



# 9<sup>th</sup> International Meeting on the Secondary Adaptation of Tetrapods to Life in Water

Virtual Meeting

CHILE

April 19-23, 2021

## ABSTRACT BOOK

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**9<sup>th</sup> SECAD**  
**2021 CHILE**

## Keynote Presentations

## **BONE BIOLOGY IN SECONDARILY AQUATIC TETRAPODS**

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<sup>1</sup>Northeast Ohio Medical University, Anatomy and Neurobiology, 4209 State Route 44, Rootstown, USA

Most lineages of secondarily aquatic tetrapods independently evolved similar changes to their postcranial skeleton, including flippers, increased bone thickness, and hindlimb loss. By studying the developmental mechanisms associated with each of these phenotypes, developmental biology may offer novel insights into the bone biology and physiology of secondarily aquatic tetrapods. Flippers evolved in marine mammals and reptiles, and sea turtles. These soft-tissue flippers are supported internally by long digits that may contain supernumerary elements. In dolphins, these supernumerary elements are likely the result of prolonged outgrowth of the limb coupled with increased joint formation under the influence of interdigital FGF and WNT protein signaling. It could be that the supernumerary digits of aquatic marine reptiles, including ichthyosaurs, also utilized a similar molecular strategy. Beyond flippers, hyperostosis is also common in modern and fossil secondarily aquatic tetrapods, including marine mammals and reptiles, crocodylians, penguins, etc. This thickening of bones has been the subject of microanatomical studies of phenotype and inferences of habitat are especially powerful with integration of evidence from stable isotopes. In at least the cetacean lineage, hyperostosis may have been an exaptation that allowed the skeleton to act as ballast to counteract body buoyancy. Study of bowhead whales showed hyperostosis in rib bones as was likely the result of inhibition of the epigenetic regulator of bone phenotype, EZH2. Finally, limb loss in secondarily aquatic taxa, including manatees and sea snakes, is probably the result of dysfunctional signaling centers in embryonic limbs, as documented in dolphins and pythons. Although these studies offer insights into some morphologies characteristic of secondarily aquatic tetrapods, we still lack an understanding of novel aspects of calcified tissue biology: prevention of skeletal senescence, production of calcium-rich baleen in mysticetes, and function of mechanosensitive osteocytes in a hyperostotic extracellular matrix.

## ICHTHYOSAURS: TETRAPODS IN A FISH SUIT

MARTA FERNANDEZ<sup>1</sup>

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Among reptiles, ichthyosaurs can be considered as representing the “summit” of secondary adaptation to marine life. They evolved after the Permo-Triassic extinction becoming major components of marine ecosystems worldwide for almost 150 million years. Their fish-body profile was only paralleled in the Cenozoic by Cetacea. Ophthalmosaurid ichthyosaurs, the youngest and more derived clade, diversified soon after they emerged and became dominant along 76 Mya until the final extinction of the group. During the last two decades, taxonomic revisions, new findings, and micro and macro morphological analyses have shown that the diversity of Ophthalmosaurids (both in terms of species richness and ecological diversity) was more significant than previously supposed. The evolutionary scenario built upon the fluctuations of diversity through time shown an increased species richness during the Late Jurassic, a peak of disparity during the Early Cretaceous followed by a fall in their ecological diversity without the subsequent rise of new phenotypes by the Cenomanian. These factors and global environmental changes contributed to the final extinction of the group in the late Cenomanian. Despite the significant advance in our understanding of the evolution of the group, changes associated with their diversification are still poorly understood. At first glance, their skeletons do not seem to have been highly diverse but, under a common “fish-suit”, amazing alternatives of morphologies are hidden. The external nares and the zeugopodium-mesopodium pattern showed significant diversity, and, independently, both regions of the skeleton showed a tendency towards increasing complexity. Of particular interest are the changes in the connectivity pattern of the proximal fin elements that could have led to diverse swimming modes (e.g., differences in maneuverability). Despite the significant paleobiological information content in the sclerotic rings, variations of the internal and external diameters (as proxies of the cornea and eyeball size) have not received much attention. Some of these features could represent ecological characters and, in this sense, could be used as other traits to detect minor shifts in the ecospace occupation by Ophthalmosaurids. Not only for the case of Ophthalmosaurids but also all Mesozoic marine reptile communities, the joint and interdisciplinary efforts from different areas such as functional morphology, comparative phylogeny, autoecology, and ecospace modeling approaches represent a promising and exciting area for future research.

## **ABOVE AND BELOW THE WAVES: MARINE DIVING AND SOARING BIRDS IN THE CENOZOIC**

DANIEL KSEPKA<sup>1</sup>

<sup>1</sup>Bruce Museum, 1 Museum Drive, Greenwich, CT, USA

Crown birds expanded into many specialized ecological niches shortly after the K-Pg extinction. Sphenisciformes (penguins) are among the first crown birds to appear in the fossil record. Recently evidence has built the case for an origin of both total group and crown group penguins in Zealandia. Fossils reveal that penguins rapidly achieved a wide range of morphologies and that the modern penguin fauna is depauperate in larger species but also shows feeding adaptations not seen in pre-Pliocene penguins. Tragically, at least one species of penguin is now known to have been wiped out by humans. Another group with a rapidly expanding fossil record is the Pelagornithidae. One of the most enigmatic groups of extinct birds, it remains uncertain which major branch of the avian tree of life pelagornithids occupy. Arising in the Paleocene, they achieved the largest known avian wingspans by the Oligocene and survived until the late Pliocene. This talk will touch on recent advances in the understanding of penguin and pelagornithid evolution and the many questions that remain.

\*Project supported by National Science Foundation award DEB1556615

## EVOLUTION OF MARINE TETRAPODS ALONG WESTERN GONDWANA: A FOCUS ON THE CONE OF SOUTH AMERICA

NICHOLAS PYENSON<sup>1</sup>

<sup>1</sup>Smithsonian Institution, National Museum of Natural History, Department of Paleobiology, 10th and Constitution NW, Washington, United States

Marine tetrapods are four-limbed vertebrates that have adapted to life in marine ecosystems. Since the end-Permian mass extinction, many different vertebrate lineages have evolved marine descendants from land ancestors, including amphibians, reptiles, birds, and mammals. The marine tetrapod fossil record reveals information about these ecological transitions (and their morphological transformations) that we otherwise would not know, including examples of convergence and unique innovations. Today, marine tetrapods living off the coasts of South America represent a coarse latitudinal mirror to those in North America (especially along the Pacific coasts), with some notably exceptions, such as penguins and walruses, which are restricted to their southern and northern realms. At different times in the geologic past, the western margin of Gondwana (or the Panthalassian coastline) had both similarities with marine tetrapods faunas elsewhere in the world. Mesozoic fossil marine tetrapods from the Triassic of Chile, Jurassic-Cretaceous age marine reptiles from the Neuquen Basin of Argentina, Torres del Paine National Park in Chile, and the late Cretaceous of central and southernmost Chile are mostly represented by globally represented taxa (e.g., metriorhynchid crocodyliforms, ichthyosaurs, plesiosaurs, and mosasaurs). By the late Cretaceous, marine reptile assemblages show the strongest similarities with Antarctica, New Zealand, and even Japan, suggesting the onset of pan-Pacific dispersal for some of these groups (e.g., elasmosaurid plesiosaurs, and sea turtles). The end Cretaceous through early Paleogene record of marine tetrapods in South America is sparse, although the Neogene record of South America from Peru and Chile is exceptional for its abundance, especially from the Pisco and Bahia Inglesa formations, respectively. This part of the record coincides with a rise in global marine productivity unrivalled by any other time in the past, and the fossil marine tetrapod assemblages from Peru and Chile essentially mirror the assemblages from western North America, sharing many co-occurring groups of marine mammals. The Neogene marine tetrapod record of South America, however, is unique in several ways: it preserves major faunal turnovers observed throughout the hemisphere (e.g., in pinnipeds and seabirds); ecomorphologically convergent extinct taxa such as *Odobenocetops* and *Thalassocnus*, found nowhere else; and spectacularly abundant fossil sites which, in some cases, preserve ecological snapshots. The increasing pace of discoveries in the past 25 years, especially from Chile and Argentina, suggest that improvements over long-standing collecting and reporting biases will reveal even more complexities to the evolution of marine tetrapods along western Gondwana.



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## **Online Presentations**

### **Symposium Online: “Eating down under: feeding as a driver for the evolution of marine tetrapods”**

Tuesday 20<sup>th</sup> April (10:30 – 13:00 GMT-4)

Moderator: Dr. Carolina Loch



## HOW MUCH KELP COULD A SEA COW EAT? IDENTIFYING CARBON SOURCES TO SIRENIAN DIETS THROUGH AMINO ACID STABLE ISOTOPE FINGERPRINTING

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The discovery of Steller's sea cow (*Hydrodamalis gigas*) during the mid 18<sup>th</sup> century marked the first documentation of a species of sirenian inhabiting high latitude, kelp-dominated waters. This habitat preference suggested that the ecology, as well as the physiology, of *H. gigas* was radically different from that of all other extant sirenians, which are restricted to tropical/sub-tropical seagrass meadows and freshwater ecosystems. Unfortunately, the quick extermination of *H. gigas* by human hunting wiped out any chance for a thorough scientific study of this unique marine mammal. Observations of kelp consumption made by Wilhelm Steller and other explorers suggest that kelp was part of the animal's diet, but identifications and descriptions of plants ingested by these animals are open to interpretation, leaving much doubt as to whether sea cows actually were significant kelp consumers. We assessed the contribution of kelp to the diet of *H. gigas* by analyzing the carbon isotopic composition ( $\delta^{13}\text{C}$ ) of essential amino acids (EAA) in bone collagen. EAA are ideally suited as source tracers because sources that biosynthesize EAA – bacteria, fungi, vascular plants, and algae – each have source diagnostic  $\delta^{13}\text{C}$  EAA patterns or fingerprints. These fingerprints remain largely intact during the trophic transfer because animals cannot biosynthesize EAA. Within aquatic primary producers,  $\delta^{13}\text{C}$  EAA fingerprints can discriminate marine kelp from seagrasses, freshwater plants, and other macroalgae. We sampled bone collagen from three species of sirenian – *H. gigas* (n = 7), *Trichechus manatus* (Florida manatee, n = 6), and *Dugong dugon* (Australian dugong, n = 3) – and compared  $\delta^{13}\text{C}$  EAA fingerprints from these samples with those recovered from representative samples of modern kelp, other macroalgae, seagrasses, and freshwater plants. Specimens of *H. gigas* included historic material from the Commander Islands in the Bering Sea (~200 years old) and fossil material of late Pleistocene age from Monterey Bay, California. Using multivariate classification methods, we found  $\delta^{13}\text{C}$  EAA fingerprints of *H. gigas* matched those of kelp, fingerprints for *D. dugon* grouped most closely with seagrass, and fingerprints for *T. manatus* were split between those grouping with seagrasses and others that clustered with freshwater plants. Our results suggest *H. gigas* was an important consumer within the kelp ecosystems that flourished along the North Pacific coastlines, and that this species favored kelp species over other producers available within these ecosystems.

\*Project supported by: National Science Foundation (SGP EAR 0847413).

## LEAVING THE TRIANGLE: MARINE TETRAPOD TOOTH GUILDS USING AUTOMATED HIGH-DENSITY 3D GEOMETRIC MORPHOMETRICS

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Defining feeding guilds based on tooth morphology is an entire subfield in marine tetrapod science, which essentially started with a seminal paper by Judy Massare in 1987. However, these assessments have mostly been qualitative, subjectively placing teeth on a triangle using a series of criteria that draw both from tooth shape, rarely preserved gut content, and killing/hunting behaviour. Moreover, some of the data at the foundation of these guilds have proven to be debatable and there is an ever clearer need for a testable, quantitative framework to assess feeding guilds. We develop a novel protocol that incorporates the pseudo-landmarking technique into high-density geometric morphometrics procedures, sampling 3D surface models of tooth crowns automatically and densely (e.g., 2000 surface landmarks) after placing just 5 fixed landmarks on each tooth. This very dense sampling of shape permits full characterisation of crown shape, and we provide the first ever quantification of dental morphospace occupation among a sample of mosasaurs, ichthyosaurs, plesiosaurs, archaeocetes, and odontocetes with conical (i.e., non-multicuspid) teeth. A crushing-to-piercing transition is evident along the first axis of the PCA-based morphospace, while the presence and shape of carinae, as well as crown curvature, is captured by the second axis. This allows an efficient visualisation of tooth shape differences and definition of regions/guilds with just two axes that explain ca. 90% of the total variance. Because crown shape has a direct functional signal, our results provide important data to better understand how marine tetrapods evolved and functioned. Despite their gigantic size, the teeth of the largest marine macropredator ever, the phyteteroid *Livyatan melvillei*, have crowns with an unremarkable shape, occupying a position close to the center of the morphospace. In fact, peculiar structures such as crown curvature or carinae are mostly recorded on medium-sized teeth, suggesting that a scaling factor is at play. Similarly, crown shapes that have rarely or never been evolved, either by certain groups or during certain time periods, also carries information. For example, the perfectly straight teeth of the Early Jurassic ichthyosaurian *Temnodontosaurus platyodon* with protruding flange-like carinae are unique and indicate neoichthyosaurs developed a unique pathway towards hypercarnivory, albeit only once. Further work will incorporate as many different taxa and tooth-shapes into the morphospace as possible to usher in a new, quantitative paradigm for understanding marine tetrapod feeding ecology.

\*Project supported by: Fonds De La Recherche Scientifique - FNRS (Grants MIS F.4511.19, FRIA fellowship); partenariat Hubert Curien-Tournesso

## FUNCTIONAL MORPHOLOGY, BITE PERFORMANCE, AND NICHE PARTITIONING AMONGST SYMPATRIC MARINE REPTILES

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Jurassic marine ecosystems were dominated by a diverse assemblage of reptiles – plesiosaurs, ichthyosaurs and thalattosuchian crocodylomorphs. These groups coexisted and partitioned the higher orders of food webs for over 50 million years. Yet, their feeding ecology have primarily been inferred from similarities of their skulls, mandibles and teeth with those of modern aquatic tetrapods – comparisons that have only rarely been tested in a quantitative manner. We assembled a dataset of 43 plesiosaurian, ichthyosaurian and thalattosuchian taxa scored for 16 continuous craniomandibular and dental characters known for their functional significance. We analysed this dataset with multivariate ordination and statistical techniques to assess functional similarities and differences amongst and within each marine reptile lineage. The results show that: (1) phylogenetically closely related taxa are characterised by similar craniodental functional features; (2) taxa with similar inferred feeding behaviours, regardless of clade membership, are characterised by analogous morphological features. For example, inferred small-prey specialists (piscivory and/or teuthophagy) have longirostrine skulls (ichthyosaurs, Peloneustes-like pliosaurids, metriorhynchines, non-machimosaurin teleosauroids), with numerous small teeth, comparatively long and shallow mandibles, smaller muscle adductor groups, which contribute to fast but less efficient biting performances. Whereas macropredators (large-bodied pliosaurids, geosaurins, machimosaurins) often had specialised dentition, comparatively deep mandibles, and enlarged muscle adductor attachments which contribute to slower but more efficient biting performances. Overall, this study reveals multiple instances of morphofunctional convergent evolution, which is concordant with previous ordination analyses based on tooth morphology. The exception are the long-necked plesiosaurs, which had an unusual combination of dental and mandibular characteristics, hints to a feeding strategy that was unique this group. With the same methodology we investigated the macroevolutionary patterns across two well-sampled formations of the Sub-Boreal Jurassic Seaway: Oxford Clay Formation (OCF – Callovian-early Oxfordian, Middle-Late Jurassic) and Kimmeridge Clay Formation (KCF – Kimmeridgian to Tithonian, Late Jurassic) of the UK. Analyses show that the ecosystems in the OCF and KCF were markedly distinct in faunal composition and structure. The transition from the OCF to the KCF involved a shift from a Middle Jurassic assemblage dominated by small-bodied specialists to Late Jurassic assemblages characterised by a wide diversity of macropredators. This trend, which occurred in concert with deepening of global and local sea levels, was primarily driven by the diversification of gigantic pliosaurids and derived geosaurins, alongside with the decline of piscivore thalattosuchians and small-bodied pliosaurids.

## MIOCENE MACRORAPTORIAL SPERM WHALES: ANATOMICAL CLUES, DENTAL DAMAGE, AND LACK OF DIRECT EVIDENCE

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Among extant cetaceans, many species feed on relatively small prey that are not processed before being swallowed. An exception to this pattern is the killer whale *Orcinus orca*; in populations of this large delphinid, collaborative hunts allow for the capture of larger prey, including other marine mammals, which are consumed by tearing the carcass into smaller pieces. Going back in time, the earliest fully aquatic cetaceans (basilosaurids) retained an heterodont dentition with grasping anterior teeth and cutting cheek teeth. With such an oral apparatus, at least some large basilosaurids were proposed to have preyed upon other cetaceans, as testified by the discovery of predators' stomach contents and bite marks on prey's skulls. Early heterodont odontocetes most likely retained the ability to cut their prey into pieces, and larger taxa (e.g., *Ankylorhiza*) were proposed to have occupied ecological niches similar to *Orcinus*. Among modern odontocete lineages, several middle-to-late Miocene members of the superfamily Physeteroidea (sperm whales) have been interpreted as macroraptorial predators. Though displaying a roughly homodont dentition, *Acrophyseter*, *Albicetus*, *Brygmophyseter*, *Livyatan*, and *Zygophyseter* display cranial, mandibular, and dental features that differ from other physeteroids and suggest the ability to prey upon large prey, including other marine mammals. Robust upper and lower jaws bearing large cylindrical teeth and voluminous temporal fossae imply the ability to produce powerful bites and to withstand the associated mechanical stresses, an interpretation that is in line with the recent observation of prominent Hunter-Schreger bands in the thick enamel of a tooth of *Livyatan* from the Miocene of Chile. More circumstantial evidence helps further supporting this interpretation. First, bony outgrowths observed along alveoli of *Acrophyseter robustus* were identified as buccal maxillary exostoses, and were hypothesized to have developed in reaction to strong loads related to powerful bites. Interestingly, a seemingly analogous condition was observed in the heterodont odontocete *Ankylorhiza*, similarly interpreted as macrophagous. Secondly, computed tomography and visual inspection of a set of 45 large stem physeteroid teeth from the Miocene of Belgium revealed chipping fractures along the crown and vertical root fractures in the apical region of the massive root; those most likely indicate contacts with hard material and, more tentatively, the application of strong and repetitive bites forces. Whereas more direct evidence (digestive tract contents and the more challenging identification of bite marks) is still missing, stable isotope analyses should allow further testing the position of these extinct sperm whales in Miocene marine trophic chains.

## **ARE PINNIPEDS HOMODONT? SHAPE ANALYSES DEMONSTRATE A DIVERSITY OF PINNIPED TOOTH SHAPES AND SUGGEST COMPLEX FEEDING ECOLOGIES**

CARLOS PEREDO<sup>1</sup>

<sup>1</sup>University of Michigan, Earth and Environmental Science, Assistant Professor, Ann Arbor, USA

Pinnipeds are a clade of marine carnivorans that evolved from terrestrial ancestors in the Oligocene and become increasingly aquatic throughout their evolutionary history. Unlike terrestrial carnivorans, extant pinnipeds, which largely feed on fish, do not masticate or process prey with their teeth before swallowing. The posterior teeth of pinnipeds are often described as homodont; several lineages of extant pinnipeds have a reduced or simplified dentition with incisiform cheek teeth. This trend towards homodonty occurs in other marine mammals, such as whales, and may represent an aquatic adaptation. But potential links between dental shape and feeding ecology remain unclear. This study quantifies shape across the cheek teeth of extant pinnipeds and demonstrates a surprising diversity of dental shapes. Both otariids and phocids preserve a remarkable diversity of dental shapes beyond the simple, incisiform, conical pegs typically associated with homodonty. The diversity of dental morphologies across both clades suggests multiple distinct functions and feeding ecologies, and calls into question whether simple, conical teeth are an aquatic adaptation.

\*CMP supported by: National Science Foundation, NSF Award #1906181

## WERE EOCENE AND OLIGOCENE STEM CETACEANS SUITED FOR SUCTION FEEDING?

ALEX WERTH<sup>1</sup>, CARLOS PEREDO<sup>2</sup>, CHRIS MARSHALL<sup>3</sup>, MARK UHEN<sup>4</sup>

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Numerous recent studies have suggested that filter feeding arose in mysticetes through an intermediary stage involving suction feeding. This explanation, which has been offered with varying scenarios and diverse evidence, generally posits that prior to the evolution of effective baleen filtration, many partly or wholly edentulous fossil species could have captured prey via subambient pressures generated intraorally, which would carry water-borne food items into the mouth. Suction feeding has evolved repeatedly in odontocetes, with at least seven odontocete lineages including fully or functionally edentulous suction feeders. But how well suited were early whales—different lineages of archaeocetes, stem odontocetes, and stem mysticetes—for generating and using suction for prey capture and transport? Our comparative investigation aims to identify the full breadth of morphologies that facilitate suction feeding in obligate suction feeders, including cranial, mandibular, and hyoid osteology, dentition, and other morphological and paleoecological data. Then, we compare these diverse morphologies to those observed in fossil taxa to establish the extent to which each may have been facultative or obligate suction feeders. For example, basilosaurid archaeocetes and some stem toothed mysticetes have differentiated dentitions, traditionally associated with raptorial feeding, suggesting that the anterior teeth may have been used for prey capture while the cheek teeth were for oral processing of prey. However, other morphological evidence, such as robust hyoids in these taxa, suggest some capacity for suction, perhaps as intraoral transport from the front to the back of the mouth and to retain food items within the oral cavity. Valuable information regarding important morphological features (notably the tongue and hyoid) of many fossil taxa remains sorely lacking, but our analysis demonstrates the utility of identifying and applying multiple morphological (osteological, dental, and soft tissue) and ecological traits to better evaluate the likelihood of different feeding mechanisms and foraging methods. We found that like many extant cetaceans, numerous extinct cetacean taxa, notably a number of stem mysticete genera, very likely could also have been effective suction feeders. Some other secondarily aquatic tetrapods could also have been effective suction feeders.



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## **Online Presentations**

**Symposium Online: “The evolutionary history and paleobiogeography  
of the Latin American fossil aquatic mammals and its connections to  
the global record – III edition ”**

Wednesday 21<sup>st</sup> April (10:00 – 14:00 GMT-4)

Moderator: Drs. Mónica R. Buono & Carolina S. Gutstein

## PLATANISTOIDEA AND THEIR PREVIOUSLY UNKNOWN HISTORY IN MIOCENE SOUTH AMERICAN WETLANDS

ALDO BENITES-PALOMINO<sup>1,2</sup>, JOHN J. FLYNN<sup>3,4</sup>, CHRISTIAN DE MUIZON<sup>5</sup>, GABRIEL AGUIRRE-FERNÁNDEZ<sup>1</sup>, DIANA OCHOA<sup>6</sup>, JULIA TEJADA-LARA<sup>2,3,4,7</sup>, ALI ALTAMIRANO<sup>2</sup>, PATRICE BABY<sup>8</sup>, RODOLFO SALAS-GISMONDI<sup>2,3,6</sup>

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Extant *Platanista gangetica* (Ganges river dolphin) is the sole survivor of Platanistoidea, a highly diverse clade that once thrived oceans around the world. The fossil record indicates a peak diversity of Platanistoidea during the early Miocene, followed by an abrupt decline towards the middle/late Miocene. This diversity included mainly marine taxa, with a broad range of body sizes and rostral morphologies that might represent occupation of a wide array of ecological niches; evidenced by their variety of skeletal muscle scars, dentition patterning and rostral proportions. Little is known about the marine-freshwater transition and evolution of these animals, as their fossil record from freshwater environments is scarce. During most of the Miocene, the northwestern region of South America was occupied by the Pebas mega-wetland system, a vast aquatic environment that spanned areas surrounding the borders of Peru, Colombia, Ecuador and Brazil. The two sole findings of freshwater Platanistoidea known so far correspond to fragmentary rostral remains and two isolated earbones from the Fitzcarrald Arch, Peru and La Venta, Colombia. Those findings indicate that Platanistoidea species independently invaded freshwater environments in South America before the extant Amazon river dolphin (*Inia*). New well-preserved cranial material from marine-influenced deposits of the Pebas Fm. in Peru and the Querales Fm. in Venezuela (both middle Miocene) indicate the presence of two new *Platanista* relatives within coastal to inland deposits of tropical South America. Our preliminary observations indicate that these new taxa display some characters solely found in *Platanista*, such as the conspicuous pneumatization pattern and dorsal projection of the maxillary crests, suggesting that these structures were present ancestrally in the South American platanistoid clade and the related extant Ganges river dolphin. In contrast to the highly modified eye and greatly reduced vision in extant *Platanista*, the orbital region in these new fossils shows no significant differences relative to that of other Miocene marine platanistoids, thus their sense of vision probably was not



reduced or otherwise substantially modified. These new findings indicate that the ambiances of the northwestern region of South America should have held an unknown diversity of Platanistoidea; which greatly contrast the extant distribution of the modern Ganges river dolphin, the sole survivor of this group.

