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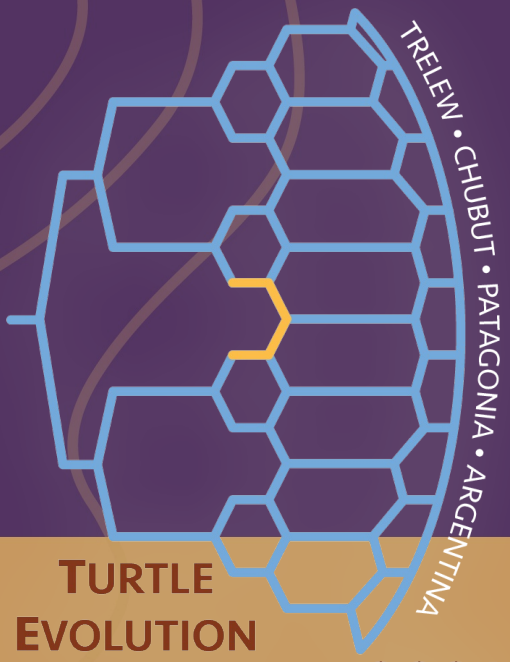
TURTLE EVOLUTION SYMPOSIUM 2021



BOOK OF ABSTRACTS

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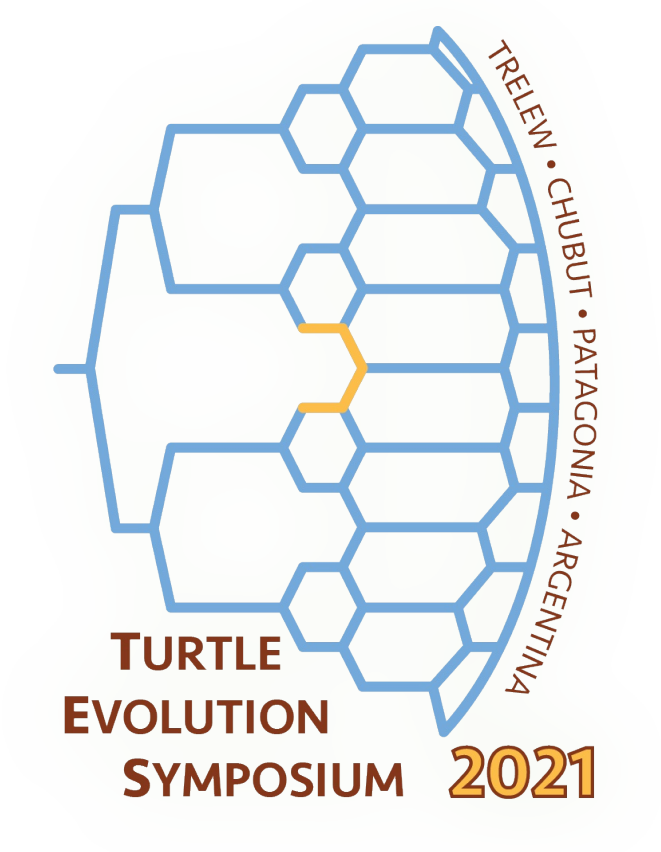

BOOK OF ABSTRACTS

November 10–12, 2021

Organizing Institutions

Museo Paleontológico Egidio Feruglio

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PREFACE

The main goals of the "Turtle Evolution Symposium 2021" (TES 2021) are: to present, promote, communicate, and discuss the latest advances and original results about the evolutionary history of turtles, since their origin and early evolution until the present. It is an international meeting that gathers all turtle researchers and students around the world that work in specific topics like anatomy, evolution, nomenclature, taxonomy, phylogenetic relationships, fossil record of extinct turtles, conservation, among others.

TES 2021 is the seventh meeting since 1983 and the second in South America. In the last decades TES acquired certain regularity and it is organized each 3 years. In this TES 2021, we honor Dr. Marcelo S. de la Fuente. Dr. de la Fuente is the first researcher in South America dedicated to the study of extinct turtles and who marked a before and after in our discipline at regional level whose studies reached a global impact.

The election of Argentina as the place to organize TES 2021 is the result of the ongoing growth of paleoherpetology in the country during the last decades. Nowadays, the country accounts for more than 400 occurrences and more than 40 species of extinct turtles, being the most rich and important record of turtles in South America and one of the most important and extensive in the world.

