on the visual apparatus of extinct birds and other dinosaurs