## PALEOECOLOGY AND TAPHONOMY OF NEOGENE CETACEANS: NEW PERSPECTIVES FROM THE SOUTHWESTERN ATLANTIC OCEAN

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The Neogene was a key time for cetaceans diversification and cosmopolitan distribution, mainly driven by important changes in global climate and ocean productivity. Neogene deposits from the Atlantic and Pacific Oceans and the Mediterranean and North Seas provide a rich cetacean fossil record from this critical evolutionary time. In the Southwestern Atlantic Ocean, Miocene outcrops in Patagonia (Argentina) hold an important, albeit still poorly known, fossil record of modern lineages (= Neoceti) which in the last ten years have been continuously and exhaustively explored from a systematic, paleoecological, and taphonomic points of view. The most fossiliferous cetacean's outcrops comprise the lower Miocene Gaiman Formation, the upper Miocene Puerto Madryn Formation, and the Bajo del Gualicho Formation of uncertain Miocene age. Numerous specimens were collected in the XIX century, and many have been recently studied taxonomically and anatomically. Modern fieldwork efforts have resulted in new and more well-preserved specimens, increasing the taxonomic diversity of the assemblage but also the taphonomic and paleoecological information. This record has yielded an ecologically and taxonomically diverse cetacean community composed of odontocetes (the dominant group including ziphiids, platanistoids, physeteroids, kentriodontids, eurhinodelphinids, and stem odontocetes) and mysticetes (balaenids, neobalaenids, cetotheriids and balaenopteroids). Odontocetes are composed of small to large size marine forms, displaying a variety of feeding strategies (i.e., raptorial, combination suction, capture suction). Moreover, mysticetes are also represented by small to large size forms with ecological specializations ranging from skim to engulfment feeding. For the Gaiman Formation, two stratigraphically distinct cetacean assemblages are identified: one including small-sized odontocetes (mainly platanistoids), preserved mostly in inner shelf embayment deposits and dominated by isolated postcranial and cranial elements to associated cranial-postcranial skeletons. The other comprises large-size odontocetes and mysticetes (mainly physeteroids and balaenopteroids), preserved in open inner shelf deposits with isolated cranial elements as the most common category of preservation. Environmental, ecological, and biological factors have been identified as the main aspects controlling the cetacean assemblages in shelf environments from the Gaiman Formation. Preliminary results for the Puerto Madryn Formation show a variety of preservation styles, ranging from isolated cranial or postcranial elements to articulated specimens. Ongoing studies will allow determining which factors-controlled preservation and distribution of cetaceans in this unit as well as in the remaining Miocene fossiliferous outcrops in Patagonia. Integrative studies of the Patagonian record will be of great value to characterize the evolution of cetacean's communities during the Neogene in the Southwestern Atlantic Ocean.

## WHAT WE KNOW AND WHAT WE DON'T ABOUT THE FOSSIL MARINE MAMMALS ASSEMBLAGES OF BAHIA INGLESA FORMATION: A REVIEW OF TAPHONOMIC BIASES, TURNOVERS AND PALEOBIOGEOGRAPHIC RELEVANCE

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The Bahia Inglesa Formation (BIF, Northern Chile) is a marine Neogene sequence that includes a variety of environments preserved from deep to shallow water and transitional environments. BIF is known for hosting a great diversity of marine vertebrate fossil elements, with more than 70 taxa already recognized. The marine mammals are an important component of this fauna, with a sirenian, a few marine sloths, abundant and diverse phocids, and several cetacean taxa. In this manner, the BIF registers a variety of environments associated with this fauna as well as an array of phylogenetic and paleobiogeographic stories put together in the same geographic area. For example, the pinnipeds show a turnover between this sequence and the overlying Pleistocene unit (Estratos de Caldera), with 7 phocid morphotypes in the late Miocene as opposed to scarce records of the family in the Pliocene and only species of Otariidae in the Pleistocene. Meanwhile, the delphinidans apparently change their species composition and family representation between strata from the late Miocene to the early Pliocene. Among these, the Pontoporiidae (Inioidea) is the best-represented family and the most abundant in fossil remains. Nevertheless, these are virtually absent from the upper levels, where delphinid records are more common. Taphonomically there are also important differences between the 5 most productive fossil strata (bonebeds). The bias that those differences can produce is under study. The Cerro Ballena assemblage is interpreted as resulting from synchronic catastrophic records, produced by recurrent mass mortalities and transport of carcasses to a taphonomic trap. Contrastingly, the “fosforita” is a hardground formed during sedimentation hiatus in a deeper environment near the coast (pronounced slope), which accumulated skeletal elements through time, and constituting the most productive and diverse layer so far (over 60 vertebrate taxa). Bahia Salado, El Morro (Late Miocene) and Los negros (Early Pliocene) localities consist of similar fine sandstone strata with differences in species composition, age, and probably paleoenvironments. The observed differences in species composition can be affected by each

of these factors, a topic that is part of our ongoing research. The marine mammal assemblages present species, genus, and family level richness, making BIF relevant for understanding the evolution and paleobiogeography of these groups. BIF shows similarities to the coeval fauna of the Pisco Formation (Peru), with particular differences (presence of Balaenidae), while it differs substantially from the older record of the West South Atlantic (Argentina).

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## FROM HIND LIMBS TO GIANT TEETH AND LONG SNOUTS, AND FROM BALEEN TO GUT CONTENTS: RECENT CONTRIBUTIONS FROM THE EAST PISCO BASIN TO CETACEAN EVOLUTION IN THE SOUTHEASTERN PACIFIC

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For more than four decades, the study of the marine deposits of the East Pisco basin (southern coast of Peru) has led to the description of a large number of extinct marine mammals from the Paleogene and Neogene, revealing the existence in the past of surprising creatures, like the marine sloth *Thalassocnus* and the walrus-like dolphin *Odobenocetops*. The last fifteen years have seen further integration for the marine mammal studies in that basin, being gradually coupled with detailed investigations in fields ranging from sedimentology to taphonomy, and from chronostratigraphy to geochemistry, which are ultimately leading to a better understanding of the temporal framework and paleoenvironments of the discovered taxa, as well as the taphonomic processes underlying the exquisite preservation of so many marine vertebrate remains. Whereas earlier works focused predominantly on the extremely rich late Miocene levels of the Pisco Formation, an increased prospection effort and the organization of several larger-scale, multidisciplinary field campaigns targeting geologically older deposits in the basin revealed the great potential of several localities for the middle Miocene part of the Pisco Formation, the lower Miocene Chilcatay Formation, and the middle to upper Eocene Paracas Formation. From a paleobiogeographic viewpoint, new finds provided clues about the early dispersal of quadrupedal whales in the Pacific and Southern Hemisphere, and antitropical distribution of late Miocene beaked whales. Other discoveries shed new light on key steps of the evolutionary history of cetaceans, including the earliest mysticete, the late Eocene *Mystacodon*, and records of early members of the clades Cetotheriidae (middle Miocene *Tiucetus*) and Physeteroidea (early Miocene *Rhaphicetus*). Previously unknown feeding strategies and cranial morphotypes were revealed, including evidence of evolution towards suction feeding in the tooth-bearing *Mystacodon*, a unique feeding strategy for the cetotheriid *Piscobalaena* (suggested by the extent of the fossilized baleen rack on its narrow rostrum), a great disparity of rostrum shapes in early Miocene platanistoids, and macroraptorial sperm whales with proportionally large teeth and robust

jaws (e.g. the giant *Livyatan*). Finally, rare cases of fossilized digestive tract contents (for the basilosaurid *Cynthiacetus*, a large-sized cetotheriid, and the beaked whale *Messapicetus*), as well as shark bite marks on cetacean bones (including *Piscobalaena*), yielded valuable insights on local trophic networks. More fragmentarily preserved specimens in the collection of the MUSM (Lima) and preliminary prospection in new localities suggest that the East Pisco basin is still far from having revealed all its marine mammal treasures.

## ILLUMINATING A GLOBAL DARK AGE IN CETACEAN EVOLUTION

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The earliest Miocene, or Aquitanian, is a global dark age in cetacean evolution, from which few toothed whales (odontocetes) and virtually no baleen whales (mysticetes) are yet known. Global Oligocene cetacean assemblages are rich and dominated by archaic groups like mammalodontids, aeticoetids and xenorophids. With the onset of the Miocene, odontocete diversity decreases and mysticetes temporarily disappear from the records of Australia, Europe and the Americas. Following the Aquitanian, assemblages recover but also appear notably more modern. The reasons behind this transition, and its significance to cetacean evolution, remain obscure. New Zealand is one of few places globally where Aquitanian cetaceans are preserved. Well-dated sequences provide an almost unbroken record across the Oligocene-Miocene boundary, and have yielded the first confirmed Aquitanian mysticetes, as well as a variety of comparably aged odontocetes (*Prosqualodon cf. davidis*, *Tangaroasaurus kakanuiensis*, and a new squalodelphinid). Overall, the baleen whale assemblage appears comparatively modern, with no toothed forms, no obvious eomysticetids, and at least one species resembling the younger *Isanacetus* and *Parietobalaena*. This may suggest a relatively rapid turnover event, with most archaic groups disappearing close to the Oligocene-Miocene boundary.

## THE WESTERN PACIFIC CORRIDOR LINKING THE RIGHT WHALES ON BOTH SIDES OF HEMISPHERES

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One of the most intriguing distributional patterns is antitropical distribution that closely related species reside in high latitudes of Southern and Northern Hemispheres, but not in between. Of the abundant examples, the right whale (Mysticeti, Balaenidae, *Eubalaena*), reaching 18 m long, represents the largest antitropical distribution pair – *Eubalaena australis* solely inhabiting the Southern Hemisphere whereas *E. japonica* and *E. glacialis* occupying the Northern Hemisphere. However, the *Eubalaena* interchange remains poorly explored. Here we describe a newly-found tympanic bulla from the Pleistocene of Taiwan. The specimen was dredged from the sea bottom between Penghu and Taiwan, resulting in the uncertainty of its geological age (likely to be the Middle/Late Pleistocene, ranging from 0.78 to 0.01 million years ago, but not excluding the possibility of Holocene in age). Morphology of the left tympanic bulla is almost identical to the extant *Eubalaena*, including relatively large size (the anteroposterior length is 117 mm); rectangular outline in medial view; short anterior lobe, judging from the remaining of the lateral furrow; the squared anterior margin in anterior view; squared Eustachian outlet; prominent transverse creases on the involucrem; transversely compressed in anterior view; well-developed and rounded outer lip; and parallel involucrem and main ridges. Albeit incompletely preserved, the diagnostic power of the cetacean earbone (the tympanic bulla and periotic) allows a reliable taxonomic assignment to *Eubalaena* sp. The occurrence of a tropical *Eubalaena* could be interpreted as an extra-limital record of the North Pacific right whale (*E. japonica*). Alternatively, given the superabundance of Pleistocene fossils from the sea bottom between Penghu and Taiwan, we consider the *Eubalaena* bulla reasonable to be a bona fide Pleistocene existence. Thus, the discovery of a fossil *Eubalaena* from the Pleistocene of Taiwan, situated on the southern margin of the western North Pacific, suggests that the western Pacific may be the corridor linking the extant *Eubalaena* spp. exclusively on high latitudes of both hemispheres, leading to the origin of current antitropical distribution. Besides, the cause and time of driving the latitudinal movements, crossing the equator, and eventually resulting in the antitropical distribution have often been attributed to the repeated glaciations and interglaciations in the Pleistocene without concrete evidence. The Pleistocene *Eubalaena* from the tropical area, for the first time, corroborates the hypothesis of the Pleistocene interchange due to the glacial/interglacial. In addition, further deciphering the paleobiogeographical interchange of *Eubalaena* should help contribute to the unresolved speciation and phylogeny of extant *Eubalaena*.

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## A SIRENIAN FROM THE MIDDLE EOCENE OF PERU

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South America is home to one of the few extant sirenians, the Amazonian manatee (*Trichechus inunguis*), which is found throughout the Amazon River basin. Meanwhile, the fossil record of sirenians in South America consists mainly of mid-late Miocene records of dugongids in marine deposits, and early Miocene to Pleistocene trichechines found in mixed to freshwater environments. This largely contrasts with the fossil record across the Greater Antilles and North America which represents a nearly continuous record spanning from the Eocene through the Pleistocene and including representatives of stem (prorastomids and protosirenids) and crown sirenians (Trichechidae and Dugongidae). Because of the close relationship between sirenians and seagrasses, this disparity between their North and South American fossil record has led some researchers to suggest that seagrasses may have been far less common or even absent in the southern continent during the Paleogene. Herein we report the first Paleogene sirenian from South America which challenges this assumption. The specimen consists of cranial and postcranial remains from the middle Eocene (Lutetian) Paracas Formation in the Pisco Basin, southern Peru. A preliminary phylogenetic analysis suggests that the Paracas sirenian represents a new basal form, similar to species in the paraphyletic genus *Eotheroides*. Species in this genus are known from mid-late Eocene deposits in India, Madagascar, Europe, northern Africa and eastern North America, and together with other Eocene taxa form a grade of phenetically similar species basal to crown Sirenia. More specifically, the Paracas sirenian forms a monophyletic group with *Eotheroides sandersi* and *E. lambondrano*, from Egypt and Madagascar, respectively. The close relationship between these species suggests a westwards dispersal from Africa via the South Atlantic and Central American Seaway towards the eastern South Pacific, similar to what is hypothesized for the semiaquatic protocetid *Peregocetus pacificus*. The apparent disparity in the fossil record of sirenians between North and South America may be a result of a number of factors, spanning from availability of the rock record to differences in collecting and research efforts. Other marine mammals from the Paracas Fm. include several species of basilosaurid and protocetid whales that have only been described over the last 10 years. Finally, the discovery of sirenians in the Lutetian of Peru helps fill the apparent temporal gap in their fossil record in South America and, additionally, can be used as an indicator for the presence of seagrasses in the eastern South Pacific at least since the middle Eocene.



## HEARING THE PUZZLE: THE INNER EAR EVOLUTION OF PLATANISTOIDEA (CETACEA: ODONTOCETI)

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Hearing is one of the key senses for modern cetaceans (Neoceti) to hunting and communication, adapted for either infrasonic (Mysticeti) or ultrasonic (Odontoceti) frequencies. Among odontocetes, the Platanistoidea comprises a single extant riverine representative (*Platanista gangetica*) but numerous extinct marine species from the late Oligocene onward. *Platanista* is a critically endangered odontocete species that possess unique morphological characteristics, but their evolutionary patterns remain mostly unknown. Studying extinct platanistoids' hearing abilities might contribute a piece to the complex evolutionary puzzle of this group to understand its drastic diversity reduction. Thus, we describe for the first time the inner ear morphology of 6 late Oligocene–early Miocene extinct marine platanistoids from New Zealand and Patagonia (Argentina). These species represent the most diverse moment in the evolutionary history of Platanistoidea. In this study, we hypothesized that extinct marine platanistoids lacked a specialized inner ear like *P. gangetica* and thus, their morphology and inferred hearing abilities were more similar to extant marine odontocetes. Based on microCT scans and 3D models, we took 15 measurements, 3 ratios, and estimated their low-frequency limit. Then, we applied 3D geometric morphometric and statistical analyses to inner ear models of 7 platanistoids, 2 stem odontocetes, 9 extant odontocetes, and 1 archaeocete species (n=21). We did not find a “typical” platanistoid cochlea but rather a disparate range of high-frequency hearing morphologies in the group, supporting an early-acquired specialized underwater hearing ability in odontocetes. *Notocetus* and *Platanista* share a loosely coiled and wide cochlea, and a low number of turns that are widely separated. Stem odontocete *Prosqualodon australis* and platanistoid *Otekaikea huata* are the only species that possess a tympanal recess, of yet unknown function. *Aondelphis talen*'s inner ear morphology indicates it had lower high-frequency hearing than other platanistoids. As expected, *Platanista* has the most derived cochlear morphology and is always distant in the morphospace from its sister genus *Zarhachis*, adding to evidence that it is an outlier within the group. Inner ear morphology, pneumatized maxillary crests, and pterygoid sinus system, among other unique characteristics, would have ultimately allowed the survival of *Platanista* to the present day. New fossil platanistoids, particularly from the middle–late Miocene onward, will help test these hypotheses.

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### **Symposium Online: “Palaeopathologies of secondarily marine tetrapods”**

Thursday 22<sup>nd</sup> April (12:00 – 14:00 GMT-4)

Moderators: Drs. Judith Pardo-Pérez & Erin Maxwell

## CRANIAL PALAEOPATHOLOGIES IN A LATE CRETACEOUS MOSASAUR FROM THE NETHERLANDS

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Here we describe multiple pathological skeletal elements in a specimen assigned to a globidensine mosasaur as *Prognathodon cf. sectorius*. This individual, NHMM 2012 072, was recovered from the upper Lixhe 3 Member (Gulpen Formation, upper Maastrichtian) near Maastricht, the Netherlands. Various injuries are visible on the anterior sections of the premaxillary, left maxillary and left dentary. In all likelihood, it was bitten in the snout by a large, possibly conspecific mosasaur – and survived this attack. The specimen described here is among the very few with clear and unambiguous evidence of (very likely intraspecific) agonistic interactions amongst mosasaurs. Despite significant injuries, including partial amputation of the premaxilla, this animal initially recuperated from the encounter, but the subsequent infectious processes as a result of this attack were still ongoing at the time of death. As a result, a vast amount of bone is dissolved in the maxillary, creating multiple anteroposteriorly oriented tubules and even starting to affect the enamel of the first maxillary tooth base. Radiological and morphological features suggest chronic osteomyelitis which probably hampered its ability to feed, potentially contributing to its demise. The underlying nature of such an encounter between two (or more) proportionally similar mosasaurs is highly speculative. However, the identification of more such encounters in the fossil record, suggests either intra- or interspecific competition or predation. According to the size of the victim and the suggested attacker(s), the latter would appear unlikely. Surprisingly, the specific immune response of this mosasaur to the chronic infection seems to hint at differences relative to the typical response of extant analogues including snakes. This case study illustrates the potential of integrative three-dimensional approaches in palaeopathological studies to provide a much more comprehensive and detailed description of alterations and underlying physiological processes. Ideally pathological studies should aim to incorporate both histological and radiological techniques (including 3D-visualizations) to supplement traditional external morphological descriptions as suggested by previous authors. This allows for a much higher degree of certainty in identifying a causative factor, as well as providing a much more detailed description of skeletal processes on a tissue level.

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## **LIFE WASN'T MEANT TO BE EASY: PATHOLOGIES OF MIOCENE MARINE VERTEBRATES FROM THE PISCO FORMATION AT SACACO (SOUTHERN PERU)**

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Pathologies in skeletal remains have been instrumental to decipher the ecology and life history of extinct taxa, but this distinct fossil evidence was barely documented within marine vertebrate communities of the Cenozoic. Here, we present the first record of pathological bones in marine vertebrates recovered from five localities (9~4.5 million years ago [Ma]) of the Pisco Formation in the Sacaco area, north of Arequipa, Peru. The macroscopic study of 535 specimens from five fossil-bearing localities allowed the identification of 24 pathological bones, including representatives of cetaceans, marine sloths, seals, crocodiles, birds and cartilaginous fishes. Hueso Blanco (HB) at the Aguada de Lomas locality encompasses more than half (15/24; 62.5%) of the injured bones identified, whereas in the other four localities (i.e., Sacaco Sur, Sacaco, Montemar, and El Jahuay) pathologies (associated to ankylosis, trauma with signs of healing and joint disease) are less common (9/24; 37.5%). In HB, ten of the fifteen injured bones (67%) are articular diseases (possibly infectious arthritis and osteoarthritis). In this site we also record putative evidence of tumors (13%) in a phocid metacarpus and a lamniform vertebra, and three bones with healed traumas (20%). Injured bones from HB showed that phocids are particularly affected (53%) by articular diseases with possible signs of infection. In general, the fossil record of vertebrates in Sacaco comprises skeletons in anatomical connection but bones in HB are usually isolated and several bearing shark predation marks. Whilst predation could have been a cause for the development of observed pathologies, we cannot rule out other origins, so further studies are required. Macroscopic studies will be contrasted with analyses of the microstructure of the pathological areas of the bone through thin sections. This will allow obtaining details of the histological anomalies, pattern and level of development in bone remodeling.



## PALEOEPIDEMIOLOGY IN DEEP TIME: WHAT PALAEOPATHOLOGIES TELL US ABOUT THE LIVES OF ICHTHYOSAURS

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The prevalence of injuries in fossil populations over evolutionary time scales can elucidate intrinsic and extrinsic factors affecting organism health, and shed light on ancient ecosystems and organismal palaeobiology. We used ichthyosaurs as a model system to examine factors affecting the prevalence of osteopathologies, surveying 624 specimens from museum collections and from three representative lagerstätte: Middle Triassic Besano Formation (BF; 242 Ma, Swiss-Italian Alps), Early Jurassic Posidonia Shale Formation (PF; 182 Ma, Germany) and Middle-Late Jurassic Oxford Clay Formation (OC; ~163 Ma, England). Whereas the first two formations preserve a diverse ichthyosaur fauna spanning numerous trophic levels, the latter assemblage only yields a single mid-sized taxon (*Ophthalmosaurus*). We quantified the type of bone anomalies macroscopically observed and the anatomical units affected to assess if the incidence of osteopathologies is related to changes in palaeoecology and/or body plan. Top predators from the Triassic and Early Jurassic formations were the most prone to traumatic injury. However, the Middle Jurassic *Ophthalmosaurus*, considered to be a dietary generalist, also showed substantial skeletal trauma. Pathologies in *Ophthalmosaurus* predominantly occurred in the skull (20%; 16/81) and pectoral girdle/forefin (12%; 10/84), similar to Early Jurassic top predators like *Temnodontosaurus* and higher in comparison with the similar sized Early Jurassic *Stenopterygius* (4% affecting skulls and 2% affecting forelimbs). Of the three formations analyzed, the highest prevalence of pathological specimens was observed in the OC (15%; 29/188) followed by the PF (14%; 32/236) and lastly the BF (6%; 12/200). Increased detection in the OC assemblage might be caused by observer bias: unlike the two older formations, material from the OC consists of isolated elements prepared free from surrounding matrix, potentially increasing the probability of detection of osteopathologies by up to 50% relative to slab-mounted specimens. Pathologies are concentrated in the anterior portion of skeletons in *Ophthalmosaurus*, similar to in Early Jurassic ichthyosaurs, supporting a link between body plan, swimming style and osteopathologies. *Ophthalmosaurus* was the only taxa with presence of avascular necrosis from all the surveyed specimens, suggesting contrasting palaeoenvironments compared with older formations, with individuals diving deeper, potentially for food. The higher number of cranial traumas suggests a similar amount of intraspecific aggression to top predators like *Temnodontosaurus*. Besides avascular necrosis we also detected ankylosis of phalanges and cases of possible tumor in the pectoral girdle of *Ophthalmosaurus*. We expect to complement the macroscopical observations with CT scan in selected pathological bones in the future of this research.