Due to the pandemic caused by the virus SARS-COV-2, TES 2021 is developed completely in a virtual mode. However, going virtual allowed this TES meeting to be the biggest of all with more than 75 attendees from more than 25 countries around the world. During the symposium, 52 works and 2 keynote presentations were communicated. These presentations have covered different topics about extinct and extant turtles, like history, development, systematics, nomenclature, histology, anatomy, evolution, phylogeny, faunas, conservation, among others.

The abstracts of all these 54 presentations can be found in this Book of Abstracts, published in the Publicación Electrónica de la Asociación Paleontológica Argentina, a Diamond Open Access journal published by the Asociación Paleontológica Argentina.

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A SLATE, A SWIMMING POOL, A TURTLE AND OTHER MISCELLANIES: THE BEGINNING OF AN INTERESTING HISTORY

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Although Patagonia is famous worldwide for its fossils, an interesting story about extinct Patagonian reptiles began in an urban context in Buenos Aires Province (Argentina) when the paleontologist Osvaldo Reig discovered a carapace including in a decorative slate surrounding a swimming pool. The origin of the slate was determined as a quarry in Las Lajas (Neuquén), and the turtle was formally described in 1961 as the new Late Jurassic turtle *Notoemys laticentralis*. A few years later, a small collection of rocks and fossils from the Neuquén Province became a natural history museum at Zapala city and began to gather an increasing collection of Jurassic marine reptiles (mainly from the Vaca Muerta Formation), including other turtles as the Thalassochelydia *Neusticemys neuquina*. Although these records documented the co-occurrence of different lineages in marine environments, their significance was somehow overlooked for a couple of decades until they called the attention of Marcelo de la Fuente. Marcelo was working on his Ph.D. project on Cenozoic chelids and testudinids of Argentina, and, for the first time in Argentina, he was developing a project based on turtles. Since then, de la Fuente's former project became a research program that triggered new research lines and strongly influenced subsequent generations of paleontologists. In this talk, I will present a brief account of de la Fuente's contributions focused on those referred to Jurassic marine forms and how "miscellaneous" events in a proper context can be transformed into a promising field for scientific research.

PRESENT AND FUTURE OF THE PALEONEUROLOGICAL STUDIES OF TURTLES

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Compared to most reptilian clades (particularly arcosauriforms) the neuroanatomical and sensory evolution of turtles is understudied. So far, several cranial endocasts of extinct taxa have been described. However, and also contrarily to other reptilian groups –such as squamates and birds– turtle cranial endocasts are poor predictors of the soft tissue anatomy making difficult to interpret many aspects of their sensory biology. This talk will summarize the history of the paleoneurology of the group, including the influence of the use of new technologies -such as computed tomography- in the high increment of the studies along the XXI Century, the problematics that paleontologists face trying to reconstruct soft tissues based on osteological correlates in the turtle skull, and which are the current advances in the field, and future trends towards more comprehensive studies.