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## PALEOEPIDEMIOLOGY OF THE EOSAUROPTERYGIA FROM THE VOSSEVELD FORMATION (TRIASSIC, ANISIAN), WINTERSWIJK, THE NETHERLANDS

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The locality of Winterswijk (the Netherlands), representing a coastal to neritic paleoenvironment, is unique among the various localities within the Germanic Basin, because of its westernmost position and in that it not only yields a large number of isolated bones but also has preserved articulated and associated skeletons and skulls of marine vertebrates as well as tracks and trackways of terrestrial vertebrates. Among the numerous eosauropterygian remains from Winterswijk locality, several bones with osteopathologies have been identified. A jaw with a healed fracture indicates that the afflicted individual of *Nothosaurus* managed to survive a severe injury and, despite it, it was capable of food intake. Another individual had its clavicle broken with displacement, the healing of which also proves it to be non-lethal. The most curious examples of pathologies are rickets of the humerus of pachypleurosaur *Anarosaurus heterodontus*, which was possibly caused by a vitamin D deficiency (osteomalacia), and osteofibrous dysplasia, probably the oldest case in the paleontological record, which affected an eusauropterygian rib and could also be related to bone metabolism disorder or trauma. Such case studies have the potential of bringing novel data about the health condition of ancient animals, their locomotion, feeding, the way they functioned in their environment, and environmental hazards they had to endure. Furthermore, they inform about the physiology of extinct animals and their healing processes. This is particularly meaningful for the groups which lack extant representatives, and whenever they have modern ecological analogs, they may allow inferences on the impact of the mode of life on biological processes.

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## WHAT DO WE REALLY KNOW ABOUT PAST PENGUIN DIVERSITY?

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Although the evolution of penguins have been assumed to be driven by global cooling, the correlation between penguin diversity and large-scale environmental changes have rarely been evaluated in a deep-time scenario and, in consequence, their evolutionary drivers remain largely unknown. The present study explores in deep the global diversity of penguins through time, testing the correlations between multiple palaeodiversity accounts and environmental/stratigraphic proxies, to elucidate the relations between these charismatic birds and their environment, taking in to account the possible impact of sampling biases and taxonomic instability. The correlations and models tested show a persistent influence of the number of formations with vertebrate records in the Southern Hemisphere over the known richness of penguins, particularly during the last 23 Ma and when we analyse the Cenozoic as a whole. This suggests the existence of sampling and/or preservation biases. We also identified two gaps in our current knowledge of penguin palaeodiversity, one during the early Oligocene and the other in the middle Miocene. Nevertheless, in Eocene and Neogene data, the strength of the environmental proxies increases during model fitting, allowing the identification of potential drivers. Our results point towards sea temperature as a possible driver of penguin diversity during the Eocene; whereas sea level, carbon burial ratio and plankton composition maybe linked to their radiation during the Neogene. Thus, the available evidence allows the identification of significant patterns in the evolution of penguins, showing that their fossil record is incomplete but informative. These macroevolutionary trends allow us to tackle some key aspects regarding the origin of penguins, what are the differences between basal and modern penguins, and the potential drivers of their evolution. It also helps us to identify areas and subjects which need to be prioritized in the immediate future, regarding sampling effort and analysis.

## THE OSSIFICATION OF THE FALX CEREBRI IN SIRENIANS: EVOLUTION AND PHYLOGENETICAL SIGNAL

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Both cerebral hemispheres are separated by a membrane projection of the brain dura matter, which is attached to the ventral surface of the parietal named the falx cerebri. Another membrane, the tentorium cerebelli, separates the upper surface of the cerebellum and the occipital lobes. These membranes ossify in some mammals such as primates, marsupials, some cetaceans and sirenians, among others. These ossifications, named the bony falx cerebri and the tentorium osseum, which meet in the internal occipital protuberance, can be preserved in the endocranial surface of the skull of fossil taxa. Holocene sirenians possess all these structures, except for *Hydrodamalis gigas*. Nevertheless, they are not present in all the fossil sirenian taxa. Traditionally, the absence of these structures has been considered diagnostic for the Eocene family Protosirenidae. Some authors, however, have suggested that the absence or almost absence of these endocranial ossifications could be a primitive condition to Trichechids and Dugongids. New skull bones assigned to perinatal to young adult individuals of *Sobrarbesiren cardieli* from the Lutetian (middle Eocene) of Spain, and a deep study of the type specimens, have revealed a bony falx cerebri absent, combined with a low tentorium osseum and a blunt internal occipital protuberance in this stem sirenian. In base to these observations, three phylogenetic characters related to the endocranial surface of the parietals are added to previous phylogenetical matrix together with characters of the basioccipital bone. The topology of the tree obtained resolves the polytomy for Eocene Pan-sirenians, but *Prorastomus sirenoides*, from previous phylogenetical proposals. Furthermore, the reconstruction of the characters supports the hypothesis that the absence of these endocranial structures is the plesiomorphic condition for pan-sirenians, and therefore, it is discarded as diagnostic for Protosirenidae. The ossification of the falx cerebri would have appeared during the Lutetian with the Egyptian taxa *Eotheroides aegyptiacum*. Nevertheless, the lack of bony falx cerebri in *Sobrarbesiren* but the presence of the tentorium osseum and internal occipital protuberance suggest an asynchronous development of these structures, which are already present in perinatal individuals and therefore, they ossify before birth as in extant *Dugong dugon*. Consequently, the inclusion of characters of the endocranium in the phylogenetical analysis can be useful to resolve the phylogenetical relations of stem Pan-Sirenia and further studies in this line must be made.

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## ORIGIN, DIVERGENCE TIMING AND EARLY PALEOBIOGEOGRAPHIC HISTORY OF CAIMANINAE (CROCODYLIA): INSIGHTS FROM THE FOSSIL RECORD

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Today, caimanine crocodylians are restricted to Central and South America but the fossil record of their sister clade, Alligatorinae, strongly implies a North American origin. An incomplete fossil record, however, hampers reconstructing the early biogeographic history and divergence of Caimaninae. The oldest unambiguous fossils of the clade are known from the early Paleocene (ca. 63 Mya) of South America, whereas more controversial occurrences may push back their origin well into the Late Cretaceous (ca. 80 Mya) of North America, in contrast with most molecular divergence estimates. By revising previous fossil morphological taxon-character datasets, as well as integrating molecular backbone constraint topology from extant taxa, we present a comprehensive maximum parsimony analysis of early Caimaninae phylogeny. The inclusiveness of stem-group Caimaninae is sensitive to the scarcity of well-sampled unambiguous basal caimanine taxa, and highlights our poor understanding of the ancestral morphology in the primary alligatoroid clades. Our fossil phylogeny suggests an origin of the total group (stem and crown) no earlier than the latest Cretaceous (ca. 66 Mya) in North America. This was followed by a rapid dispersal to South America at latest by the early Paleocene (ca. 63 Mya), in accordance with hypothesized emergence of temporary land connection with North America during this time. We reinterpret previously hypothesized Paleogene back-dispersals to North America as an equally plausible hypothesis to the persistence of North American endemic stem taxa until the middle Eocene, age of the youngest caimanine occurrence on the continent, ca. 42 Mya. This alternative, however, would imply a second Paleogene dispersal to South America for the divergence of the clade containing the crown-group. Our phylogeny suggests that crown-group Caimaninae diverged in South America, but the timing is poorly constrained by fossils. Future molecular divergence estimates, however, could yield promising insights when calibrating the crown to a hard minimum of 18.8 Mya (the age of earliest definite crown fossil).

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## PRELIMINARY REVISION OF THE EUROPEAN RECORD OF THE SQUALODONTIDAE (ODONTOCETI) OFFERS MORE ACCURATE DIVERSITY OF THIS HISTORIC CLADE

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The Squalodontidae is one of the most historic families of Cetacea, with *Squalodon* named in 1840. Since its initial description, workers in the 1800s were eager to assign heterodont cetacean teeth to this family; as a result, it is now a wastebasket taxon with many species based on fragmentary remains. Taxa possessing complete skulls reveal that the Squalodontidae possess a mixture of ancestral and derived traits: they exhibit polydonty as most modern odontocetes do, but their teeth are still differentiated into incisor and molariform types. The Squalodontidae are most prevalent in the North Atlantic with most occurrences reported from early to middle Miocene deposits, though the earliest records of the Squalodontidae extend into the late Oligocene. Several workers have revised the record of the Squalodontidae in the Americas, resulting in a drastic reduction in diversity represented on the east coast of North America. However, this work has not yet been done for species named from European specimens. Here, we present the results of a preliminary taxonomic revision. A literature review of historic papers describing various “squalodont” fossils reveals that at least eight of twenty formal species of *Squalodon* described from Europe should probably be declared *nomina dubia* and should be referred to as Odontoceti indeterminate. These species were named from holotypes now considered nondiagnostic: isolated teeth, rostral or mandibular fragments, or isolated postcranial elements. This work reveals that the number of species of the Squalodontidae in European waters is halved from what was previously thought. However, it gives us a better picture of the diversity in this historic family.



## **NEW DATA ON THE STRATIGRAPHIC DISTRIBUTION OF MARINE MAMMAL ASSEMBLAGES IN SOUTHERN CALIFORNIA**

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The fossil record of Southern California includes one of the most continuous sequences of marine mammal assemblages from the Miocene of the North Pacific. Since some of the major transitions in the evolutionary history of marine mammals are recorded within these deposits it should be possible to look at the timing of these events at a refined scale. Unfortunately, a lack of reliable ages for many sites combined with a lack of recent synthetic studies have obscured these patterns. Over the past few years we have collaborated on studies aimed at refining the age of sites and formations in the Los Angeles Basin and documenting the fossils of marine mammals from the region. We reviewed published observations and added new data from Miocene-Pliocene marine mammals based mainly on the NHMLA collections. Although the focus of this report is on Southern California, our broader data set includes comparisons with specimens from other formations in the eastern North Pacific from as far north as Washington to as far south as Baja California Sur. Our occurrence data are vetted on a site-by-site basis, with updated chronostratigraphic and taxonomic information, allowing for more precise first and last appearance dates. In this presentation, we will 1) Review evidence for the last global occurrence of toothed mysticetes; 2) Compare the chronostratigraphic ages and marine mammals assemblages of species-rich units from the Middle Miocene Climatic Optimum (Topanga Formation and Sharktooth Hill bonebed); 3) Distinguish, for the first time, two distinct marine mammal assemblages from the Monterey Formation. In all three cases, chronostratigraphic data from multiple sources provides new insights into the evolution of marine mammal assemblages and establishes an increasingly robust framework for more comparisons in the North Pacific. Ongoing work aimed at narrowing the chronostratigraphic range of other poorly constrained formations in California and Mexico will allow us to further test the geographic extent of the patterns we present.

## THE EARLIEST ICHTHYOPTERYGIAN BONEBED

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Ichthyosaurs are a major group of Mesozoic marine reptiles ranging from the Triassic to the mid-Cretaceous. The earliest representatives (Ichthyopterygia) of this group appear to have a near-global distribution already in the latest Early Triassic (early to middle Spathian). Recent excavations in central-Spitsbergen in the Vendomdalen Member, Vikinghøgda Formation in Svalbard, revealed a large amount of ichthyopterygian remains. These form part of a vertebrate bonebed, the “*Grippia* bonebed”. All elements are disarticulated, largely uncompressed and represent at least two different taxa and ontogenetic stages. Using PCA analysis, we present the evidence that these remains include a large-bodied ichthyosaur (*Cymbospondylus/Pessopteryx*), a grippidian ichthyopterygian (*Grippia longirostris*) as well as possibilities for additional taxa. This new material is not only temporally important, but also taxonomically. There is limited amount of fossil material referred to *G. longirostris*, with the holotype lost in WWII. As such, the disarticulated cranial material described from the *Grippia* bonebed helps understand, the poorly preserved skull morphology as well as ontogenetic development in this taxon. The sheer amount of material, as well as the diversity in size and palaeoecology, demonstrate a larger biodiversity of ichthyopterygians than previously suggested at such an early stage of their evolutionary history.

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## A GIANT NEW EARLY MIDDLE TRIASSIC ICHTHYOSAUR AND A COMPARISON WITH WHALE BODY SIZE EVOLUTION

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Evolution of giant body size (>10 t) is a pervasive trend in the history of both marine and terrestrial amniote clades. The largest marine amniotes are today's cetaceans, followed by giant ichthyosaurs of the Triassic. Here we describe a new giant ichthyosaur (skull length close to 2 m, est. total length 18 m, est. body mass ~ 27 t) from the early Middle Triassic Fossil Hill Member of Nevada, USA. The giant ichthyosaur is the largest member of a diverse fauna including several other large ichthyosaur species. This fauna existed only 6 million years after the appearance of marine reptiles in the fossil record and in the absence of the highly productive marine ecosystems of today. Cetaceans, which are the closest living analog to ichthyosaurs, appear to have evolved much more gradually, both in their late appearance after a mass extinction event and their slower size increase. Using phylogenetic comparative methods and a newly compiled consensus phylogeny of all cetaceans, we quantitatively compared size evolution in the two clades. We chose skull length as size proxy in ichthyosaurs and bizygomatic skull width in cetaceans. Our analysis documents an amazingly rapid size increase from *Chaohusaurus* in the Olenekian at 248.5 ma (skull length 117 mm) to the new giant (skull length 1890 mm) a mere 2.5 ma later. This rate of evolutionary size increase fits an early burst model and far surpasses that seen in the origin and early evolution of whales. In this clade, size evolution was much more gradual. It took whales 15 ma to reach a comparable body size (*Basilosaurus*) to the new giant and to reach their first size peak. Both groups dominate the pelagic ecosystems and diversified into different niches and a wide morphospace in the first 50 ma of their evolution. The early burst model for ichthyosaurs underscores the notion of explosive evolutionary body size increase in ichthyosaurs. This is consistent with the early burst previously detected in diversity and morphological disparity in ichthyosaurs. Why was whale size evolution slower than ichthyosaur size evolution, and why is there a delayed return to the sea in whales, 15 ma after the end of the Cretaceous? Possibly, eutherian mammals were more constrained in aquatic adaptation despite having one precondition, life birth, that most reptiles lack.

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## CRETACEOUS MARINE TETRAPODS FROM BENTIABA, ANGOLA

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Since 2005, our multinational collaboration, Projecto PaleoAngola, has focused on the exploration and documentation of the geological and paleontological heritage of Angola. In conjunction with our scientific goals, we have an active outreach and exchange program that ranges from field and lab training of Angolan undergraduate and graduate students, and development of museum exhibits, including the exhibition currently on display at the Smithsonian National Museum of Natural History. Since the project's inception, numerous localities from Cabinda in the north to Tombua in the south of Angola have been documented; however, one site stands out as an exceptional example of Angola's geoheritage. That site is near Bentiaba, Namibe Province, in the south of Angola. It has yielded a rich fauna of marine tetrapods, including mosasaurs, plesiosaurs and turtles, and in terms of fossil density, it is arguably the richest Mesozoic marine tetrapod site of the Southern Hemisphere. Most of the fossils at Bentiaba have been recovered from the lower Maastrichtian part of the section, the so-called 'Bench 19' interval; however, ongoing work in the upper part of the section is also sampling a late Maastrichtian fauna, and new fossils have been discovered below Bench 19 in recent field seasons. The species diversity in the Bench 19 interval is striking, with ten mosasaur, two plesiosaur, and four marine turtle taxa discovered thus far. Additionally, the locality preserves both young and old individuals, as well as evidence of trophic interaction including multiple examples of exceptionally well-preserved gut content. Diversity of body size and tooth form evidence niche partitioning, and isotope-based evidence allows to discern segregation of foraging area. Thus Bench 19 provides a snapshot of an early Maastrichtian South Atlantic ecosystem, set at 26 degrees paleolatitude, and likely reflects an upwelling setting, similar to that supporting the Benguela Current Large Marine Ecosystem, which today is one of the world's most productive fisheries. This contribution is intended to provide an overview of our fieldwork and research so far, and to highlight education and outreach initiatives, as well as ongoing efforts to further safeguard the rich geoheritage at Bentiaba.





## **CENOZOIC MARINE TURTLE RECORD FROM SOUTHERN SOUTH AMERICA: NEW INSIGHTS FROM THE MIOCENE OF PATAGONIA, ARGENTINA**

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The study of marine turtles is a challenging topic because of the cosmopolitan nature of its fossil record and current distribution. Thus, it might be difficult to study and compare specimens, but sometimes even the smallest fragments or isolated occurrences might provide significant new information for the whole group. The Cenozoic fossil record of marine turtles (Pan-Chelonioida) in South America is scarce with less than 10 published occurrences. The southernmost published record corresponds to a fragmentary and undetermined specimen of pan-dermochelyid (MPEF-PV 565) from the lower Miocene Gaiman Formation in Chubut province, Patagonia, Argentina. However, recent fieldwork has significantly increased the record of marine turtles from northeastern Chubut. The fossil record of pan-dermochelyids was increased with two findings from the Gaiman Formation: one fragmentary consisting of two ossicles (MPEF-PV 11360) and an almost complete carapace with associated postcranium (MPEF-PV 10918). Furthermore, also from the Gaiman Formation, a lower jaw of a pan-cheloniid (MPEF-PV 11382) was found. This group was also recently found in the upper Miocene Puerto Madryn Formation, represented by shell and postcranial remains (MPEF-PV 10929) and a skull (MPEF-PV 2577) coming from Gaiman or Puerto Madryn formations. In summary, we can conclude that: (1) the northeastern Chubut presents the most diverse and abundant record of chelonioid turtles in the Atlantic coast of South America; (2) the reported pan-cheloniid specimens expand the stratigraphic and geographic range of the group in the Atlantic coast in the Neogene; (3) the almost complete carapace of a pan-dermochelyid represents one of the most complete specimens of the group found up-to-date in the world. Thus, these new findings will provide valuable information on the anatomy, taxonomy, and diversity of the marine turtles that once populated the southwestern Atlantic sea and coasts of southern South America.

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## **Recorded Presentations**

**Topic: “Fossil Record and Present Distribution”**

Modality: Poster

## **AN OVERVIEW OF THE FOSSIL RECORD OF EARLESS SEALS, PHOCIDAE, FROM THE NORTH ATLANTIC: WHERE ARE WE NOW, AND WHERE WILL WE GO TO?**

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The first published studies of fossil earless seals, Phocidae, from the North Atlantic realm date back to the middle of the nineteenth century. The description of many taxa in the nineteenth century was followed by a long stasis throughout the twentieth century, with little research interest in the subject. At the start of the twenty-first century, interest in the fossil seals from the North Atlantic has witnessed a new surge, especially focusing on the fossil records from the North Sea Basin and the east coast of the United States. Despite the renewed interest in the fossil seals from the North Atlantic, many of the historical taxa remain poorly understood: they were established and described, using nineteenth century approaches, and have not been critically reassessed. In addition, many of the recently-described fossil seal taxa from the North Atlantic have not been critically reassessed either, after their original description. This presentation gives an overview of the current state of this fossil record. We reassess the poorly-understood historical and recently-described fossil phocid seals from the North Atlantic realm. This investigation highlights two major historic flaws. First, a history of selecting questionable specimens as type specimens, strongly limiting the diagnosis and understanding of each taxon. Second, the inadequate selection of characteristics as being diagnostic, lacking quantitative proof or consensus that these characteristics are indeed diagnostic for distinguishing different taxa. In the present (re-)assessment, the validity of multiple highly fragmentarily and poorly-known phocids is questioned, including the genus *Gryphoca*, *Platyphoca danica*, and *Terranectes parvus*, thus, strongly reducing the known diversity of seals from the North Atlantic in geologic time. Through biostratigraphy and literature research, the geologic ages of many of these fossil seal taxa have been finetuned or updated. Most notably, dinoflagellate cyst biostratigraphy revealed that most of the Pliocene fossil seals from Belgium are in fact of late Miocene age. The presented reassessment of the fossil seal record and of the temporal framework aims to spark a radical change in the description of new material and a more careful selection of type specimens in future studies.

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## A REVISION OF THE PHYLOGENY AND PALEOBIOGEOGRAPHY OF KENTRIODONTIDS (CETACEA: ODONTOCETI)

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The kentriodontids are small to medium-sized extinct dolphins that have been known throughout the world from the early to late Miocene (18–10 Ma). Although kentriodontids are often thought to be a paraphyletic or polyphyletic group of stem taxa in the Delphinida, their phylogenetic relationships have remained controversial. Currently, more than 20 species of kentriodontids have been described, and they are common in the eastern North Pacific, western North Atlantic and Paratethys. Recently, two well-preserved fossil crania of kentriodontid-like dolphins were recovered from the middle Miocene of the northern Honshu, Japan. Since only a few kentriodontid species have been described from the western North Pacific, these new specimens are important to understand the phylogenetic relationships, pattern and process of evolution and diversification of kentriodontids. Here, we conducted a phylogenetic analysis based on a data matrix combined from previous studies. It was based on 103 taxa including almost all the kentriodontids and 387 morphological characters, with a tree constraint based on the molecular evidence for the relationships of extant odontocetes. As a result, the two new specimens were included in the same clade as kentriodontids. It means that all the known kentriodontids were recognized as forming a monophyletic group, supported by 12 synapomorphies. The monophyletic Kentriodontidae was recovered as sister group to the crown Delphinoidea. Because of the strong support for the clade Kentriodontidae, not much lower than the support for Delphinoidea (18 synapomorphies), the former clade may be raised to a superfamily rank, like Delphinoidea. In addition, the clade Kentriodontidae was subdivided into two clades. Accordingly, such clades could be raised to a family rank. Also, we reconstructed the process of kentriodontid diversification through time based on the Statistical Dispersal Vicariance Analysis (S-DIVA). The result indicates that the common ancestor of the kentriodontids is considered to have emerged in the Northern Hemisphere in the early Miocene. Subsequently, the initial diversification of the subclade including *Wimahl* and *Kentriodon* occurred in the North Pacific, while another subclade including *Delphinodon* and *Lophocetus* diversified in the North Atlantic. Both groups dispersed globally before the temporal closure of the Central American Seaway in the middle Miocene. The fall of the kentriodontids may have been affected by extreme environmental changes during the late middle Miocene, and they were replaced by early crown delphinoids and went extinct during the Tortonian.

## THE IBERIAN RECORD OF THE UPPER JURASSIC COASTAL TURTLE *PLESIOCHELYS*: AN UPDATE

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Thalassochelydia (Testudines, Eucryptodira) is currently recognized as the most diverse clade of turtles in the Upper Jurassic fossil record of the Iberian Peninsula. The Upper Jurassic genus *Plesiochelys* is a member of a successful clade of coastal turtles belonging to Thalassochelydia: the exclusively European clade Plesiochelyidae. This genus shows a relatively abundant record in several European countries (i.e., Switzerland, France, and United Kingdom). Although it has also been recognized in the Iberian Peninsula, only scarce and fragmentary material was identified there, from Tithonian levels. These remains come from two localities, one in Spain and the other in Portugal. The limited availability of characters in these fossils did not allow their specific attribution, so that they were identified as *Plesiochelys* sp. New and well-preserved Iberian shells attributable to *Plesiochelys*, found in two Tithonian outcrops where no remains of this genus had been recognized until now (both located in the Portuguese area of Torres Vedras, in levels corresponding to the Sobral Formation), are presented here. Shell characters not preserved in the previously identified fossils from Spain and Portugal, but considered in the specific diagnoses of the members of the genus, are identified for the Iberian material for the first time. Despite the relatively abundant record of *Plesiochelys* in Europe, no species that inhabited during the Tithonian was recognized by the shell. Therefore, the new Iberian remains could increase the diversity of the group, or the stratigraphic and geographical distribution of some of the species until now exclusive to other European countries. Furthermore, the potential reattribution to *Plesiochelys* of one of the oldest thalassochelydian shells identified so far, corresponding to a Spanish Oxfordian specimen with doubtful genetic attribution (i.e., the holotype and only known specimen of '*Hispaniachelys prebetica*'), is discussed. The confirmation of this hypothesis would expand the stratigraphic range of the genus, until now restricted to the Kimmeridgian and Tithonian. Taking all this into account, the specific diversity of *Plesiochelys* in the Iberian fossil record is discussed.



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**Topic: “Histology, Morphology, Comparative Anatomy and  
Paleobiology”**

Modality: Oral Presentation

***ANTARCTICOLITHUS BRADYI* AND POSSIBLE REVERSAL TO OVIPARITY IN MAASTRICHTIAN MOSASAURS FROM THE LÓPEZ DE BERTODANO FORMATION (ANTARCTICA)**

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The ootaxon *Antarcticoolithus bradyi* is the largest known soft-shelled egg (~29 x 20 cm). It was found in ~68 Myo (Maastrichtian) nearshore marine deposits of the López de Bertodano Formation (LBF) on Seymour Island, Antarctica. Unfortunately, the producer of the egg is unknown since no embryonic remains are preserved. The eggshell structure is most consistent with a large oviparous lepidosaur; formed by a thick proteic membrane overlain by a considerably thinner calcareous layer. Unlike in the “soft” eggs of several Testudines and some Dinosauria, shell units are absent. Interestingly, the eggshell is proportionally thin; reaching approximately 1/3 of the estimated thickness inferred by allometric scaling for a lepidosaur egg of its size. The only known lepidosaurs from LBF are all mosasaurs; large to gigantic specialized marine squamates. Mosasauroids (aigialosaurs + mosasaurs) are presumed to have been viviparous; embryos preserved within the body cavity of a gravid female has been described in at least two species. However, reproductive strategies show remarkable evolutionary plasticity within Serpentes, the closest living relatives of mosasaurs. These range from oviparity with differing intervals of in utero egg retention, to viviparity where females give birth to fully developed neonates; bimodality where a given species has both oviparous and viviparous populations; and even derived oviparity, acquired through reversal from viviparity, with two widely accepted cases (Viperidae: *Lachesis*, Boidae: *Eryx*). In the case of *Eryx*, reversion occurred 60 million years after the acquisition of viviparity in Boidae. Here, we propose that *Antarcticoolithus* is the egg of a mosasaur with derived oviparity. Studies that have examined the process of reversal from viviparity all associate this transition with a warm climate, which makes successful embryonic development and hatching in a nest possible, thus eliminating the greatest advantage of viviparity. During the late Cretaceous, the Antarctic was a cool environment, with mean annual temperatures (MAT) as low as 5°C. However, two recent paleoclimatic reconstructions have independently identified a warming event during the Maastrichtian (~68,5-67,5 Mya) that may have increased MATs by as much as 9°C. This marked increase in temperature may have triggered the reversal to oviparity in viviparous mosasaurs; a hypothetical scenario that is also consistent with the conspicuously thin eggshell, similar to that of extant snakes with derived oviparity.

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## LEVIATHANS UNLEASHED: SKULL ECOMORPHOLOGICAL EVOLUTION DURING THE INITIAL AQUATIC RADIATIONS OF MOSASAURS AND CETACEANS

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The repeated return of tetrapods to aquatic environments provides many iconic examples of convergent evolution, with various groups of mammals and reptiles independently evolving streamlined body shapes and similar feeding strategies. One comparison that has received little attention is that between mosasaurs (a group of Late Cretaceous marine squamates) and early cetaceans (middle to late Eocene ancestors of modern whales and dolphins). These two groups share broad similarities in skull morphology, filling a wide range of niches and achieving global distributions. The earliest fully aquatic members of both groups had serpentine bodies and swam by axial undulation, before evolving more efficient caudal oscillatory locomotion and colonising open ocean niches. Cetaceans continued to diversify after reaching this form whereas the evolutionary history of the mosasaurs was cut short by the end-Cretaceous mass extinction. Here, we investigate possible parallel evolutionary trajectories of skull morphology that occurred during these initial aquatic radiations. A series of functionally informative ratios were calculated from 32 species of mosasaurs and early cetaceans. These were subjected to ordination techniques to reconstruct patterns of functional ecomorphospace occupation, and putative examples of convergence were tested statistically. Preliminary results show that the earliest mosasaurs had gracile skulls, specialised for smaller prey, from which they radiated in several waves across the ecomorphospace. There is considerable variation within certain genera, such as *Mosasaurus*. By contrast, basilosaurid cetaceans occupy a relatively constrained megapredatory niche and cetaceans only evolved new ecomorphologies after the late Eocene split into odontocetes and mysticetes. Oligocene odontocetes explore a new area of morphospace away from the basilosaurids, evolving a long, narrow snout with an increased number of small teeth. The earliest toothed mysticetes have a similar ecomorphology to the basilosaurids, with aetiocetids appearing to radiate in a similar direction to the odontocetes. The late Oligocene *Janjucetus*, which has a highly unusual ecomorphology, plots away from other cetaceans. Despite showing striking similarities to the mosasaur *Prognathodon* (e.g short robust snout and large eyes), the two taxa were not found to be statistically convergent. However, cranial convergence was found between the mosasaur *Mosasaurus hoffmanni* and the basilosaurid *Dorudon atrox*. Future work will investigate these results using 3D landmark analyses, and the evolutionary trajectories in early mysticetes will be extrapolated by including toothless species.



**A COPROLITE CONTAINING A UNIQUE, THREE-Dimensionally PRESERVED PECTORAL GIRDLE AND FORELIMB OF *KEICHOSAURUS HUI* (PACHYPLEUROSAURIA; EOSAUROPTERYGIA); ELUCIDATING PACHYPLEUROSAUR LOCOMOTION**

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The first, three-dimensionally preserved pectoral girdle and forelimb of *Keichousaurus hui* was recovered from the Middle Triassic of Guizhou Province, China. Using a high-definition CT scanner capable of penetrating rock, the specimen was found inside of a coprolite, presumably left by a nothosaurid. The CT scans allowed for the pectoral girdle and forelimb to be segmented in 3D Slicer 4.10.2 and articulated in Meshlab 2020.12. Specimens of *K. hui* are typically found flattened on a bedding plane of mudstones or marls, with the original morphology having been deformed through geologic compaction. This preservational bias left much uncertainty in prior interpretations of mobility at the shoulder and elbow joints. However, a more accurate 3D reconstruction of the bones forming these joints is possible using the newly uncovered specimen, revealing hitherto unknown anatomy of the shoulder and elbow, because the degree of bone deformation is limited in the nodule formed by the coprolite. For instance, the dorsal process of the scapula is notably longer in this specimen compared to taphonomically compressed specimens. Such a tall blade would facilitate easier elevation of the humerus than with short blades of deformed specimens. The linear and rigid articulation of the elbow joint, commonly seen in prior *K. hui* specimens, is likely due to taphonomy since disarticulation is evident from the wide range of variation in preserved relationships between the humerus and the forearm bones. Our 3D reconstruction suggests that the elbow joint was not likely locked in place but instead allowed bending of the elbow during underwater locomotion, as seen in paddling motions of freshwater turtles—similar motions have previously been inferred for some eosauropterygians, such as nothosaurids. Our methodology can be reciprocated if the predator does not chew the prey item and if the bones

of the specimen are small enough to fit inside a fecal pellet. Furthermore, our study exhibits how taphonomic processes affect the articulation of specimens, such as post-mortem rotation of the humerus in fully articulated *K. hui* specimens, which questions the validity of the articulation of limbs in situ and should be considered when performing skeletal reconstructions in other marine reptile groups.

## MORPHOLOGICAL DIVERSITY OF OPHTHALMOSAURID FOREFINS

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Ichthyosaurs were a diverse group of secondary marine reptiles that colonized the oceans from the beginning of the Triassic (Olenekian) until the Late Cretaceous (Cenomanian). One of the most significant events in the evolutionary history of the lineage took place in the Aalenian-Bajocian interval (Middle Jurassic) with the rise of the ophthalmosaurids. Upper Jurassic marine deposits worldwide depict ophthalmosaurid ichthyosaurs as one of the more prolific and successful components of marine tetrapod communities. One of the major traits characterizing this clade is the complexity of their stylopodium-zeugopodium morphology. The ophthalmosaurid forefin has been a source of taxonomic characters since the first attempts to understand their phylogenetic relationships, and it is frequently used to diagnose genera and/or species. Here we analyse the morphological diversity of these regions of the appendicular skeleton of the ophthalmosaurids, using 2D geometric morphometrics of the humerus and disparity analysis of the zeugopodium. We found a peak of zeugopodial disparity occurred during the Kimmeridgian, followed by a decrease by the end of the Jurassic and then a recovery by the Early Cretaceous. Our results also reveal a long duration disparate humeral morphotype characterizing *Arthropterygius* spp. and closely related taxa.

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## PARANASAL SINUS SYSTEM, UPPER RESPIRATORY TRACT, AND SALT GLAND EVOLUTION IN THALATTOSUCHIAN CROCODYLOMORPHS

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Thalattosuchian crocodylomorphs were a diverse clade that predominately inhabited coastal ecosystems during the Mesozoic. Thalattosuchia is comprised of two subgroups, Teleosauroidea and Metriorhynchoidea. Teleosauroids and basal metriorhynchoids were semi-aquatic predators that lived in freshwater, brackish and coastal environments. However, within Metriorhynchoidea there was a major macroevolutionary transition, analogous to that seen during cetacean evolution. Derived metriorhynchoids within the subclade Metriorhynchidae evolved flippers, a tail-fin and became obligately pelagic. Until recently the study of this transition has largely focused on osteological changes, while internal craniofacial changes have been neglected. This is especially true for the paranasal sinus system. In extant crocodylians the rostrum has numerous pneumatic diverticula originating from both the nasal cavity and nasopharyngeal ducts, that become more extensive (in terms of size and number of diverticula) during ontogeny. Herein we investigate the evolution of the paranasal sinus system along with the anteriormost part of the respiratory system (nasal cavity and nasopharyngeal ducts) in Thalattosuchia, by reconstructing the internal anatomy in CT scans of seven thalattosuchian skulls including one teleosauroid (*Plagiophthalmosuchus gracilirostris*), two basal metriorhynchoids (*Pelagosaurus typus* and *Eoneustes gaudryi*), and four derived pelagic metriorhynchids (*Metriorhynchus superciliosus*, *Cricosaurus araucanensis*, *Cricosaurus schroederi* and *Torvoneustes coryphaeus*). Our outgroup taxa were three extant crocodylians (*Gavialis gangeticus*, *Tomistoma schlegelii* and *Crocodylus rhombifer*) and one basal crocodyliform (*Protosuchus haughtoni*). We found that metriorhynchoids had exceptionally reduced paranasal sinus systems, solely comprising the antorbital sinus. In both the teleosauroid *Plagiophthalmosuchus gracilirostris* and the basal metriorhynchoid *Pelagosaurus typus* the antorbital sinus is partially located medial to a reduced external antorbital fenestra, and broadly communicating with the dorsal alveolar canal. In pelagic metriorhynchids, the antorbital sinus is more extensive than in basal taxa and possibly performed an active function associated with a hypothetical accessory suborbital diverticulum. Although our reconstructions alone are insufficient to confirm the presence of a suborbital diverticulum they are consistent with specimens that preserve a contiguous soft-tissue structure exiting the antorbital cavity into the orbit. The nasopharyngeal ducts in metriorhynchids are dorsoventrally enlarged compared to crocodylians and basal

thalattosuchians, and bordered ventrally by thickened palatines. The larger transverse area of the ducts possibly enabled stronger ventilation. The nasal cavity in most metriorhynchoids exhibits posterior dorsolateral expansions, which we identify as a possible osteological correlate for hypertrophied salt glands. The acquisition of internal craniofacial adaptations shows a mosaic pattern, predating the major skeletal adaptations. We hypothesise that these internal craniofacial adaptations occurred while metriorhynchoid were still semi-aquatic.

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## **TIMING OF CROWN DEVELOPMENT IN A MOSASAURINE MOSASAUR (SQUAMATA: MOSASAUROIDEA) AND THEIR APPLICATION FOR RECONSTRUCTING THE DENTAL ONTOGENY OF MOSASAURS**

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We describe the dental ontogeny of a partial right dentary of the mosasaurine mosasaur *Prognathodon sectorius* from the Upper Cretaceous of Liège, northern Belgium. The enamel of all teeth in the dentary preserves discolored, pathological growth marks that probably resulted from episodic deficiencies of calcium or phosphate related to environmental factors. Across most of the tooth crowns, these discolored lines occur in two distinct sets, representing two separate cycles during which the teeth experienced calcium or phosphate shortages. Based on the different crown heights at which these lines occur, the order of tooth eruption can be reconstructed. As tooth growth occurs distally from the crown apex, teeth with discolored lines close to the apex are younger than teeth in which the lines start further away from the apex. The consistency of the discoloration pattern allows isolated, rootless teeth that were found together with the fragmented dentary to be referred to the specimen with certainty. These rootless teeth exhibit traces of resorption at their crown base, discolored lines that are distant from the apex, and a comparatively high amount of wear, indicating that they are the oldest teeth of the jaw. These teeth refute previous models of tooth replacement in which old teeth are shed together with their root while the replacement tooth is still in early development. We provide an updated model of mosasaur tooth replacement based on these observations of the teeth of the dentary. Replacement teeth of mosasaurs grew in expanding resorption pits positioned posterolingually to the functional tooth. The continuous resorption cuts the root of the old tooth off along the contacting area between the dentine and the bulbous surrounding tissue of the root known as osteocementum. Eventually, only the crown of the functional tooth remained, which stayed attached to the jaw through gingival tissue until it eventually fell out. Comparisons to isolated rootless mosasaurine teeth from Khouribga, Morocco, confirmed that old mosasaur teeth are shed after root resorption.

\*Project supported by Alexander von Humboldt Foundation.

## BONE STRUCTURE AND WEIGHT DISTRIBUTION IN THE POSTCRANIAL SKELETON OF THE EOCENE CETACEAN *BASILOTRITUS* (CETACEA: BASILOSURIDAE)

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Modern cetaceans have an osteoporotic postcranial skeleton, an adaptation for a pelagic lifestyle. However, Basilosauridae, early fully aquatic cetaceans, had osteosclerotic or, sometimes, pachyosteosclerotic ribs. Moreover, there were a few Eocene cetaceans, the best known of which is *Basilotritus* from Ukraine, which had sirenian-like heavy skeletons with pachyosteosclerotic ribs, vertebrae and limb girdles. This morphotype, highly unusual for cetaceans, needs to be studied in depth. Two specimens of *Basilotritus* provide unique information about bone macro- and microanatomy in this genus. Ground thin sections and CT scans were produced for this study. The specimen 1 includes cervical and thoracic vertebrae, ribs, fragments of humerus and innominate. Cervicals and anterior thoracics are made of spongy bone, the posterior thoracics are moderately pachyostotic, and the distal ends of anterior ribs are pachyosteosclerotic. The sternebra differs from other ribs in being made of extremely dense bone (compactness 0.99). The proximal part of the humerus at the cross section consists of spongy bone. The innominate is pachyostotic and its dorsal margin is composed of layered cortex. The specimen 2 includes cervical vertebrae, a sternebra, a thoracic rib, lumbar vertebrae, sternal elements, an innominate and a scapula. The cervicals and the sternebra have the same bone microstructure as specimen 1. The inner part of the lumbar vertebra is composed of two cones of cancellous bone (making an hour-glass shape), covered by layered cortex. The rib at the mid-length cross section has anteromedially located spongy medulla and dense cortical bone filling most of the rib. Sternal elements are composed of spongy bone, and the scapula is moderately pachyostotic. Microstructure of cortex layering is different in torso vertebrae and ribs. In ribs the cortical layers are divided by lines of arrested growth (LAG), whereas in vertebrae they are separated by lines consisting of vascular canals (only one weakly visible LAG present). There are resorption cavities and other traces of intensive remodeling in the cortex of vertebrae and ribs. Thus, the skeleton of *Basilotritus* is a mosaic of light and heavy bones. The heaviest bones are concentrated in two regions, the torso vertebrae and some ventral parts of the skeleton, therefore producing two mass centra on the dorsal and ventral sides of the body. This weight distribution may help to provide buoyancy control. Intensive resorption in the deep layers of vertebral cortex may indicate using the axial skeleton as a source of nutrient resources during early postnatal ontogeny.

## THE BIOMOLECULAR INVENTORY OF SOFT TISSUES FROM AN EOCENE CHELONIID: IMPLICATIONS FOR THE EVOLUTION OF SEA TURTLE INTEGUMENT

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Recent work on exceptionally preserved body fossils from Konservat Lagersätten around the world has demonstrated that traces of endogenous biomacromolecules, under certain conditions, can persist long after the organism has perished. One such Lagerstätte that has received growing attention over the last decade is the early Eocene Fur Formation of Denmark. Marine deposits of this formation are replete with animal and plant fossils that derive from both terrestrial and coastal marine environments, with many specimens retaining carbonaceous remnants of soft-tissue structures. A partial, yet articulated skeleton of a hard-shelled (Cheloniidae) sea turtle with extensive soft-tissue remains, including blackish outlines of a flipper and epidermal scute, was recently discovered in diatomaceous deposits on Mors Island, northern Jutland. Examination of the flipper tissue indicates a soft, wrinkly skin devoid of scales. Furthermore, based on an integrated experimental approach that included scanning and transmission electron microscopy, time-of-flight secondary ion mass spectrometry, and infrared microspectroscopy, abundant ovoid microbodies with a predominantly eumelanic biochemistry were detected; these are interpreted as remnant integumental melanosomes. The relict cellular organelles were partially embedded in a fibrous to sheet-like matrix with a morphology similar to keratin fibers of extant sea turtle skin. Molecular analyses further revealed chemical signatures consistent with heme, a porphyrin likely derived from degraded hemoglobin, together with possible proteinaceous residues. Collectively, these novel data indicate that stem cheloniids had limb integument comparable to the scaleless skin of extant soft-shelled turtles (Trionychidae) and adult individuals of the leatherback sea turtle (*Dermochelys coriacea*).

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## NETWORK MORPHOSPACE OF THE HINDLIMBS OF DIVING BIRDS

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Diving has convergently evolved many times within birds. The underwater propulsion can be performed by using the forelimbs, as in penguins and auks, or the hindlimbs, as in cormorants, loons, and grebes. Furthermore, the hindlimbs in penguins, and highly-diving foot propelled birds (grebes and loons) are proximally included within the abdominal wall, with only the foot emerging from the body. Unquestionably, this characteristic has structural and functional consequences. In order to study their hindlimb musculo-skeletal architecture, we compared musculo-skeletal networks of wing propelled divers (Alcidae and Sphenicidae), non-divers (Numididae and Anatidae) and foot-propelled divers (Phalacrocoracidae, Podicipedidae, and Gaviidae). The anatomical networks are undirected multigraphs where bones and muscles were considered as nodes and the physical junctions among them as the edges. From each network we obtained different parameters, as the plain number of nodes and connections, or connectivity parameters as the density of connections, average path length, diameter, average cluster coefficient, average degree, parcellation, and heterogeneity. With the different parameters as variables, we performed a principal component analysis (PCA), with the three first principal components accounting for 98% of the variation. In the resulting morphospace, the first PC (73.9%) segregates the wing propelled divers, with the penguins clustered in the lowest values and the auks scattered in the lower portion of the second PC (16.9%). Non-divers and highly and lesser foot-propelled divers occupy the positive quadrant delimited by the two first PC, with the highly diving grebes and loons segregated from the rest by having higher values for both components. The PCA results show that in foot propelled birds the paths in the network are longer, and the heterogeneity and parcellation are higher, while in wing-propelled divers the networks are denser and with higher cluster coefficient and degree. According to these results, the musculoskeletal structure in the hindlimbs of both highly diving foot-propelled divers and wing-propelled divers, is different from non-divers and lesser foot-propelled divers, probably related to the inclusion of the proximal part of hindlimbs within the abdominal wall. Nevertheless, the musculoskeletal structure in the hindlimb of wing-propelled divers is more integrated, with fewer nodes and a denser architecture, while in foot-propelled divers is less integrated, with longer paths and homogeneous modules.

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## DIVERSITY AND DISPARITY OF PLIOCENE RIGHT WHALES FROM THE NORTH SEA

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Extant right whales (balaenids) comprise two anatomically similar genera – *Balaena* and *Eubalaena* – characterised by an arched rostrum, a large head, long baleen plates, high lips, a finless back, fused cervical vertebrae and a relatively short forearm. By contrast, extinct balaenids are more disparate, as exemplified by the recently described *Antwerpibalaena liberatlas* from the late Pliocene (Oorderen Sands Member, Lillo Formation; 3.21-2.76 Ma) from northern Belgium. Compared to its living relatives, *Antwerpibalaena* has a slenderer flipper and an atlas that is not fused to the remaining neck vertebrae, indicating that certain purported ‘balaenid’ synapomorphies may only apply to the extant genera. The balaenid fossil record from the North Sea is surprisingly rich and besides *Antwerpibalaena* also includes *Balaenula balaenopsis*, *Balaenotus insignis*, *Balaenella brachyrhynchus* and *Eubalaena ianatrix*. The former two are represented by abundant ear bones, but in need of a detailed review based on more complete specimens. Preliminary comparisons reveal an impressive diversity of ear bone morphologies and associated body sizes, perhaps suggesting a more complex history of balaenid gigantism than hitherto assumed.

## CHANGES IN LIMB AND BODY PROPORTIONS LINKED WITH MAJOR HABITAT SHIFTS IN CROCODYLOMORPHA

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Over their ~230 million year history crocodylomorphs evolved into a wide variety of forms, ranging from cursorial terrestrial forms to fully pelagic species. Thalattosuchian crocodylomorphs are a textbook example of tetrapods secondarily adapting to life in water. Within Thalattosuchia, the subclade Metriorhynchidae is the only known pseudosuchian group to have adapted to a fully pelagic lifestyle. Whilst recent studies have revealed some of the morphological and neuroanatomical transformations that accompanied this transition, the changes in thalattosuchian body and limb proportions, and their timings, are still not well-understood. Here, we compiled a large dataset of extinct and extant pseudosuchians and scored them for skeletal measurements (i.e., the lengths of stylopodia, propodia, metapodia, and trunk) that have been shown to capture locomotory differences in crocodylians. We used this dataset to examine similarities and differences amongst crocodylomorph groups in a phylogenetic, ecological, and functional context and used the results to determine whether changes in body proportions accompanied major habitat shifts in Crocodylomorpha, with particular focus on Thalattosuchia. Our analyses show that the relative length of the limbs compared to the trunk, and the relative proportion of each limb region (stylopodial and propodial) are good indicators of habitat preference and inferred locomotory behaviour. For instance, the pelagic metriorhynchids are characterized by an absolute and relative shortening the limb regions compared to the trunk length — patterns seen in other aquatic groups. Fully terrestrial species had relatively short trunks and proportionately long limbs, with semi-aquatic species filling the intermediate of these two extremes. The forelimb and hindlimb proportions of metriorhynchids are unique, with their propodials (ulna/radius, tibia/fibula) being proportionately short when compared to their stylopodia (humerus, femur). These extreme conditions are not seen in basal metriorhynchoid or in their sister taxon Teleosauroidea, but they were gradually acquired, but only reached their zenith in fully pelagic forms. A notable exception is the teleosauroid *Aeolodon priscus*, belonging to a lineage potentially adapted to deep-diving, which shows a pattern of limb reduction similar to that of derived metriorhynchids. Similar patterns are seen in another teleosauroid lineage, Machimosauridae, and in other sea-dwelling crocodylomorphs group such as Tethysuchia, but these groups do not show the same extent of limb reduction as in metriorhynchids. This perhaps indicates that whilst tethysuchians were able to make long-distance marine migrations, they were not suited to a fully pelagic lifestyle.

## MORPHOLOGICAL COMPARISONS OF THE ARM BONES ACROSS SECONDARILY AQUATIC CLADES: ANCESTRAL TERRESTRIAL ANATOMY AND CONTROL ON TRANSITIONS

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In terrestrial and secondarily aquatic clades, the humerus, ulna, and radius together operate as the mover of the forelimb. In secondarily aquatic clades the way the forelimbs are moved depends on the locomotory style, with primary usage ranging from maneuvering and stabilization as in axial swimmers, to subaqueous flight as in many paraxial swimmers, or a combination of both. The aquatic locomotory unit formed by these elements is directly modified from a terrestrial locomotory unit, and there are functional differences in how these bones are anchored to the body across secondary aquatic amniotes. Ancestral terrestrial posture and differences in skeletal anatomy mostly split secondary aquatic “reptiles” (sauropsids) and mammals, with, for example reptiles possessing a coracoid and sprawling posture, and most mammals lacking a coracoid and having upright posture. To investigate if these anatomical differences might shape the morphological and functional pathways of secondary aquatic transitions, the humerus, ulna, and radius, of thirty taxa across four secondary aquatic clades (mosasauroida, pinnipedomorpha, cetacea, sauropterygia) were measured via linear homologous landmarks. Size was corrected for by dividing by the geometric mean of all values per taxon then input into a principal components analysis and a morphospace highlighting each clade was produced. All clades exhibit similar patterns of long bone shortening, indicated by PC1, a known change across secondarily aquatic groups. The arm bone morphology of definitive derived subaqueous flight (sauropterygians and otariids) does not overlap in the morphospace at all. Cetacean arms occupy the widest morphospace area, logical given that they transitioned from paraxial to axial swimming through their evolution, but also have similar degrees of overlap in long bone shortening as mosasaurs, with which they share derived axial swimming styles. Sauropterygians, have the least arm overlap with the other three clades, only occupying a shared portion of the morphospace in early members. Pinniped arm bone morphology is partially nested within cetacean morphospace. These findings may be signals for the controls that ancestral anatomy and functional morphology have in secondary aquatic transitions, with convergence in aquatic locomotory functions achieved through different morphological pathways. The role of other elements in the forelimb (e.g., the manus) may unite or further separate secondarily aquatic clades by locomotor function. Overall, these results set the groundwork for the next stage of this project to examine more morphology associated with function across these clades in the context of ancestral terrestrial anatomy.

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## SELECTIVE PRESSURE BY PREDATORS COULD DRIVE MULTIPLE EVENTS OF BODY SIZE DIVERSIFICATION IN CETACEAN EVOLUTION

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Cetaceans developed at least two opposite life history strategies protecting them from large warm-blooded aquatic predators. One of them is diminishing the body size along with development of cryptic communication and echolocation signals unheard by a predator: this is seen in modern small beaked whales (*Ziphiidae*), pygmy sperm whales (*Kogiidae*) and porpoises (*Phocoenidae*) which escape modern killer whales *Orcinus*. Importantly, all these groups rose earlier, during the Middle to Late Miocene, and, possibly, evolved under the pressure by giant predator sperm whales. Another anti-predator strategy is enlarging the body size, a characteristic of modern giant baleen whales. The rise of gigantic baleen whales goes back to the Middle to Late Miocene, as well as kogiids and porpoises, and thus can also be driven by pressure from the killer sperm whales like *Livyatan*. Therefore, at least two events of cetacean body size diversification (Miocene and Pleistocene) are suggested to be driven by predator pressure, with top predators themselves evolving to gigantic forms. Interestingly, the rise of modern cetaceans (Neoceti) during the Late Eocene coincided in time with existence of another gigantic cetacean top predator, *Basilosaurus*. The earliest Neoceti evolved in two ways, as small-sized toothed whales (Odontoceti) producing high frequency communication signals and ultrasound echolocation signals and baleen whales, the earliest of them including gigantic *Llanocetus*. Also, non-neocete or stem neocete cetaceans of that time showed size disparity including small-bodied *Stromerius* and gigantic “*Platyosphys einori*”. Similar to the later diversification events, these evolutionary pathways could be driven by pressure from a gigantic predator with poorly developed high frequency hearing, as *Basilosaurus* was. Moreover, another less noticeable body size diversification event is suggested for the Oligocene-Miocene boundary to the Early Miocene: large-bodied baleen whales and dwarf toothed whales evolved during that time, as well as the earliest toothed whales with narrow-band frequency hearing. Little is known about cetaceans of that time hunting marine mammals. However, at least some cetaceans, e.g., an early squalodontid *Kelloggia barbarous*, had features indicating their predation on large-sized prey. Thus, in total at least four events of cetacean body size diversification can be referred to predation pressure by other cetaceans, and this driver could also contribute to evolution of high frequency signaling which shaped the evolution of toothed whales.

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## ANOTHER PIECE IN THE PUZZLE: EOCENE SEA COW REMAINS FOUND UNDER UNUSAL CIRCUMSTANCES – *PROTOTherium AUSETANUM* (SIRENIA, DUGONGIDAE) FROM CATALONIA (SPAIN)

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Taxonomic and morphological approaches on Eocene sirenians from Catalonia (Spain) benefit from a newly discovered specimen found in a quite unusual locality, the pedestrian zone in the City of Girona. Two fossil-bearing limestone slabs were dated to the middle Eocene (late Bartonian) making the Girona sea cow one of the oldest sirenian finds in Europe. In the following, the limestone slabs had been removed and substituted from the pavement and were CT-scanned to gain more information about the obscured fossil content. The specimen most likely represents *Prototherium ausetanum* based on our results in morphology, palaeobiogeography, and stratigraphy, and hence complements the available information of the holotype and hitherto only known specimen of that species. The Girona specimen is an adult, but small individual that corroborates *P. ausetanum* as a generally small-sized species compared to other known *Prototherium* taxa. This is especially indicated by comparisons of the molars, which are distinctly smaller compared to those from *P. veronense* and *P. intermedium* from the late Eocene of Italy, but very similar in size and proportions compared to *P. ausetanum*. Post-processing of the CT scans and subsequent 3D-reconstruction of the Girona sea cow also provides new insights into the evolutionary history and diversity of Eocene dugongids. The Dugongidae have a long and rich fossil record, but the phylogenetic interrelationships, especially of Eocene taxa, are the subject of controversial debates. As such, any new find that morphologically complements the knowledge of hitherto less well-known taxa like *P. ausetanum* holds the potential of better resolved interrelationships. On a higher level, any new sirenian find from the Eocene of Europe also may contribute to support the Tethytheria hypothesis. While morphological and (molecular-) genetic data reveal sea cows to be most closely related with elephants and hence, corroborate their origin in the former Tethyan realm, the earliest known sirenians date back over some 50 Ma into the late early to early middle Eocene (late Ypresian to early Lutetian) of Jamaica. A geographic paradoxon that is still awaiting to be answered. However, there appears to be a central European hot-spot of diversification with several species known from the Lutetian to Bartonian of Spain, including the Girona sea cow, and the Bartonian to Priabonian of France and Italy. Taken together, there are good reasons to rather assume the origin of sea cows in the Tethys with a fast dispersal westward.

## CONVERGENT EVOLUTION OF FORELIMB-PROPELLED SWIMMING IN SEALS

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Modern pinnipeds (true and eared seals) employ two radically different swimming styles, with true seals (phocids) propelling themselves primarily with their hind limbs, whereas eared seals (otariids) rely on their wing-like foreflippers. Current explanations of this functional dichotomy invoke either pinniped diphyly or independent colonizations of the ocean by related but still largely terrestrial ancestors. Here, we show that pinniped swimming styles form an anatomical, functional and behavioral continuum, within which adaptations for forelimb swimming can arise directly from hind limb-propelled bauplan. Within phocids, southern seals (monachines) show a convergent trend towards wing-like, hydrodynamically efficient forelimbs used for propulsion during slow swimming, turning, bursts of speed, or when initiating movement. This condition is most evident in leopard seals, which have well-integrated foreflippers with little digit mobility, reduced claws, and hydrodynamic characteristics comparable to those of forelimb-propelled otariids. Using monachines as a model, we suggest that the last common ancestor of modern seals may have been hind limb-propelled and aquatically adapted, thus resolving the apparent contradiction at the root of pinniped evolution.

## LIFE HISTORY TRAITS OF MOSASAUROID LIZARDS REVEALED BY RIB HISTOLOGY

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Mosasauroida is a highly evolved and specialized group of squamate reptiles that radiated rapidly into the oceans of the world, reaching gigantic body sizes and streamlined body shapes during the Late Cretaceous. However, how they reached such a body size and mass remains unclear. Bone histology has been a key tool in reconstructing life histories in fossil and extant vertebrates, since bones provide mechanical support and reveal information about the animal's anatomy, biology, behavior and ecology. Previous research shows that rib bones of sauropods preserve a good growth record due to their simple morphology and relatively low bone apposition rate. Here we show the utility of mosasauroid rib fragments for histological analyses of life history and ontogeny, based on the principle that rib growth happens primarily from proximal to distal, producing a change in cross-sectional shape during ontogeny. Two complete dorsal ribs, one of *Platecarpus sp.* and the other of *Clidastes propython*, were sectioned in different positions along the proximodistal axis. Both taxa, although phylogenetically distant, show a similar microanatomy of longitudinally vascularized primary bone tissue which is replaced by secondary cancellous bone surrounding the medullary cavity. Rib growth shows distinct cycles, ending in lines of arrested growth. After mapping the histology along the ribs, the best growth record was found to be located just distal to the rib head, a few centimeters distal to where the shaft first assumes a figure-eight cross section. The best record of primary cortical bone is preserved here because it is least replaced by secondary cancellous bone, and at most one growth cycle was lost to remodeling. Despite their phylogenetic distance, both mosasauroid lizards reached skeletal maturity at an age of approximately 10 years old. This is indicated by the initiation of an external fundamental system at this cycle count. Sexual maturity was already reached in both specimens at the age of 7-8 years old, visible in the thin section as a sudden decrease in growth mark spacing. Considering that both individuals must have had a body mass of several hundred kilograms, their life history resembles that of similar-sized dolphins. This suggests a higher basal metabolic rate in mosasauroids than in extant squamates.

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## BONE HISTOLOGY AND SEXUAL MATURITY OF *KEICHOSAURUS HUI* (DIAPSIDA, EOSAUROPTERYGIA) FROM MIDDLE TRIASSIC OF SW CHINA

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*Keichosaurus hui* is a small pachypleurosaur from the late Ladinian Xingyi Fauna of the southwestern Chinese provinces Guizhou and Yunnan. The taxon is known from thousands of specimens including whole growth series and gravid females. Like many other pachypleurosaurs, *Keichosaurus* shows a pronounced and easily recognized sexual dimorphism, particularly in humerus shape. The males have an angular humerus shaft, and their humerus is distally expanded. The females, on the other hand, show simplified humerus morphology that includes a round shaft cross section. Here we describe the long bone histology of *Keichosaurus* for the first time. In addition, for the first in an amniote, humeral midshaft microanatomy reveals the onset of sexual maturity. This happened in the second growth cycle, corresponding to the second year of life of *Keichosaurus*. The first cycle has a more organized bone tissue than the second one, during which sexual maturity occurred. In the males, during the second cycle, the shaft cross section changes from round to triangular. The corners of the triangle represent the angular shaft cross section of the mature males. Interestingly, the less organized bone tissue of the second cycle occurs in both sexes, but the females continue to grow with a round or oval cross section. In addition, sex identification appears to be possible histologically even in juvenile specimens and even without external sexual dimorphic characteristics. Although a difference in growth rate between the two sexes was not observed in this study, this may be due to the small sample size. Our life history data furthermore show earlier sexual maturation of *K. hui* males compared to other pachypleurosaurs. Estimated maximum age is greater than nine years. The bone tissue deposited in *K. hui* humeri pertains to the lamellar-zonal type. Bone compactness of both sexes is high, and there are no differences between sexes. Like other pachypleurosaurs, the very small medullary cavity of the humerus indicates osteosclerosis, which fits with the morphological evidence for secondary aquatic adaptation in *K. hui*.

## ANATOMICAL INSIGHTS FROM ARCTIC ICHTHYOSAURS

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Ichthyosaurs transitioned from land to sea probably a very short time after the Permian-Triassic mass extinction and became important marine predators. After experiencing another extinction event at the Triassic-Jurassic border, the group lost variation in terms of body shape and size. From the Jurassic onwards, the ichthyosaurs acquired the shape most commonly associated with them: A streamlined body for a life in the open ocean, strikingly similar to dolphins and porpoises. The adaptations were very successful and preserved for their remaining millions of until their extinction in the Late Cretaceous. But even if the shape of a derived ichthyosaur is familiar, much is unknown about its actual anatomy, and whether all parts of the body do in fact display a convergent pattern to modern odontocetes. Understanding skeletal anatomy is necessary for analyzing evolution of new features, adaptation to life at sea and biomechanics. The aim of the work was to explore poorly known portions of the skeleton including the basicranium, the pectoral girdle, ribs and the pelvic girdle. Previously, there has been a bias towards phylogenetic characters from the humerus and selected portions of the skull, and future analyses will benefit from knowledge on additional parts of the skeleton. The newly excavated (2004-2012) assemblage from the Arctic archipelago of Spitsbergen was used, consisting of 26 specimens from the latest Jurassic and earliest Cretaceous. The analysis of basicranial elements showed that this region is influenced by rapid evolution and a conserved need for a stable basicranium. With regard to the hyobranchial arch, the material from Slottsmøya preserve hyoids in at least four specimens, adding shape and size information that has been lacking for ophthalmosaurid ichthyosaurs. Some of the ichthyosaurs from Spitsbergen show unique traits that should be investigated further to understand how widespread they actually are, as well as their function. This includes the greatly enlarged parietal foramen in two specimens, but also a previously unrecognized variation in the shape and the size of the pelvic girdle that might be explained by either locomotion or reproductive biology. Pelvic girdles and femora from Spitsbergen combined with new findings from South America can shed light on the reason why ichthyosaurs, compared to whales, did not lose their external hind fin in the transition to the sea nor to the open ocean.

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## DID TAXONOMIC TURNOVER CONSTRAIN CRANIAL MORPHOFUNCTIONAL DIVERSITY IN MOSASAURS? A GLOBAL OUTLOOK THROUGH THE CAMPANIAN AND MAASTRICHTIAN

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Mosasaurians represent one of the most prominent Late Cretaceous marine reptile clades. There is evidence from multiple sites worldwide that global mosasaur community structure was affected considerably through the Campanian and Maastrichtian. In this study, we use a suite of biomechanical traits and functionally descriptive ratios to investigate whether observed taxonomic turnovers are reflected in functional diversity (disparity) in mosasaur communities from the early Campanian to late Maastrichtian. Using measurements from 3D laser surface scans and scaled images, we calculated 17 functional traits from 96 mosasaur specimens across 57 species (>75% of known taxa). Traits included biomechanically informative ratios (e.g., mandibular lever arms) and sensory/physiological features (e.g. relative nares size). Functional traits were evaluated for completeness, standardised (z-transformation), and patterns of trait variation assessed using ordination techniques to generate ecomorphospaces and functional disparity through time. Ordination results largely corresponded in clustering of species in ecomorphospace. Groupings with discrete morphofunctional similarities were observed, including taxa with strongly recurved dentition (*Plioplatecarpus*, *Tethysaurus*) and gracile preorbital rostra (*Ectenosaurus*, *Gavialimimus*). Large megapredatory species (e.g. Plotosaurini & Tylosaurinae) tended to cluster together. Discrete, phylogenetically-independent clusters were uncovered using only feeding traits, with clear groupings in both Campanian and Maastrichtian ecomorphospaces. Global mosasaur functional disparity decreases significantly across the C/M boundary; however, this overall pattern appears to be driven by a steep decline in feeding disparity between early and late Maastrichtian. In fact, global functional disparity is higher in the early Maastrichtian than in the late Campanian. Localised mosasaur communities undergo discrete patterns of cranial ecomorphospace occupation and functional disparity during this time: Western Interior Seaway and Antipodean communities experience significant declines through the Maastrichtian, whereas those in the Northern and Southern Tethys Provinces show constant or increasing disparity through the Campanian and Maastrichtian. We conclude that the worldwide turnover in mosasaur community composition from Early Campanian to Late Maastrichtian does not appear to be reflected by a global reduction in functional variability. Rather, geographically localised community structures appear to have undergone discrete changes (extinctions, speciation and migration), influencing the diversity of cranial function in mosasaurians on the provincial level. Our results demonstrate that in several key geographic locations, mosasaur functional diversity was in decline prior to their demise during the K/Pg mass extinction.

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## THE EVOLUTION OF CAUDAL REGIONALIZATION IN ICHTHYOSAURS

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Regionalization within the caudal skeleton of vertebrates is well-documented, especially in actinopterygian fishes where the distal axial skeleton is modified to support the caudal fin rays. However, the caudal region in amniotes is rarely discussed, making commonalities over longer evolutionary time scales uncertain. In mammals, three discrete regions are recognized posterior to the sacrum: a proximal, a transitional, and a distal caudal region. Among diapsid reptiles, three regions are also recognized: a pygal region, consisting of vertebrae with ribs but lacking haemal arches, an intermediate region bearing both ribs and haemal arches, and a distal region lacking ribs. Although it is likely the proximal region of the mammalian caudal skeleton is homologous to the pygal region, the homologies of the posterior two regions are less certain. Among secondarily aquatic tetrapods relying on axial propulsion, caudal regionalization is associated with dedifferentiation between the posterior dorsal and proximal caudal regions, combined with increased regional differences within the caudal series. Distal caudal vertebrae are often modified to support a propulsive organ. Here, I use ichthyosaurs as a model group in which to explore problems related to the evolution of caudal regionalization in a constrained phylogenetic context. In ichthyosaurs, all three caudal regions can be identified in basal taxa; however, the proximal region becomes dedifferentiated during the Early Jurassic. The tail fin is derived from vertebrae of the distal caudal region, but the position of the tail bend relative to the intermediate – distal regional boundary appears to shift posteriorly over time from within the distal region to the intermediate-distal regional boundary when defined by the loss of rib apophyses. However, when haemal arch morphology is considered, the tail bend consistently correlates with the regional boundary. Large-scale meristic changes within regions are correlated with body plan evolution. For instance, the intermediate region increases substantially in length, from 5-10 vertebrae in the ichthyosauriform *Chaohusaurus* to >30 in the baracromian *Stenopterygius*. This increase cannot be explained solely by dedifferentiation of the proximal region, and is correlated with the presence of a semi-lunate tail fin. This synopsis of caudal regions in a group in which a regionalized tail is primitive highlights several key problems: 1) which morphological structures best define regions in the caudal skeleton; 2) whether vertebrae involved in the tail bend should be considered a novel region; and 3) if a shared caudal patterning framework being is coopted across clades to produce a regionalized tail skeleton.



## PRENATAL OSSIFICATION STAGES OF THE EARLY JURASSIC ICHTHYOSAUR *STENOPTERYGIUS QUADRISCISSUS* AND PALEOBIOLOGICAL IMPLICATIONS

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Viviparity is a common adaptation for marine tetrapods to accommodate reproduction in an aquatic habitat. The Ichthyosauria acquired viviparity early in their evolutionary history, likely around the time they entered their aquatic habitat or even as an exaptation. *Stenopterygius quadriscissus* is an Early Jurassic ichthyosaur, well-known for the many specimens of gravid females with well-preserved embryonic material. To date, that material has mostly been designated as “embryonic” and few attempts have been made to study prenatal osteological development. We studied embryonic material from eight gravid females of *S. quadriscissus*. We recognize four potential stages of prenatal development on the basis of cranial ossification; differing in both the degree of ossification of the individual elements as well as in the sequence of ossification. The circumorbital elements ossify early relative to the rest of the cranium, followed by the cheek area and dermatocranial elements of the lower jaw. The parietal and frontal lag behind these areas in ossification throughout prenatal ontogeny, as does the palate. Splanchnocranial and chondrocranial elements (braincase, articular, quadrate) are latest in ossification. The lag in ossification of the chondrocranial and splanchnocranial elements compared to the dermatocranial elements is seen throughout Diapsida. The cranial midline elements of the skull roof as well as the anterior girdle are not fully developed and the antimeric sutures of the parietal, frontal and coracoid are not closed perinatally. We hypothesize that weak midline ossification relative to anteroposterior ossification functions to prevent damage to the embryonic skull during birth, similar to the cranial fontanelles in mammals. Although fontanelles are present in many oviparous reptiles, delayed closure of the midline sutures relative to transverse sutures is rare, especially regarding the frontal, and is therefore here considered to be associated with viviparity and as a possible adaptation to an aquatic lifestyle. Perinatal embryos are on the whole well-ossified and possess functional teeth, ossified jaw elements and well-formed flippers. It is probable that the neonates were precocial, able to swim and feed immediately after birth. This is corroborated by the fact that juveniles and adults had differing diets and therefore occupied different niches. Moreover, many females of *Stenopterygius* had litters of multiple (up to 10-11) embryos, and provisioning so many young would have been challenging.

## AN ARCHAIC NEW ZEALAND SEAL (FAMILY PHOCIDAE) AND THE EVOLUTION OF MULTIPLE MORPHOLOGIES FOR UNDERWATER HEARING IN “EARLESS” SEALS

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Fossils from Australasia have revealed that southern true (“earless”) seals (Subfamily Monachinae) largely evolved in the Southern Hemisphere, with fossil representatives of all three extant monachine Tribes (Monachini, Miroungini, Lobodontini) identified in New Zealand. This contrasts with the fossil record for South Africa and South America, from which more ancient true seals are found. Today, true seals are remarkable for displaying a surprising amount of variation in the morphology related to the round window. The separation of the round window from the rest of the tympanic cavity in true seals enables effective underwater hearing, whilst retaining the ability to hear in-air, via the “traditional” mammalian auditory pathway. As ancient true seal fossils are rare worldwide, including in Australasia, the origins of the disparate morphology related to underwater hearing displayed within the group today is unknown. We report the fossil basicranium of an archaic true seal from Motunau, New Zealand. This cranium was found in a reworked concretion from the Greta Formation, with dating constrained using fossilised barnacles adhering to the specimen (13–3 Ma). The internal anatomy of fossil and extant true seals was investigated by using micro-computed tomography (micro-CT) scanning. The Motunau seal possesses an archaic form of auditory morphology, reminiscent of ancient monachines and the stem-true seal *Devinophoca*. A subsequent total-evidence fossilised birth-death Bayesian analysis resolved this seal as an early diverging true seal. A morphological ancestral state estimation of the round window morphology of true seals reveals that the Motunau specimen possessed transitional morphology related to underwater hearing, hinting that modern diversity in underwater hearing morphology has ancient origins. This suggests that effective aquatic hearing was likely an early adaptation in true seals.

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## **SURVEY OF THE PELVIC AND THORACIC GIRDLES OF DYROSAURID AND THALATTOSUCHIAN CROCODYLIFORMES**

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Dyrosauridae is a clade of neosuchian crocodyliformes that diversified in fluvial and marine environments across the Cretaceous-Paleogene transition. Thalattosuchia is a clade of aquatic crocodyliforms which spanned over the Jurassic period and disappeared during the Early Cretaceous. Both clades crossed extinction events (i.e., Jurassic-Cretaceous boundary for Thalattosuchia; Cretaceous-Paleogene for Dyrosauridae). The postcranial anatomy of both groups has long been overlooked in anatomical descriptions and diagnoses, obscuring their disparity and their locomotive adaptations. We surveyed the morphology of the postcranial skeleton of Dyrosauridae, Thalattosuchia, and Crocodylia, in order to identify osteological correlates for ecology and behaviour as well as test for the existence of evolutionary trends. We thoroughly surveyed the anatomy of crocodyliformes, creating 187 morphofunctional ratios that span the entire skeleton, more than 80% of which being postcranial. Ordination techniques on this extensive dataset reveal the existence of a distinctive postcranial anatomy for both Dyrosauridae and Thalattosuchia which are both markedly distinct from that of crocodylians. As a result, modern crocodylians are likely not a good functional or ecological analogy for extinct crocodyliform groups. It also appears clear that postcranial data is an important component of crocodyliform disparity. A focus on thoracic and pelvic girdles reveals a wide occupation of the morphospace for coastal taxa, even though Dyrosauridae, Thalattosuchia, and Crocodylia occupy clearly separated areas of the morphospace. Within Thalattosuchia, three main clusters are observed regardless of phylogenetic affinities, putatively hinting at global morphotypes within the clade. The most discriminant features between our samples appear to concern primarily the femur (e.g., posterior curvature, fourth trochanter, head protrusion, etc.) with contributions from the pubis, sacra, and the ilium.

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## CRANIAL NEUROVASCULATURE AND PNEUMATICITY IN THALATTOSUCHIAN CROCODYLOMORPHS

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During the Mesozoic, thalattosuchian crocodylomorphs underwent a major macroevolutionary transition, evolving from semi-aquatic taxa into pelagic forms (Metriorhynchidae). In order to investigate the land-to-sea transition seen in Thalattosuchia, and the evolution of the pelagic metriorhynchids, our team CT-scanned and digitally segmented the cranial endocasts of 16 extinct and extant crocodylomorphs. Our results document that early diverging crocodylomorphs ('sphenosuchians') had distinct brain, vasculature, and sinus morphologies, noticeably different from extant species. However, protosuchian-grade taxa had the entire suite of pneumatic structures seen in extant crocodylians, suggesting crocodylian sinus patterns originated over 200 million years ago. Interestingly, 'protosuchians' had highly pneumatic crania (far more so than extant species) with pneumatization of the laterosphenoids and frontals. Thalattosuchians had a unique array of endocranial vasculature and pneumatic anatomies; with hypertrophy of venous sinuses and vasculature canal endocasts. Compared to the circulatory patterns of extant species, thalattosuchians would have had far greater blood flow entering and exiting the orbital and nasal regions. This corresponds to their proportionally large orbits, and hints that the salt glands observed in Metriorhynchidae evolved at the base of Thalattosuchia. All thalattosuchians had less extensive cranial pneumatic sinus systems when compared to 'sphenosuchians', 'protosuchians' and extant species. Rather than having discrete diverticula, the sinuses were confluent with the tympanic cavity and hard to individualize. The lack of the intertympanic diverticula suggests thalattosuchians had poor acoustic coupling of the middle ears, with limited directional hearing when compared to extant species. Our results suggest that some of the major soft tissue adaptations that underpinned the metriorhynchid radiation



into the pelagic realm occurred much earlier in thalattosuchian evolution, prior to the reorganisation of the post-cranial skeleton. This corresponds to our already published work on the inner ears: the major endocranial changes occurred at the base of Thalattosuchia, with incremental changes occurring towards and within Metriorhynchidae.

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## A NEW SPECIMEN OF THE TRIASSIC BIZARRE SAUROPTERYGIAN *PALUDIDRACO MULTIDENTATUS*

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El Atance is an Upper Triassic fossil site located on the coast of the El Atance reservoir near Sigüenza (Guadalajara Province, Spain). The site has provided several remains of sauropterygians, including two recently described new taxa, the placodont *Parahenodus atancensis* and the eosauroptrygian *Paludidraco multidentatus*. The latter is the most abundant sauropterygian there, several individuals being recovered. However, all the information published so far about this form is limited to that corresponding to a relatively complete skeleton (the holotype) and an isolated skull (the paratype), only a brief description being currently available about them. *Paludidraco multidentatus* is a bizarre simosaurid nothosauroid closely related to *Simosaurus gaillardoti*, from the Middle Triassic of Europe. Opposite to *Simosaurus gaillardoti* and other Triassic eosauroptrygians, *Paludidraco multidentatus* has been interpreted as a slow swimmer with filter-feeding habits. Thus, it shows a highly pachyostotic postcranial skeleton and displays a specialized cranial anatomy. Here we present an unpublished specimen of *Paludidraco multidentatus*, currently under study. This specimen is represented by a partially articulated postcranial skeleton. It presents some posterior cervical vertebrae, the complete dorsal series, and some vertebrae of the sacral region, as well as some appendicular elements and both pectoral and pelvic girdles. This individual is larger than the holotype, and the pachyostosis of the vertebrae and ribs being more developed. Its detailed study, and the comparisons with the holotype, will provide new anatomical information about the species, and will help to broaden the range of intraspecific variability of *Paludidraco multidentatus*.

## IMPROVING THE IMPACT OF YOUR RESEARCH: ADVICE FOR EARLY CAREER RESEARCHERS BASED ON BIBLIOMETRIC ANALYSIS OF THE PAST DECADE OF MARINE MAMMAL PALEONTOLOGY

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Early career researchers typically need multiple high impact publications when applying for grants, fellowships, and jobs. Here, we explore the benefit of Open Access for improving research impact, using a dataset based on the past decade (2010-2020) of marine mammal paleontology papers indexed in Clarivate Web of Science (WoS) (n = 596). We selected marine mammal paleontology papers to focus on a single community of practice, maintain an easily studied dataset, and minimize the potential influences of worker bias on other secondarily aquatic tetrapod groups. The Open Access (OA) citation advantage is a well understood phenomenon, yet typically is not explored along the different types of OA, such as author-pays or article processing charge (APC) model (Gold OA), free to publish or no APC model (Diamond OA), or author provided copy model (Green OA). It is implicit in the name of the first that the author must pay out a hefty cost--within our dataset, APC costs of 172 Gold OA articles ranged from \$871 to \$5,560 (mean APC = \$2,426). A one-way analysis of variance (ANOVA) was carried out on the citations-per-year of these different groups of articles. Significant differences were found between the different models of OA in their citations-per-year. In order of highest average citations-per-year for OA articles, Gold OA was first (2.1708), Green OA was second (1.8009), and Diamond OA was last (0.6135). Toll articles (no OA of any kind, not even Green OA) still had a mean citations-per-year of 1.5059. However, in pairwise comparisons, there was no significant difference between Gold OA or Green OA articles (p = 0.45352) or Green OA and toll articles (p = 0.64218). This suggests that early career researchers would be better served publishing where they can and making their work available through Green OA options rather than paying the high costs of APCs required by Gold OA. Green OA options for disseminating their work could include disseminating their work through their personal websites, institutional or scholarly repositories, or academic social networking sites like Academia.edu or ResearchGate. While among OA papers only available as Green OA, ResearchGate is more heavily used among marine mammal paleontologists versus Academia.edu, there is no significant difference in the citations-per-year of papers on either site. Institutional and scholarly repositories remain critically underutilized by marine mammal paleontologists (only 20% of the papers).

## FIRST STEPS FOR A MORPHOMETRIC APPROACH TO THE SEXUAL DIMORPHISM OF EUROPEAN EXTINCT PLEURODIRAN TURTLES

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The study of sexual dimorphism in the fossil record can provide relevant data about the social structure of several extinct species. Information about this variability is unknown for most vertebrate extinct species, since a considerable sample size and a good preservation are generally necessary to perform such studies, especially when the objective is to analyze sexually variable characters through a quantitative approach. Turtles are a peculiar group of reptiles, characterized by the presence of a shell. Some characters associated with sexual dimorphism can be recognized in this osseous structure. Given that several turtle lineages are part of the current biodiversity, the analysis of their dimorphism can help to understand that of some extinct forms. Thus, a wide variety of sexually dimorphic characters has been demonstrated for extant taxa, opposite trends for some characters occurring between males and females of several lineages. However, relatively few studies focused on sexual dimorphism in extinct forms are available. This study aims to analyze and synthesize the sexual dimorphism present in one of the two clades that is part of the crown Testudines: Pleurodira. This clade is known from the Upper Jurassic to the present and, although it is currently restricted to intertropical regions, its distribution in the past was much greater, being very abundant in both the Upper Cretaceous and the Eocene records of Europe. To achieve the proposed objective, sexual dimorphism was evaluated in the most relevant and best-represented lineages of pleurodiran turtles in the European record, especially considering the taxa recorded in south-western Europe, which belong to Dortokidae, Bothremydidae and Podocnemididae. The morphotypes of the analyzed European species recognized as potentially attributable to sexual dimorphs were compared not only with other extinct forms but also with extant representatives of Podocnemididae, Pelomedusidae and Chelidae. Comparisons were made both by the first-hand study of some specimens and by analyzing the information available in the literature. The sexual variability was analyzed through a quantitative approach, with the landmark-based geometric morphometric method, providing precise results through objective analysis and graphic tools for its quantification and visualization. Thus, several statistical techniques were used to extensively identify and characterize the shell elements affected by sexual variation. The results evidence a significant sexual dimorphism in most pleurodiran lineages, specifically, in the morphology of the anal notch. The comparison of the sexual dimorphism between the main clades provides information to understand different trends acquired throughout the evolutionary history of Pleurodira.

## A NEW SPECIES OF MACROPREDATOR DOLPHIN (CETACEA: KENTRIODONTIDAE) FROM MIDDLE MIOCENE, PISCO FORMATION, SOUTH COAST OF PERU

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Kentriodontidae is a family of fossil delphinidan dolphins with historically debatable monophyly, but the situation has changed in the last few years. Their fossil record is extensive, from the late Oligocene to the late Miocene (23.3-9 Ma), and shows greater diversity during the Miocene in Europe, Asia, America, and Oceania. This family is composed of two subgroups according to the last phylogenetic analysis, being this second group composed of the largest known Kentriodontidae: *Hadrodelphis*, *Liolithax*, *Lophocetus*, and *Macrokentriodon*. Three previous kentriodontid dolphins were described and the present authors have formerly reported two large kentriodontids, all from the Pisco formation, Ica region, Peru. The Pisco Formation (Middle Miocene-Pliocene) presents lithology composed of whitish silty claystones, diatomaceous lutites, diatomites, some intercalations of a few compact fine sandstones, and tuffaceous gravels with a neritic sedimentary environment attributed to the inner platform. The present specimen of Kentriodontidae sp. indet. (MUSM 4268) was previously reported in an abstract of 2018 without a detailed description. We are now describing in detail MUSM 4268, which comes from the P0 Sequence of Pisco formation (middle Miocene age) from Cerro Yesera de Amara located 25 km Southwestern from Ocucaje city, Ica region, southern coast of Peru. MUSM 4268 is composed of one partial skull with mandibles, periotic and fragmentary tympanic bulla, this skull (condylobasal length: 679mm; bizygomatic width: 252 mm) compared with other large species of the second group of Kentriodontidae display transversally narrow nasals differing from *Lophocetus*, frontals exposed at the vertex, wide temporal fossa and convex anterodorsal margin of the supraoccipital as seen in *Lophocetus*, *Hadrodelphis*, and *Liolithax*. However, the presence of transversally narrow nasals along their entire length, low vertex, and robust rostrum morphology resembles *Liolithax pappus* but differs from this taxa by having slightly elongated and narrow antorbital processes and wide antorbital notches. Also, it presents powerful mandibles with robust teeth, premaxillae laterally inflated slightly anterior to level of antorbital notches and periotic with higher pars cochlearis, similar to *L. pappus*. Considering these cranial characters, MUSM 4268 probably represents a new species related to *L. pappus* or a related new genus. MUSM 4268 probably was a macro-predator kentriodontid dolphin from Pisco Formation (middle Miocene) and represents the third record of large kentriodontids for South America. Previous records include a kentriodontid probably related to *Macrokentriodon* also from the Pisco Formation (Late Miocene), Peru, and a kentriodontid probably related to *Hadrodelphis* from the Caujarao Formation (middle-late Miocene), Venezuela.

## FIRST THREE-DIMENSIONAL NEUROANATOMICAL AND CRANIAL RECONSTRUCTION OF A BOTHREMYDID TURTLE (TESTUDINES, PLEURODIRA)

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The use of computed axial tomography scans for the neuroanatomical studies is a very useful and non-invasive technique to analyze the inner cranial cavities and structures. Since the end of the 20th century, the use of these tools has been employed to study various extinct taxa of vertebrates. The application of this technique for the analysis of extinct turtles is more recent than in other groups such as crocodylians, dinosaurs or mammals. Thus, the first neuroanatomical reconstruction for an extinct turtle, corresponding to that of the European Upper Jurassic *Plesiochelys etalloni*, was published less than ten years ago. Despite three-dimensional models corresponding to the neuroanatomical reconstructions of different clades of turtles (both basal and derived taxa) are now available, the information about the neuroanatomy of Pleurodira is still very scarce. In fact, although some partial neuroanatomical reconstructions of extant members of Pleurodira have been included in comparative studies, only those of two fossil species were published. Both species are members of Podocnemididae. The extinct clade Bothremydidae is one of the best represented pleurodiran lineages in the Cretaceous and Paleogene fossil record of several continents, in both Laurasia and Gondwana. Despite the abundant and diverse record available on this successful group, the only studies currently available on its neuroanatomy were published in the 1960s and 1970s, prior to the use of computed axial tomography scans for these analyzes. The first one corresponds to the analysis of an artificial latex cast, and the second to that of a natural endocast, both belonging to North American taxa. Therefore, a complete reconstruction of the neuroanatomy of this group is not currently available. As a result, the first three-dimensional reconstruction of the cranial anatomy and neuroanatomy of a bothremydid turtle is presented here. In addition, a comparative framework is established through the neuroanatomical reconstruction and analysis of various species of extant pleurodires, corresponding to several lineages, observing that the most variable neuroanatomical characters for this group correspond to the shape of the olfactory region, the lateral expansion of the cerebral hemispheres, and the development of the vidian branches of the facial nerves.

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## **ANATOMY OF A DWARF MIOCENE SEAL *MONACHOPSIS PONTICA* FROM THE EASTERN PARATETHYS**

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*Monachopsis pontica* is one of the smallest species of seals that had ever lived. It was described by Eichwald, 1850, however, findings of complete or partial skeletons were missing until recent time. Newly found specimens of *M. pontica* include new parts of the skull (such as maxilla, mandibular, tympanic bulla), which help understand the phylogenetic position of this dwarf pinniped. Material: A partial skeleton (10246), including the skull, vertebrae, limbs, etc is stored in the Feldman Family Museum, Kharkiv, Ukraine. Another partial skull (CH00-01) and isolated teeth are stored in V.I. Vernadsky Taurida National University (Simferopol, Ukraine), and the lectotype is SPMI 17-113 (St Petersburg, Russia). *M. pontica* lived in a shallow temperate sea of the Eastern Paratethys in the Tortonian (from 8.6 to 7.6 Ma). It was about 80-90 cm in body length and its condylobasal skull length was about 140 mm. New findings of facial skulls show that *M. pontica* had three incisors in the maxilla. The 4th premolars and the 1st molars were double rooted, divided by a diastema. All the double rooted premolars and molars have a similar size with a large protoconid, a tiny metaconid and a paraconid. The scapula is elongated, the inner edge of the scapula is semicircular, and the upper edge is only slightly protruding dorsal to the neck of the scapula. The deltoid crest of the humerus is high and so long that its distal edge is situated near to distal epiphysis of the humerus. The sacrum contains four fused vertebrae (Monachinae usually have 3 and Phocinae have 4). The femur is short and wide, with a large greater trochanter. The neck of the femur is short and the distal epiphysis is relatively wide. The tibia and fibula are not fused with each other. Phylogenetic analysis shows that *M. pontica* belongs to the subfamily Phocinae and nests this species in the separate branch at the base of the extant Phocinae, the hypothesis needing further testing. *M. pontica* has a few autapomorphies including the shape of humerus and femur. Meanwhile, its facial skull anatomy shares a few traits with the extant harp and ribbon seals.





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## **Recorded Presentations**

**Topic: “Evo-devo”**

Modality: Oral Presentation

## **TERRESTRIAL AND AQUATIC SHIFTS IN TESTUDINES ASSOCIATED WITH DIFFERENCES IN WATERBORNE ODORANT-DETECTING OLFACTORY RECEPTORS AND NASAL CAVITY MORPHOLOGY**

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The shift from aquatic to terrestrial environments and vice versa is accompanied by major morphological changes in feeding, respiration, and locomotion. Yet, much less is known about how these shifts affect the detection of novel environmental cues. Chemoreceptor genes compose the largest proportion of the vertebrate protein-coding genome and are among the fastest evolving, likely rapidly responding to a diverse and ever-changing chemical space. At the molecular level, it has long been speculated, though rarely tested outside of model organisms, that subfamilies Class I and Class II of olfactory receptors show distinct responses to waterborne or volatile chemical cues, respectively. If this were the case, aquatic and semiaquatic animals possess larger repertoires of Class I receptors and the opposite for terrestrial vertebrates. We discovered testudines (turtles and tortoises) exhibit among the largest diversity of chemoreceptors and aquatic turtles do indeed have a higher proportion of Class I receptor genes. At the anatomical level, the testudines nasal cavity contains four chambers that contain olfactory receptor-expressing epithelia, and the volumes of these chambers is highly variable across species. The spatial distribution of these chambers may correlate with the expression of Class I and Class II receptor genes, potentially demonstrating shifts in size of nasal cavity regions that relate to waterborne versus airborne compounds. We compare the embryo series of several species of turtles with different ecologies, comparing the nasal cavity development of the four chambers using iodine-stained  $\mu$ CT-scans. We find substantial differences in the sizes and heterochrony of the different chambers, potentially reflecting differences in space devoted to the expression of Class I and II receptors. This study sheds light on the ecological basis of the largest vertebrate gene family within a clade in which chemosensation is largely underappreciated. Our study has implications for understanding how gene duplication and related anatomical structures can facilitate habitat-specific sensory processing.

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## **Recorded Presentations**

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## ICHTHYOSAURIAN AFFINITY OF OMPHALOSAURS ILLUMINATED BY NEW DISCOVERY FROM THE LOWER TRIASSIC OF SOUTH CHINA

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After the devastating Permo-Triassic extinction, ichthyosauromorphs rapidly occupied the marine predator niche during the Early and Middle Triassic. *Nasorostra* Jiang et al. 2016, a clade including *Sclerocormus* and *Cartorhynchus* from the Lower Triassic of China, is among the earliest such members. Here we report a new specimen of *Sclerocormus* from the Early Triassic Majiashan quarry in Chaohu, Anhui Province, China, which preserves the skull, cervical vertebrae, shoulder girdle, anterior trunk, and forelimb elements. The new specimen exhibits a set of the diagnostic characters for *Sclerocormus*: elongated large nasal reaching the tip of the snout, pre- and postorbital parts of the skull subequal in length, large orbit, deep trunk, robust gastralia, and single-headed ribs with expanded proximal ends and blunt distal ends. The new specimen also shows a stack of button-like maxillary and dentary teeth with irregularly pitted enamel surfaces as in *Omphalosaurus* from the Lower and Middle Triassic of North America and Europe. These tooth characteristics suggest that *Sclerocormus* preyed upon shelled invertebrates. A new phylogenetic analysis including the new specimen and *Omphalosaurus* supports the monophyly of *Omphalosaurus*, *Sclerocormus*, and *Cartorhynchus*, suggesting the single origin of durophagy in this clade, for which the name Omphalosauridae Merriam 1906 is readily available. *Nasorostra* thus is a junior synonym of Omphalosauridae, and the long enigmatic *Omphalosaurus* thus turns out to be an early-branching ichthyosaur. Further study may reveal *Sclerocormus* and *Cartorhynchus* to be junior synonyms of *Omphalosaurus*.



## A REVISION OF *TEMNODONTOSAURUS ZETLANDICUS* (SEELEY, 1880) NOV. COMB. AND THE PHYLOGENETIC RELATIONSHIPS OF EARLY JURASSIC ICHTHYOSAURIANS

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Parvipelvia is a major clade of ichthyosaurian marine reptiles that diversified during the Triassic-Jurassic transition. However, the interrelationships of early parvipelvians are unclear and many genera are poorly diagnosed, such as *Temnodontosaurus*, an iconic genus from the Early Jurassic of Western Europe. We redescribe the holotype of *Ichthyosaurus zetlandicus* (CAMSM J35176) as well as a new specimen attributable to this taxon (MNHNL TU885) from the Toarcian of Luxembourg. *Ichthyosaurus zetlandicus* is currently referred to as a junior synonym of the problematic taxon *Temnodontosaurus acutirostris*. We find that *I. zetlandicus* is a valid taxon that can be referred to as *Temnodontosaurus* with confidence. *Temnodontosaurus zetlandicus* nov. comb. shares numerous synapomorphies with *T. trigonodon* such as the morphology of the jugal and the parietal and the presence of a prominent mediolateral crest on the postfrontal. However, *T. zetlandicus* is characterized by a smaller skull, a narrower postorbital region, the absence of dental carinae, two nasal posterior processes that overlap the anterior edge of the postfrontal thus adopting a V-shape and a dorsal region of the lacrimal less extended and marked by a notch. These distinct craniodental architectures suggest that *T. zetlandicus* and *T. trigonodon* occupied different ecological niches. Our phylogenetic analyses of a new cladistic dataset thoroughly sampling Early Jurassic species under implied weighting maximum parsimony and Bayesian inference confirm the strong links between *T. zetlandicus* and *T. trigonodon*. *Temnodontosaurus acutirostris* is systematically recovered as a Stenopterygiid baracromian, confirming that *T. zetlandicus* and *T. acutirostris* are distinct taxa. Moreover, species currently included within *Temnodontosaurus* are scattered across non-ophthalmosaurid neoichthyosaurians and the monophyly of this genus needs to be thoroughly investigated.

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## WHERE DOES THALATTOSUCHIA BELONG IN CROCODYLOMORPHA? AN UPDATE ON THE CROCSUPERMATRIX PROJECT

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Perhaps the most peculiar clade of crocodylomorphs is Thalattosuchia, a predominately marine group that lived during the Jurassic and Cretaceous. Within Thalattosuchia there was a major evolutionary transition, encompassing the shift from semi-aquatic to pelagic forms (the Metriorhynchidae). However, where in Crocodylomorpha they belong is contentious. There are four major hypotheses on the position of Thalattosuchia: 1) sister taxon to Crocodyliformes, 2) sister taxon to Metasuchia, 3) basal neosuchian clade, and 4) a member of a ‘longirostrine aquatic’ neosuchian clade with pholidosaurids and dyrosaurids. At first glance, this wide range of possible positions for Thalattosuchia, a major crocodylomorph clade, is surprising. However, thalattosuchians evolved a suite of over 40 osteological, soft-tissue and neuroanatomical characters that underpinned their aquatic and/or marine adaptations. Over the past five years the authors here have been merging their phylogenetic datasets to investigate areas of uncertainty in the crocodylomorph tree, in particular Thalattosuchia. This led to the CrocSuperMatrix project. Here we report progress on this project. Thus far the datasets of Alexander Hastings and Mark Young are merged, and the merging with the Andrade et al. (2011) dataset is over half complete. Moreover, CT-based endocranial data from the University of Edinburgh CrocTransition project has also been incorporated. At present our dataset recovers Thalattosuchia in hypothesis two – as the sister taxon to Metasuchia. This position is recovered regardless of weighting regime used. Four key problems are revealed through our merging of these matrices: (1) Thalattosuchia is a group where a substantial number of characters reflect clade specialisations, few characters provide links to other branches, and it becomes difficult to differentiate secondary homology from convergence; (2) a Norian–Pliensbachian gap in the crocodylomorph fossil record means we lack information on the origin of most of the crocodyliform lineages (Gobiosuchidae, Hsisosuchidae, Shartegosuchoidea, Notosuchia, Neosuchia and Thalattosuchia); (3) the multiple lineages of “sphenosuchians” present in the Jurassic have no known Triassic forebearers (including Hallopodidae, the sister taxon to Crocodyliformes); (4) these issues all imply a poor distribution of characters on the consensus topologies. These three problems will affect any matrix and sample of characters. As a result, any crocodylomorph matrix or supermatrix will suffer from too much noise (problem 1), or missing data (problems 1–4). These problems seem to explain such disparate hypotheses (and poor support) for the position of Thalattosuchia. A substantial input from the fossil record is needed to overcome this gap.

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## THE PHYLOGENY OF NEOGENE BOOBIES AND GANNETS (AVES, SULIFORMES) OF THE SOUTHEAST PACIFIC

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Boobies and gannets, family Sulidae, are exclusively marine birds which specialise in hunting by plunge diving from up to 30 m high, catching its prey deep into the water with little or no pursuit. The family currently includes ten species on three genera (*Morus*, *Sula* and *Papasula*) distributed mainly in tropical and subtropical regions. Nowadays, boobies (*Sula*) are more diverse in the Pacific Ocean, whereas gannets (*Morus*) are restricted to the Southwest Pacific and are completely absent in the East Pacific. The most extensive fossil record of sulids in the Southern Hemisphere comes from the Pacific coast of South America, specifically from the Neogene of the Pisco Formation (Peru), where eight species of *Sula* and *Morus* have been described, along with an extinct genus: *Ramphastosula*. Unfortunately, very little is known about how these extinct species relate to the extant lineages. The present study attempts to elucidate their relationships through a parsimony analysis using 136 osteological characters for 10 living species along with all 7 Pisco's fossil species. The single tree recovered when only type specimens are considered for fossil species, shows *Papasula* as the sister group of a clade joining *Sula* and *Morus*. The fossil species *Sula figueroae*, *S. sulita*, and *S. magna* are placed within the crown *Sula*, whereas *S. brandi* appears as sister taxa of *Papasula*. On the other hand, *Ramphastosula* is recovered within *Sula*, indicating that the latter might be a paraphyletic genus. In addition, several alternative tests incorporating additional material which may belong to *Sula magna* or *Ramphastosula* were carried out. These inclusions only reduced the overall performance of our analysis. Size and geographic distribution were also analysed using our primary results, suggesting that the extant sulids may have originated as medium size birds on the South Pacific, whereas the acquisition of giant and small sizes tends to be autapomorphic.





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## **BREAKING THE MOLD: TELESCOPING DRIVES THE EVOLUTION OF MORE INTEGRATED AND HETEROGENEOUS SKULLS IN CETACEANS**

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The skull of modern cetaceans (= crown Cetacea or Neoceti) experimented along its evolutionary history dramatic changes in the arrangement of cranial bones linked with the acquisition of a novel feature in mammalian skull configuration: the telescoping (i.e., skulls with a combination of extensive bone overlap and extreme proximity of anterior and posterior cranial elements). Cetacean telescoping not only shows radical changes in the position of bones, but also in the arrangement of cranial sutures, with large areas of bone overlap (= horizontal sutures). This represents a new level of bone-suture configurations, breaking the typical mammalian skull design, and exploring new morphospaces that might bias the exploration of new ecological and behavioural strategies. Despite telescoping being investigated in the last years from different perspectives, the impact of the novel sutures configurations in the topographical organization and integration of the cetaceans skull has never been addressed. In this study, we applied Anatomical Network Analysis to examine the level of organization and integration of archaeocete, odontocete and mysticete skulls. We constructed networks of six cetacean skulls (*Dorudon*, *Aetiocetus*, *Yamatocetus*, *Eubalaena*, *Balaenoptera*, and *Tursiops*) based on the most complete published skulls and/or first-hand examinations. Our results show that crown cetaceans occupy a previously unoccupied place in the tetrapod skull morphospace, with better integrated, slightly simpler, and mainly more heterogeneous skulls in comparison to other mammals. PERMANOVA shows a statistically significant difference between the skulls of cetaceans and terrestrial tetrapods, suggesting a unique skull network specialization of cetaceans linked with their transition to the aquatic environment. The evolution of telescoping in modern cetaceans promotes new sutural contacts between skull bones without loss or fusion (except interparietal), but rather adding new connections in those bones mainly involved in the telescoping process (e.g., supraoccipital). Among mysticetes, the most extreme skull integration and complexity is observed in *Eubalaena* spp., and might reflect the disparate skull anatomy of balaenids in relation to their specialized skim feeding behaviour. Telescoped skulls in neocetes are more modular compared to their ancestors, and four main modules are detected: two dorsolateral, one palatal and another one in the posterodorsal region. Telescoping mostly alters the composition of the posterodorsal module, which expands to include bones that would otherwise form part of the dorsolateral modules. Anatomical Network Analysis allows looking at the telescoping of cetacean skulls through a different lens, magnifying the connectivity pattern of their bones that potentially mirrors aspects of their evolution.

## THE EVOLUTION OF EYE SIZE IN ODONTOCETE WHALES

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For many marine tetrapods, vision remains the primary way of finding food and navigating underwater. Adaptation to seeing underwater has necessitated increases in eye size to capture light in dim ocean depths. However, odontocete whales rely instead on echolocation. We tested whether the evolution of echolocation may have influenced eye size, and examined how eye size evolved over time. Using measurements of orbit length and bizygomatic width, we calculated proportional orbit size for 70 extant and 29 fossil whale taxa, with an emphasis on Odontoceti. We then performed ancestral character state reconstruction using the R package Phytools on a time-calibrated composite phylogeny. Our analysis revealed that there was no shift in proportional orbit size from archaeocetes through stem odontocetes. Proportional orbit size increased in *Mesoplodon*, Phocoenidae, and *Cephalorhynchus*. In *Mesoplodon* this may be an adaptation for finding prey at great depth, while within the latter two lineages increase in orbit size is a result of retention of juvenile features from progenesis. Proportional orbit size decreased in *Physeter* and river dolphins. Decrease in orbit size within *Physeter* may be a result of eye size no longer increasing at the same rate as body size in very large animals. Decrease in orbit size in river dolphins represents the reduced importance of eyesight in sediment-filled river environments. This study reveals that eyesight continues to be an important sense for whales and the evolution of echolocation did not affect it.

## CRETACEOUS MARINE PREDATORS FROM COLOMBIA AND THEIR CONTRIBUTION TO THE UNDERSTANDING OF THE EVOLUTION OF SOUTH AMERICAN MARINE ECOSYSTEMS

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During the Early-Cretaceous, the final phase of fracturing of Pangea was accompanied with a global sea level rise that, together, created an oceanic connection between the ancient Atlantic and Pacific Oceans in the region of what is now the Neotropics, that started during the Jurassic (the Hispanic-Corridor). This connection allowed the marine ecosystems of each Ocean to mix for the first time after over 120-million-years of relatively isolated evolution. Sedimentary basins in Europe and South America preserve an extraordinarily rich fossil record that span this event and offer unprecedented details of their respective ecosystems. Uniquely, a basin in central Colombia was deposited during the formation of the Hispanic-Corridor and has thus far yielded fossil taxa that are shared between each Ocean and a suite of endemic species. These rocks are part of the Paja-Formation that was deposited over 15-million-years in a shallow sea during the Early-Cretaceous (Hauterivian-Aptian), and has already yielded several specimens of ichthyosaurs, fishes, turtles, plesiosaurs, a fragmentary dinosaur, and abundant molluscan faunas. Nearly each new fossil specimen represents a new species indicating extremely high endemism levels in this place and time, containing one of the few fossil assemblages with sufficient material to test the correlation between environmental factors and biodiversity. New and published fossil material of crocodylians, plesiosaurs, ichthyosaurs and turtles suggest the Paja-Formation to be a potential biodiversity hotspot. The marine vertebrate fauna of the Paja-Formation records a shift in marine predator communities that would last for the following 50-million-years. This transition involves the origin and demise of several lineages. The Paja-Formation has already yielded the earliest stem marine turtles and long-necked plesiosaurs and the last surviving pliosaurs, ichthyosaurs, and teleosauroids. These taxa were the dominant predators of an ecosystem filled with ammonite, bivalve, and fish species, and were eventually replaced by several lineages of non-pliosaurid plesiosaurs, mosasaurs, tethysuchian crocodyliforms, and more derived marine turtles. Although this research is in progress, the description of the youngest teleosauroids demonstrated that teleosaurs survived the J/K extinction. Our recent description of a new ichthyosaur from Colombia recognized its unique dentition that presents several discrete tooth morphologies that range from piercing to cutting to crushing. This large ichthyosaur presents a revival of hypercarnivory in the clade that was last present in the Early-Jurassic. Together, a preliminary food web is constructed and compared to older and

younger marine ecosystems demonstrating that these systems were not static during the final breakup of Pangea.

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## **WHEN PHYSIOLOGY AND ECOLOGY MEET: THE INTERDEPENDENCY BETWEEN FORAGING ECOLOGY AND REPRODUCTION IN OTARIIDS AND THEIR IMPLICATIONS FOR THEIR EVOLUTIONARY HISTORY**

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Otariids (fur seals and sea lions) have a semiaquatic lifestyle, feeding in the water and breeding and nursing on land. They also exhibit an overall income breeding system where the females alternate between trips to the foraging grounds and periods at the breeding colony to feed the pup. How far and how long lactating females can be away from their breeding colony is ultimately dictated by ecological and physiological tradeoffs, which also indirectly rule other aspects of their life history, including their distribution. Here, we examine the interrelations between behavior, ecology, and physiology and how they affect the reproductive, foraging, energetics, life history, and, likely, the evolutionary history of otariids. As income breeders, otariid females are limited to forage near their reproductive colonies, constraining them to inhabit highly productive oceanographic regions. Further, sea lions are generally larger than fur seals; therefore, they are capable of deeper and longer dives resulting in fur seals tending to feed closer to the surface in the epipelagic regions. In contrast, sea lions tend to forage in deeper environments on benthic, epipelagic, and mesopelagic prey. These diving and foraging differences translate into divergent patterns of resource acquisition and allocation and energetic balance between fur seals and sea lions, which drive, in turn, the current distribution and demographic trends during the last decades. Finally, we discuss how these physiological and ecological trade-offs would have influenced otariids' evolutionary history in the geologic past, promoting a more comprehensive and interdisciplinary perspective for assessing the ecological and physiological transitions associated with the evolutionary history of marine mammals.

## FINGERS ZIPPED UP OR BABY MITTENS? TWO MAIN TETRAPOD STRATEGIES TO RETURN TO THE SEA

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The application of network methodology in anatomical structures offers new insights on the connectivity pattern of skull bones, skeletal elements, and their muscles. Anatomical networks helped understanding better the water-to-land transition and how the pectoral fins were transformed into limbs via their modular disintegration. Here, we apply the same methodology to the forefins of 19 tetrapods that have been secondarily adapted to the marine environment, including turtles, ichthyosaurs, mosasaurs, plesiosaurs, metriorhynchid crocodylomorphs, and mammals (whales, dolphins, sea lions, seals, and sea cows). We find that these animals achieved their return to the sea with four types of morphological changes, which can be grouped into two different main strategies. In all marine mammals and the majority of the reptiles the fin is formed by the persistence of superficial and interdigital connective tissues, like a “baby mitten”, whereas the underlying connectivity pattern of the bones does not influence the formation of the forefin. These tetrapods managed to explore regions outside the known morphospace, attempting higher disintegration of the limb or some moderate reintegration — but without losing their digits. On the contrary, ichthyosaurs “zipped up” their fingers and transformed their digits into carpal-like elements, forming a homogeneous and better-integrated forefin, showing a costly reintegration of their limb to a modular pattern that is analogous to fishes, with the addition of interdigital bony elements and lateral connections. These strategies led these vertebrates into three different macroevolutionary paths exploring the possible spectrum of morphological adaptations. Mosasaurs and plesiosaurs placed new limits in the disintegration of the limb, by adding numerous new phalanges on their digits, increasing its modularity, while reducing its density and integration. Marine crocodiles, and possibly basilosaurids, lost elements and increased connections of the metapodials, resulting in forefins that were more complex and better integrated. The most impressive changes are noted in the forefins of ichthyosaurs, who reintegrated their digits into the mesopodium with the addition of anterior and posterior contacts and articulations. Their metacarpals and phalanges radically adopted the connectivity pattern of carpal bones (increased clustering, betweenness centrality, and degree), forming forefins that were highly integrated and homogeneous. However, this strategy allowed ichthyosaurs to have forefins that did not lose much of their modularity. Anatomical networks help understanding that all these secondary adaptations to the marine

environment are not the same, and to speculate that they are the result of different developmental mechanisms, but also physical, phylogenetic, and morphological constraints.

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## THE ECOLOGICAL DIVERSIFICATION AND EVOLUTION OF TELEOSAUROIDEA (CROCODYLOMORPHA, THALATTOSUCHIA), WITH INSIGHTS INTO THEIR MANDIBULAR BIOMECHANICS

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Throughout the Jurassic, a plethora of marine reptiles dominated ocean waters, including ichthyosaurs, plesiosaurs and thalattosuchian crocodylomorphs. These Jurassic ecosystems were characterized by high niche partitioning and spatial variation in dietary ecology. However, while the ecological diversity of many marine reptile lineages is well known, the overall ecological diversification of Teleosauroidea (one of the two major groups within thalattosuchian crocodylomorphs) has never been explored. Teleosauroids were previously deemed to have a morphologically conservative body plan; however, they were in actuality morphofunctionally diverse and evolved a bizarre body-plan (i.e., proportionally large heads). Here we investigate the ecology and feeding specializations of teleosauroids, using morphological and functional cranio-dental characteristics. We assembled the most comprehensive dataset of multiple teleosauroid taxa (approximately twenty species) and ran a principal component analysis (PCA) to categorize them into various feeding guilds based on seventeen dental characteristics (forty-one specimens) and sixteen functionally significant mandibular characters (nineteen specimens). The results were examined in conjunction with our comprehensive thalattosuchian phylogeny (153 taxa and 502 characters) to evaluate macroevolutionary patterns and significant ecological shifts. Multiple taxa fall into the pierce and crushing guilds (including intermediate forms), and there is increased bite efficiency shifting from longirostry to brevirostry in Machimosaurini (a subgroup within machimosaurids). Teleosauroid taxa with slender teeth, an elongate mandible and comparative small adductor muscle attachments have a lower mechanical advantage than taxa with robust teeth, a shortened mandible and large muscle attachments. Machimosaurids display the well-developed following ecological shift: from (1) a slender, pointed tooth apices and an elongate gracile mandible; to (2) a more robust, pointed teeth with a slightly deeper mandible; and finally, (3) rounded teeth and a deep-set, shortened mandible with enlarged musculature. Teleosaurids display pointed, unornamented, slender teeth and an elongate mandible with comparatively smaller muscles/muscle attachments and are more phenotypically plastic. Overall, non-machimosaurin teleosauroids display a slight array of overlap, particularly in the dental analyses; this suggests that multiple taxa may have exploited relatively similar food sources and possibly lived in similar habitats. However, this contradicts the cranial anatomy, which shows an extraordinary number of diverse characteristics within teleosauroid species.

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## HEAD-OR TAIL-FIRST BIRTH IN ICHTHYOSAURIA AND ITS IMPLICATIONS FOR THE ORIGIN OF VIVIPARITY: EVIDENCE FROM A NEW CYMBOSPONDYLID FROM THE ANISIAN OF NEVADA

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Viviparity offers great selective advantages to marine reptiles because it obviates the need of oviposition on land and the associated difficulties and dangers as well as the need to retain minimal terrestrial capabilities. Among marine reptiles, only sea turtles are unequivocally not viviparous since recent work suggests viviparity even in thalattosuchian crocodiles. The oldest example of viviparity in ichthyosaurs is *Chaohusaurus* from the Early Triassic of China. The early-branching position of this taxon and its apparent head-first birth position has been used to argue that viviparity in the clade, and in marine reptiles in general, had already evolved in their terrestrial ancestors. However, more derived ichthyosaurs show usually (although not all) a tail-first birth position. The argument that the rarer head-first birth position in derived ichthyosaurs documented death in labor is invalidated by embryos preserved just outside the mother and can be neglected. It seems more reliable that the birth position seems to be variable and to depend in which direction the embryos “uncoil” themselves in an elongated position shortly before birth. Cymbospondylid ichthyosaurs are an early-branching clade of primarily large-bodied and pelagic ichthyosaurs from Middle Triassic open-water sediments from Spitzbergen and Europe, but best known from coeval marine sediments in Nevada, USA. The holotype skeleton of a new species of *Cymbospondylus*, the medium-sized (~3.5-4.3 m body length) *C. duelferi* from the late Anisian of the Augusta Mountains, Nevada, is interpreted as a pregnant female. Ventral to the dorsal column of the *C. duelferi* holotype, are three straight strings of small articulated vertebrae and for one individual anterior can be identified. This individual has anterior opposite to the dorsal vertebrae of the large specimen. The small vertebrae are on average 32% of the size of the large ones. Due to the small size of these strings and their position within the trunk region, they most likely represent fetuses. The holotype of *C. duelferi* represents the geologically second-oldest record of viviparity in ichthyosaurs. This ichthyosaur from Nevada thus indicate that head-first birth was possible even in pelagic ichthyosaurs that certainly gave birth under water. This questions the argument that this

position indicates a terrestrial origin of viviparity. Here, we explore the implications of the new find from Nevada for the general discussion on the “head or tail” first birth position and the competing hypotheses about the origins of viviparity (terrestrial vs. marine) in marine reptiles from the Permian to the Cenozoic.

## NEW INSIGHTS ON THE PALEOECOLOGY OF THE FOSSIL WALRUS *ONTOCETUS EMMONSI* INFERRED FROM STABLE ISOTOPES

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Today, there is one living walrus species, *Odobenus rosmarus*, which is highly adapted to sea ice habitats and is essentially distributed around the North Pole. Conversely, in the geologic past, walruses were more taxonomically diverse, varied greatly in ecomorphology and body size, and had a much wider geographic distribution across the Northern Hemisphere. *Otocetus emmonsi* is one of the closest extinct relatives of modern walruses. This species inhabited the North Atlantic during the Pliocene; based on the possession of enlarged tusks and large body size, it has been inferred to have a foraging ecology analogous to living walruses but deployed in a warmer environment. Nevertheless, this hypothesis has not been thoroughly tested. In this study, we analyzed the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of the tooth enamel of *O. emmonsi* and other co-occurring marine mammals, including phocids and odontocete cetaceans, from Pliocene deposits of the Yorktown Formation (4.9 - 3.92 Ma) on the east coast of North America to investigate the foraging and habitat preferences of this extinct walrus species. We found low variability ( $\sim 0.5\%$ ) in the  $\delta^{18}\text{O}$  values for the different groups (with the exception of phocids), similar to modern fully aquatic marine mammals, indicating adequate preservation of the ecological signal in the fossil specimens. Together, *O. emmonsi* and phocids had  $\delta^{18}\text{O}$  values  $\sim 1\%$  lower than co-occurring cetaceans, which likely resulted from physiological disparities among these groups; however, the specific mechanisms underpinning these differences remain unknown. Furthermore, *O. emmonsi* had  $\delta^{13}\text{C}$  values  $\sim 1$  and  $2\%$  higher than co-occurring phocids and odontocetes, respectively, indicating predominantly coastal foraging and habitat preferences, in comparison to co-occurring marine mammals, which had offshore foraging preferences. In addition, we found remarkable variability in the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of phocids, revealing an unknown behavioral and, likely, taxonomic variability within members of this group inhabiting the area. In conclusion, our preliminary results indicate that *O. emmonsi* had coastal foraging preferences, supporting previous inferences based on morphology. We plan to analyze more specimens and additional species from this and other fossil localities on the eastern coast of North America to further explore the foraging and habitat preferences of this extinct group of walruses, including the occurrence of intraspecific variation.

## ECOMORPHOLOGICAL VARIATION IN ENDOCRANIAL SHAPE IN THALATTOSUCHIAN CROCODYLOMORPHS

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Crocodylomorphs evolved a rich diversity of ecomorphotypes during their long evolutionary history. Appearing during the Late Triassic, approximately 230 million years ago, crocodylomorphs were initially terrestrial and possibly facultatively bipedal. However, they quickly diversified especially after the Triassic-Jurassic boundary, into a wide range of semiaquatic, freshwater and marine forms. During the Early Jurassic, Thalattosuchia was the first crocodylomorph group to make the land-to-water transition. They evolved from their terrestrial ancestors and gradually moved back into the ocean. Thalattosuchians comprise two subgroups, the teleosauroids which occupied predominantly brackish and coastal environments during the Jurassic and Early Cretaceous, and the metriorhynchoids which transitioned from coastal ecosystems to open ocean environments. Within the latter, the crown Metriorhynchidae evolved paddle-like limbs, a hypocercal tail and a streamlined body. Metriorhynchids are the only archosaurs known to have adapted to an obligately pelagic lifestyle. Such evolutionary transitions involve several skeletal transformations related to new physiological requirements. Besides osteological changes, endocranial sensory systems are key to understanding such transitions, and can reveal how ecology changed over long time-scales. To explore these ecomorphological adaptations we used CT scans of extant and extinct crocodylomorphs and a high density 3D morphometric approach to extract brain endocranial shape data. We analysed the whole endocranial as well as individual sections: cerebrum and olfactory tracts, optic lobes, cerebellum, medulla oblongata and pituitary. We performed statistical analysis (e.g., principal component analysis) to test whether and which features characterise the land-to-water transition in thalattosuchians. Our results reveal that the overall endocranial shape shows a phylogenetic signal with major clades clustering together in morphospace. Thalattosuchians generally have a more elongated and tubular brain endocranial compared to their modern relatives, which might be related to their elongated

skull-shape. However, there are additional ecomorphological differences between pelagic metriorhynchids compared to the semiaquatic teleosauroids and the basal metriorhynchoid *Pelagosaurus typus*, with them occupying distinct morphospace region. One main feature is that pelagic taxa seem to have a significantly larger pituitary fossa compared to semiaquatic forms. Our results suggests that brain endocast morphology shows phylogenetic and ecomorphological signal, similar to other neurosensory systems such as the bony labyrinth, that became more compact in pelagic metriorhynchids. Those neurosensory changes combined likely helped metriorhynchids adapt to their new open ocean realm.

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**9<sup>th</sup> SECAD**  
**2021 CHILE**

## **Recorded Presentations**

**Topic: “Ecology/paleoecology”**

Modality: Poster



## **ANATOMICAL NETWORKS REVEALS NEW ADAPTIVE STRATEGIES OF CETACEAN FLIPPERS**

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Previous studies of the anatomical network analyses (AnNA) of pectoral fins of tetrapods that have been secondarily adapted to the marine environment identified two main strategies: most limbs have superficial and interdigital connective tissue which gives to the limb the shape of a "baby mitten" (observed in marine mammals and most reptiles), whereas ichthyosaurs are characterized by a homogeneous reintegration of the limb. That initial sample included only two extant cetaceans, which did not show a clear tendency to follow any of the defined adaptation paths. Cetacean flippers evolved from the forelimbs of a group of terrestrial artiodactyls. The transition to the aquatic environment entailed multiple morphological changes in the bone anatomy and the limb's soft tissues. As a consequence of these transformations, there is interspecific variation (e.g., the number of phalanges and carpals and their connections). In order to know the adaptive tendencies of the flippers in extant cetaceans and the group's morphological diversity, an AnNA was carried out with a larger sample. The anatomical networks of pectoral fins of 44 cetaceans were constructed from dissected specimens, radiographs of museum collections and figures from literature. They represent 11 families, 9 corresponding to the Order Odontoceti and 2 to Mysticeti, being the largest sample of an AnNA study on tetrapod limbs. By incorporating these samples into the morphospace established for tetrapods adapted secondarily to water, we observed an expansion of the "mitten" morphospace, allowing the identification of new adaptive strategies in cetaceans. A new trend towards a disintegration of the flippers with higher heterogeneity is observed, bifurcated into two different paths of heterogeneity: one towards complex heterogeneity and the other towards modular heterogeneity. Likewise, the expanded sample identified some cetaceans that clearly fit in two of the three previously established adaptive pathways towards a modular disintegration and complex reintegration respectively. The expanded and more representative sampling confirms that there were disparate trends in the strategies of ichthyosaurs and cetaceans, with homogeneous and heterogeneous forefins respectively. Future objectives include exploring in detail the networks within the cetaceans at the individual bone level and investigate how their connectivity patterns influence the morphological diversity of the group and their possible taxonomic and/or environmental correlations.

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## THE DIGITAL CRANIAL ENDOCAST OF *DUSISIREN DEWANA*: THE IMPLICATION FOR PALEOECOLOGICAL CHANGES OF HYDRODAMALINAE

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Sirenia is one order of mammals and includes two extant families, Dugonidae and Trichechidae. The “extant” Dugonidae includes two subfamilies, Dugoninae and Hydrodamalinae. Hydrodamalinae includes *Dusisiren* that seemed to be used to feed on kelp at or near the surface, and *Hydrodamalis* is more derived than *Dusisiren*. *Dusisiren dewana* is known for the species that revealed intermediate teeth characteristics between *Dusisiren* and *Hydrodamalis*, but there is little information about their paleoecology. 3D-digital technology allows us to “see” brains or sensory organs of extinct animals. Notably, brain endocasts are correlated to paleoecology and the evolution of extinct animals. Here we report the digital endocast of *D. dewana* to understand the paleoecology evolution of Hydrodamalinae. As a result of comparing *D. dewana* with other sirenians, *D. dewana* had character combinations with mosaic neuroanatomical features among Hydrodamalinae. *D. dewana* shared many characters with *Hydrodamalis*, but many characters with more basal dugonids, too. This feature is consistent with their dental evolution. *D. dewana* had a tiny olfactory-bulb, unlike other hydrodamalinae sea cows. These features indicate that olfactory retraction preceded the teeth loss. The relative width of the trigeminal nerves is the widest among Hydrodamalinae. A hypophysis expansion is found in the inner ear region, characterized by basal Hydrodamalinae and more basal dugonids. This feature is found in the basal Hydrodamalinae and the more primitive hydrodamalinae and *Halitherium*, but not in the derivative Hydrodamalinae. The cerebrum size was significantly larger than *Halitherium*. The height of occipital lobe is not so tall similar to *H. cuestae* but shorter than *H. gigas* and *D. jordani*. Unlike other hydrodamalinae sea cows, the olfactory-bulb size could not be seen in endocast like dugongs. These character combinations were suggested that *D. dewana* had mosaic neuroanatomical features among Hydrodamalinae, and this indicates that olfactory retraction preceded the teeth loss.

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Modality: Oral Presentation



## KOGIIDAE FROM BAHIA INGLESA FORMATION, LATE MIOCENE, CHILE

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The sperm whales, particularly the pygmy and dwarf forms (Kogiidae), are infrequent in South American (SA) marine deposits. This can be partially explained by their oceanic habitat, which is less represented by sedimentological facies in SA. We report here the first confirmed record of Kogiidae from the Bahia Inglesa Formation (BIF), late Miocene, northern Chile, based on a complete isolated periotic bone. The specimen (SGO.PV 18057) displays characteristics considered diagnostic for kogiids such as: short, medially recurved anterior process with dorsal, anterodorsal, and anteroventral spines, anterior process with a concavity for a large accessory ossicle (as in other physeteroids), and a horizontally-oriented posterior process with rounded plate-like bullar facet. To further assess the affinities of this new specimen we conducted a PCA analysis based on measurements established in previous work on kogiid ear bones. The results show that the Bahia Inglesa specimen falls within a cloud that can be described as representing a large morphotype, that is far and distinct from those of the extant genus *Kogia* (pygmy sperm whale). Only a few fossil Kogiidae are known by associated or referable skulls and periotics, which prevent a more accurate discussion of the taxonomic affinities. Previous suggestions of the presence of *Kogia* (SGOPV 1117) from BIF have been since considered as indeterminate Kogiidae, representing the small-sized morphotype. Nevertheless, the distinct morphology of the new complete kogiid periotic from BIF is shared with *Scaphokogia cochlearis* from late Miocene strata of the Pisco Formation (Peru), cf. *Aprixokogia kelloggi* specimens from the early Pliocene of Yorktown Fm. (USA), as well as kogiids of unknown affinities from the late Miocene-early Pliocene Salada Formation (Mexico), early Pliocene Bone Valley (USA) and Tirabuzon (Mexico) formations. Finally, we hypothesize that the large morphotype represents the plesiomorphic condition amongst kogiids, while the more derived morphology observed in extant taxa is unique to *Kogia spp.*, appearing by the latest Miocene at the earliest. The presence of the two forms in the phosphatic conglomerate levels of BIF (7 my) agrees with this hypothesis and highlights the potential for the geologic record of this formation to capture the diversity of pelagic taxa, with both plesiomorphic and derived morphotypes present. This pattern of mixed forms apparently in sympatry is repeated in the Yorktown and Pisco formations. Furthermore, the Pacific records (late Miocene) appear to be older than the Atlantic records, dated from the early Pliocene.

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## **SOUTH AMERICAN AND ASIAN RIVER DOLPHINS HEAD MORPHOLOGY WITH COMPARISONS ON THE EVOLUTION OF ECHOLOCATION AMONG FRESHWATER AND MARINE ODONTOCETI**

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The ancestors of different groups of river dolphins (Amazon, Yangtze, Ganges and Indus dolphins), lived in marine environments, having different timings and places for their habitat transition. Nevertheless, there are similarities that have puzzled the understanding of their evolutionary history, making the phylogeny and biogeography of these groups heavily discussed. This study compares the facial and basicranial anatomy of the head and skull of several marine, most coastal-estuarine and all riverine dolphins, emphasizing at the structures related to echolocation with comparisons between those taxa. We performed 50 measurements of the skulls for extinct and extant species from Platanistoidea (Platanistidae, n= 5); Lipotoidea (Lipotidae, n=15); Iniioidea (Iniidae, n=20, Iniioidea Incertae sedis, n=1, stem Iniioidea, n=11; Pontoporiidae, n=19); Delphinoidea (Kentriodontidae, n=14; Odobenocetopsidae, n=1; Phocoenidae, n=57; Delphinidae, n=78), and performed 3D reconstructions on computed tomography scans with AGNOSCO DICOM 2.1, and AW 4.6, for extant species. Morphometry: all statistical analysis (PCA, Cluster and LDA) were performed on PAST 4.3 software. All river dolphins were significantly discriminated from the marine species, based on skull measurements related to the morphology of the melon, bursae dimensions and nasal passages. The coastal and marine groups of dolphins present overlapping. We have verified CT scan data with the known acoustic abilities of each taxa. Additionally, skulls of fossil taxa were compared through morphometrics and specific proxy morphology established from modern species soft tissue anatomy. *Platanista gangetica minor* presents more elongate melon, symmetry of the right and left branches on the posterior portion of the melon, which were directly connected to the monkey lips dorsal bursae complex (MLDB), and the presence of two emitting surfaces. While *Inia geoffrensis* and *Lipotes vexillifer* present asymmetry and alignment of the left branch of the melon with MLDB. The presence of the “Porpoise capsule” was found in *I. geoffrensis*, *L. vexillifer* and

*Pontoporia blainvillei*. Accordingly to the current phylogenetic understanding and echolocation types, *I. geoffrensis* and *L. vexillifer* were found more similar, while *P. blainvillei* had an intermediate morphology among *I. geoffrensis*, *L. vexillifer* and Delphinoidea species. Meanwhile, *P. gangetica minor* striking differences are in accordance with its basal phylogenetic position and echolocation type (Wide Band Low Frequency) rather than the similarity of environmental conditions of the other taxa (Yangtze, Amazon). Fossil taxa were assigned to echolocation types, for example *Ischyrorhynchus vanbenedeni* (Late Miocene, Argentina) was considered a narrow-band high frequency echolocator as in other Iniioidea.

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## TIME-LAPSE STUDY ON A WHALE MASS MORTALITY EVENT IN SOUTHERN CHILE REVEALS TIMING OF DECOMPOSITION, DISARTICULATION AND TRANSPORT ON SYNCHRONIC EVENTS OF BEACH DEPOSITS

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Neotaphonomy or actualistic taphonomy is a branch of paleontology focused on systematic observation and experimentation of decomposition and disarticulation processes undergone by organisms until their final burial, in the present time. In this sense, neotaphonomy offers the basis to understand the preservation of fossil deposits and how ecological and mortality events at different environments are preserved. Therefore, this approach is crucial for accurate paleoecological and paleobiological interpretations. However, in the case of marine vertebrates, these studies are very scarce. In 2015, there was a larger mass mortality already recorded in baleen whales, with more than 300 baleenopterids attributed to Harmful Algal Bloom (HAB) intoxication in the Golfo de Penas in a remote area of southern Chile, which represents a unique opportunity for long-term neotaphonomic studies, which are in evolution. The present work analyzes daily and hourly monitoring data using time-lapse photography (May 2016) of 3 carcasses of sei whales (*Baleoptera borealis*) in the Seno Escondido (Bahía San Quintín). The decay time of the carcasses was determined to be approximately 81 days from the start of the video (thus adding approximately 1 year and 3 months since the mortality event). Disarticulation and removal by transport was observed from this period on, having a duration of 29 days for the complete disarticulation, as well as rotational and translational movements of the skeletal elements of the carcasses. In addition, the pattern for carcass disarticulation stages could be established in this order: 1) jaws, 2) pectoral fins, 3) pectoral girdle, 4) ribs and vertebrae. The skulls remained in place throughout the observed period, undergoing only minor orientation movements. Biological and physical processes control decomposition and disarticulation of carcasses, scavengers, birds and microbial decomposers regulate decomposition and initial disarticulation, while wave action (and continental watercourse) control the transport and orientation of the elements. The high decomposition time relates to the temperate climate decreasing microbial activity rate. Comparing Cerro Ballena site (Fm. Bahía Inglesa, Northern Chile) also attributed to massive mortality by HAB at, there are striking differences. At Golfo de Penas the arrangement of skeletons resulted in postcranial elements included in medium-energy beachfront deposits separated from the skulls, spaced apart (10 meters) in beach deposits. Which contrasts with the more than 20 articulated skeletons found in supratidal lagoon deposits (5x 200m) at Cerro Ballena. This fact draws attention to the potential underestimation of massive mortality events in the fossil record, depending on the deposit facies.

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## AUSTRALASIAN MONK SEALS (TRIBE MONACHINI) ‘FLIP’ THE EVOLUTIONARY HISTORY OF THE SOUTHERN TRUE SEALS (SUBFAMILY MONACHINE) TO THE SOUTHERN HEMISPHERE

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Historically, southern true seals (Subfamily Monachinae) were thought to have evolved in the North Atlantic alongside their northern counterparts (Subfamily Phocinae). The north–south biogeographic dichotomy that exists between these two groups today is thought to be the result of limited dispersal events across the equator (a barrier to marine mammal dispersal), resulting in the Antarctic distribution of elephant seals and lobodontins, and the northern tropical distribution of monk seals. These equatorial crossings were likely done by small sized seals from warmer waters, with true seals not obtaining larger sizes until the colonization of polar environments. However, this well-established evolutionary hypothesis has been affected by a research bias towards fossils from the Northern Hemisphere. It is therefore unclear how the emerging fossil record of monachines from the Southern Hemisphere fits into this hypothesis. Here we describe a new species of seal from the Pliocene (3.4–3 Ma) of New Zealand, and two fragmentary fossils from the late Miocene–early Pliocene (6.24–4.35 Ma) of Australia, which represent the first southern monk seals. A new total evidence fossilised birth-death Bayesian phylogenetic analysis tested the established evolutionary hypothesis for true seals. The new phylogeny completely flips the evolutionary history of the monachines, demonstrating an early presence in the Southern Hemisphere. Phylogenetic comparative methods were run in R to test the biogeography and environmental tolerances of true seals. It was found that the southern true seals mostly evolved in the Southern Hemisphere, rather than the North Atlantic, and crossed the equator multiple times in their evolutionary history. An ancestral state estimation and phylogenetic generalised least squares regression reveals that true seals do not conform to Bergmann’s rule, and that the multiple dispersal events across the equator are the result of broad environmental tolerances independent of body size. This revised evolutionary history for the group completely overturns how true seals are thought to have evolved in the past.

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## **TAPHONOMIC ANALYSIS OF AN ARTICULATED MYSTICETE (CETACEA; MYSTICETI) FROM THE LATE MIOCENE PUERTO MADRYN FORMATION, PENINSULA VALDÉS, PATAGONIA, ARGENTINA**

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Taphonomic studies of fossil cetaceans in Argentina are scarce and they were focused mainly in odontocetes and mysticetes from the Gaiman Formation (lower Miocene of Patagonia). These analyses propose different factors (i.e., paleoenvironmental, paleobiological and paleoecological) that controlled the preservation of cetaceans. Prospecting fieldworks on the Puerto Madryn Formation (late Miocene) result in the discovery of a well-preserved and articulated baleen whale (= Mysticeti) specimen in Peninsula Valdés, Chubut, Argentina. This specimen was the focus of a taphonomic analysis with a multidisciplinary approach including taxonomical, sedimentological, stratigraphic and ichnological analyses, with the aim of reconstructing the taphonomic processes and the paleoenvironmental conditions that played a role in the preservation of the specimen. The preliminary taxonomic analysis shows that the specimen corresponds to an adult to subadult belonging to the family Balaenidae. It displays a high degree of articulation, a low to moderate degree of fragmentation and a relatively high degree of completeness (i.e., presence of cranial bones, tympano-periotic, mandibles, maxilla, caudal, thoracic and cervical vertebrae, ribs and a fragmented scapula). Our results suggest that after death, the balaenid followed a brief biostratinomic route that can be summarized in four stages: A) death at sea, with an initial decomposition and positive buoyancy of the carcass; B) internal accumulation of putrefaction gases, reorientation, loss of connectivity of the skeletal elements and gas loss; C) sinking and deposition in ventral-up position on the seafloor and; D) a lateral re-orientation (side-up) of the postcranial region due to physical and biological processes. The high degree of bones articulation and association, the presence of mandibles, the moderate fragmentation and the lack of evidence of scavenging, indicate no lateral transport on the seabed. These observations allowed us to dismiss reflation processes of the carcass. Also, the taphonomic features (e.g., high degree of articulation, low degree of fragmentation, polymodal orientation) of the associated invertebrate fossils and the ichnogenera, support this interpretation. The final deposition of the whale carcass on the seafloor did not result in an ecological impact as is known for whale-fall communities' studies. Finally, the collected data indicates a low-energy shelf environment with normal marine oxygenation, productivity and salinity conditions, characterized by a soft bottom and a low to moderate sedimentation rate. This, combined with the high bioturbation activity, resulted in a rapid burial of the carcass because of the sediment removal. Thereby, the fossil diagenetic processes allowed the final conservation of the skeleton.

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## COMPARATIVE ANATOMY AND VARIATION OF THE PERIOTIC AND ITS COCHLEAR STRUCTURES: A CASE STUDY WITH A POPULATION OF THE LONG-FINNED PILOT WHALE (*GLOBICEPHALA MELAS*) AND ITS RELEVANCE IN PHYLOGENETIC STUDIES

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Odontocetes echolocate to perceive their environment, emitting high-frequency sounds of a varied range (40 to 140 kHz). These frequencies differ between groups, reflecting on the morphology of the tympano-periotic complex. Previous studies explored the inner and outer morphology of the periotics comparing species, but few studies have been designed to test intraspecific versus interspecific variation of these functional and phylogenetic characteristics in the different species of odontocetes. An intraspecific morphometric study of the periotic and the cochlear structure was carried out for 22 individuals of the same population of Long-finned pilot whales (*Globicephala melas*), obtained from a massive stranding (2015, Clemente Island, Southern Chile). 6 internal and 18 external measurements were taken, and body length data were compiled to the classification of relative maturity. All of these were analyzed by computerized volumetric tomography (Morita Cone-beam Scan) and processed in OsiriXPro software. These measurements were then compared with a database of tympano-periotic complex measurements of extinct and extant odontocete species (n=111; including Platanistoidea, Delphinida), for interspecific variation comparisons. All the analysis was performed on Past4 software. The measurements were standardized for size (divided by a size indicator measurement) and ordered in a PCA ( $p < 0.05$ ; > 91% of the variation explained in the first component). In the variation within the species, the most relevant measure was the total length of the periotic. For the family groups analysis, the measurements were ordered in a CVA, where *G. melas* specimens were strongly grouped together with other specimens of Delphinidae (the confusion matrix was also consistent), while Platanistidae, Phocenidae, Kentriodontidae, Odobenocetopsidae and Iniidae formed other well separated cluster of groups. The same analysis, classified by genus, shows a notable separation for *G. melas* with respect to all the other specimens indicating a rather unique shape for this species. The analysis was repeated with only inner (from Cone-beam; n=29) and only outer morphology measurements with similar results. The variation within *G. melas* was also observed within a greater range than expected, this was partially related to ontogenetic changes, however, a clear pattern of age-related variation was not observed, probably due to sample size. These preliminary results reveal that at least ontogenetic changes should be taken into consideration when making palaeobiological inferences about the type of echolocation, as well as when using these data for character coding in phylogenetic analysis.

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## **INNER EAR OF TWO MIOCENE PHYSETEROIDS (CETACEA, ODONTOCETI) FROM PATAGONIA (ARGENTINA): EVIDENCE FOR AN EVOLUTIONARY STASIS IN SPERM WHALE HEARING MORPHOLOGY?**

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The Odontoceti are known for emitting and receiving ultrasonic sounds that are captured inside the cochlea. In the last decades, the knowledge of cetaceans' cochlea anatomy has increased due to the analyses of extant and extinct taxa, including physteroids or sperm whales. Extant members of that clade are deep-diving animals and their ears are adapted to support great pressures. However, few studies have analysed the inner ear morphology of the early extinct sperm whales, which can provide information about the acquisition of these deep diving specialized hearing abilities. In this contribution, we analyse for the first time the inner ear of two Miocene Patagonian sperm whales of Argentina. Two isolated periotics of *Physeteroidea* indet. (MLP 76-IX-5-1; Gran Bajo del Gualicho Formation, Miocene, and MPEF-PV-6074; Gaiman Formation, early Miocene) were scanned using MicroCT. Posteriorly, digital endocasts were reconstructed for each. The estimation of the low-frequency hearing limit (LFL) was based on the radii ratio of the cochlea. Published illustrations of extant sperm whales endocasts were used for comparative purposes. The analyses of measures and ratios of the inner ear of the patagonian Miocene physteroids shows that their cochleae have intermediate values between extant sperm whale genera. Patagonian specimens have some values that are similar to *Physeter macrocephalus* (e.g., number of turns, basal radii, cochlear), and others that are similar to *Kogia* spp. (e.g., basal ratio, axial pitch). The comparison with available images of endocast models shows that the cochleae of Patagonian physteroids resembles that of *P. macrocephalus* more than that of *Kogia* spp., even sharing the presence of a conspicuous tympanal recess. The LFL of MLP 76-IX-5-1 and MPEF-PV-6074 are notably lower than in *Kogia* spp. with MLP 76-IX-5-1 having the lowest LFL among the studied individuals, and MPEF-PV-6074 having an LFL intermediate between the extant genera. Nevertheless, we cannot exclude that the minor differences between the estimated LFL of the patagonian specimens might be due to taphonomic processes. All these morphological comparisons show that, even though intermediate values are observed in the studied fossil specimens, the whole inner ear morphology shares more similarities with *Physeter*. These results agree with the clear differences also observed in the morphology of the tympano-periotic complex among kogiids and non-kogiid physteroids. This suggests that in physteroids the hearing morphological and functional pattern was acquired early in their evolutionary history, with a subsequent evolutionary stasis over millions of years.

## FIRST CETOTHERIID BALEEN WHALES FROM THE SOUTH ATLANTIC

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Cetotheriidae are a family of small- to medium-sized baleen whales with an unusual cranial anatomy. After long being considered extinct, some analyses now suggest that the pygmy right whale, *Caperea marginata*, may be their last living representative. Cetotheriid fossils are known from the Miocene to the Pleistocene, and ranged across the Paratethys, North Pacific, North Atlantic and the South East Pacific. In South America, they are well represented along the Pacific coasts of Chile and Peru, but so far have remained conspicuously absent from the Atlantic. Here, we report their first record from the late Miocene of Patagonia, Argentina (Puerto Madryn Formation; 11.9-9 Ma, Serravallian-Tortonian). The new specimens include an isolated left periotic resembling that of *Herentalia*, and left and right tympanic bullae of uncertain affinity. Our findings broaden the diversity of mysticetes in the Miocene assemblage of Patagonia and notably expand the geographical range of cetotheriids in the Southern Hemisphere. In addition, the presence of a genus previously only known from the North Atlantic invites a reevaluation of cetotheriid biogeography.

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Modality: Poster

## TUBERCULOSIS-LIKE INFECTIOUS SPONDYLITIS IN A CERVICAL VERTEBRA OF A PLESIOSAUR FROM THE UPPER CRETACEOUS OF PATAGONIA, ARGENTINA

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Paleopathological studies have been used to understand the history of injury and disease in extinct populations, their putative cause, and on this basis, some infer paleoecology and behavioral aspects. Paleopathologies are generally identified if they damage the skeleton. The most common in the zoological/paleontological record are traumatic injuries, post-traumatic malformations, modification of bone tissue from infection, congenital defects, and neoplasms. Although pathologies in plesiosaurs are recognized since the 1870s, and various diseases have been reported (e.g., septic necrosis, avascular necrosis, erosive osteoarthritis, vertebral fusion, and tooth-marked bones), reports of infectious diseases are still comparatively scarce. Here we report the pathological cervical vertebra of a plesiosaur recovered from the Maastrichtian (Late Cretaceous) of Argentinian Patagonia. The specimen MML-PV 1305 is explored macroscopically and by computerized microtomography. The anterior external surface shows a taphonomic artifact (in the form of cracks in the subchondral bone with central loss) as well as an elliptical, subchondral erosion with minimal new bone formation and a slight adjacent filigree reaction. The right anteroventral surfaces of the centrum bears an erosive process with a minimal bone reaction and alterations have the appearance of space-occupied masses. On the left anteroventral surface of the centrum, there are abnormal vascular channels, associated with a groove just ventral to the articular surface. X-ray examination reveals a central lytic area with weakened and collapsed trabecular bone. The combination of these features indicates that the pathological aspect of the vertebra is due to an infection. The pattern of bone abnormalities is indistinguishable from that described in Pleistocene mammal skeletons affected by the granulomatous tuberculosis infection and analogous to the abnormal ribs and cervical vertebrae of an eosauropterygian from the Middle Triassic. The latter is also identified as tuberculosis-like pneumonia. The case reported herein represents the first record of tuberculosis-like infection in a plesiosaur. As the vertebra was not part of an associated skeleton, it cannot be determined if the cause of death of the plesiosaur is unrelated or secondary due to compromised hunting ability (due to limited neck mobility) or the result of infection-related organ failure.

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## WORK IN PROGRESS: SHELL PATHOLOGY IN JURASSIC MARINE TURTLES

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The fossil record of Jurassic aquatic turtles consists of fragmentary specimens from the Kimmeridgian of Krzyżanowice, Czarnogłowy (Zarnglaff), and Wrzosów (Fritzow), as well as the Tithonian turtle *Owadowia borsukbiallynickae* from Owadów-Brzezinki. The specimen MZ (Polish Academy of Sciences Museum of the Earth, Warsaw, Poland) VIII Vr-71 from the first mentioned locality, described initially in 1968 as “*Tretosternon aff. punctatum*”, the taxon now considered invalid, was recently revised as a thalassochelydian turtle resembling *Craspedochelys* spp. This identification is supported by the histological data. The structure of the shell bones is diploe, with the external cortex generally thicker than the visceral, and histology consistent with the previously described thalassochelydians, such as *Plesiochelys* spp. Similarly to other representatives of this group known, e.g., from Switzerland, the external surface of the shell of MZ VIII Vr-71 bears numerous asymmetrical pits of varied depth and size. Historically, these pits were frequently interpreted as bite marks created by chelonophagous reptiles, such as large crocodylomorphs. Although record of predation is evident on some turtle shells from the Jurassic, in many cases the morphology of the pits is not consistent with tooth marks. Some other explanations were also proposed, such as diagenetic modifications or colonization by epibionts, either in vivo or post mortem. In MZ VIII Vr-71 the pits are numerous, resulting in an uneven surface of the shell, and predominantly localized on the carapace. The histological sections reveal that they penetrate the thick external cortex, but never seem to pierce it completely, and their appearance is not correlated with any disturbances (e.g., breakage) of the underlying trabeculae of spongiosa, seemingly refuting their mechanical origin. In some places, evidence of healing by deposition of new layers of bone is visible, in some cases completely obscuring the initial presence of the pits in macroscopic view of the shell surface. This refutes their appearance post-mortem. The most plausible explanation for their origin thus seems to be the activity of epibionts or localized bone destruction due to dermal diseases, such as, e.g., shell rot. This will be investigated further based on comparisons with extant taxa.

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