CHELONIAN REMAINS FROM THE LATE CRETACEOUS KHARGA AREA, SOUTHWESTERN DESERT, EGYPT

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The Late Cretaceous is the least known period in the Egyptian chelonian record. The Quseir Formation is a Campanian (Late Cretaceous) sequence that crops out mainly in the southwestern Desert of Egypt. The Quseir Formation comprises a clastic sequence of bioturbated mudstone and sandstone intercalations, containing rare, scattered and fragmented vertebrate remains such as shark teeth, dinosaur remains, and turtle plates. These deposits reveal a supratidal marsh environment. The turtle remains collected from the Quseir Formation east of the Kharga area are housed in the New Valley Vertebrate Paleontology Center, New Valley University. All the turtle remains are isolated plates, with no cranial elements. However, four well-preserved specimens (NVP002, NVP003, NVP004 and NVP005) have been recovered. NVP002 is a squeezed highly damaged carapace and plastron together. NVP003 and NVP004 are plastra with different sizes (NVP004 is about 45 cm long and NVP003 is almost 42 cm long). NVP005 is a well preserved articulated carapace and plastron. The character combination (trapezoidal anterior lobe, triangular gulars, V- shaped intergular, the pectoral shield does not reach either epiplastron or entoplastron, the humeral scales overlap the entoplastron, the humeral-pectoral sulcus suture is posterior to the entoplastron, the posterior end of the entoplastron does not reach the anterior margin of the bridge, the hyoplastron lateral border spreads gradually and almost straight in a lateral direction and spreading dorsally to form the axillary, humero-pectoral suture is in the mid portion of the hyoplastron and is posteriorly located to both the ento-hyoplastral and the epi-hyoplastral sutures, the hypoplastron extends laterally in the dorsal direction, forming the inguinal process, in the ventral view, on xiphiplastron surface a curved sulcus anteromedially extending is observed corresponding to the femoro-anal sulcus) recognized in the three better preserved specimens (NVP003, NVP004 and NVP005) allows us to identify mixed characters from Cearachelyini and Bothremydini. The material records the first and oldest specimens preserving characters from both Cearachelyini and Bothremydini from the Campanian in North Africa and especially in Egypt. These records help fill the missing evolutionary gap from the Late Cretaceous chelonian record in Egypt and North Africa.

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NEW FINDINGS FROM MORRO DO CHAVES FORMATION (LOWER CRETACEOUS OF BRAZIL) REVEALS THE OCCURRENCE OF ARARIPEMYDIDAE (TESTUDINES, PLEURODIRA)

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Here we report the third fossil turtle record from Sergipe-Alagoas Basin. The new finding consists of a partially preserved shell (LPUFS-5843) collected at the InterCement quarry (9.7565°S, 36.1544°W) in Morro do Chaves Formation strata, dated as Barremian. The principal mining area exposes mainly shales and coquinas layers with 75m height. LPUFS-5843 was collected in a shale layer at the base of this outcrop, while *Atolchelys lepida* was recovered from its uppermost sequence. There is no exact stratigraphic information for MCP-4721PV and therefore available data supports LPUFS-5843 as the oldest fossil turtle from Brazil. LPUFS-5843 consists in a partially preserved carapace and a cranial portion of the plastron, both in their visceral view, and possibly belong to the same individual. The small body size (6.4 cm) and the well-marked bone sutures allow identifying it as a juvenile. Therefore, some of the below mentioned features might be due to ontogeny. It seems reasonable to identify this specimen as an Araripemydidae given the presence of: (1) an arrow-shaped entoplastron; (2) a nuchal emargination; and (3) an elongated and curved third peripheral. LPUFS-5843 plastron remains preserve both epiplastra, most of the entoplastron, and the cranial portion of both hyoplastra. The rounded shaped epiplastra, like most pelomedusoids, are different to that of other Family members (elongated and "V-shaped" as in *Araripemys barretoi* and *Taquetochelys decorata*). The suture between epiplastra and hyoplastra is not straight as seen in *A. lepida*, with a pronounced notch similar to that seen in Araripemydidae. The arrow-shaped entoplastron differs from the diamond shape seen in most Pelomedusoides, including *A. lepida*. The carapace remains preserve most of the nuchal bone, four pairs of partially preserved costal bones (1 to 4), right peripherals 1 to 3 and part of neural series (1 and 2). Nuchal plate is broad, "boomerang" shaped (emarginated). The nuchal contacts with peripheral 1 and excludes costal 1 of the carapace margin (as in *T. decorata*). Costal 1 exhibits an elongated and parallel axillar buttress and laterally contacts caudal margin of peripheral 2 and the entire preserved peripheral 3. The elongated, curved and caudally expanded peripheral 3 is similar to that of *Ara. barretoi* but the most cranial portion of the carapace bridge is placed at peripheral 3, as in *T. decorata*. Given that character state combination, the specimen may consist of a new species of Araripemydidae that extends back the minimum age for the family from Aptian to Barremian, reducing its ghost lineage in 15 Ma.

* Project funded (scholarship) by: CAPES (Financial Code 001).

ATOLCHELYS LEPIDA (TESTUDINES, PLEURODIRA) - AMENDMENT DIAGNOSIS AND REVIEW OF THE EARLY HISTORY OF CROWN-PELOMEDUSOIDES

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Atolchelys lepida is a side-necked turtle from the Upper Barremian of Brazil (Morro do Chaves Formation; Sergipe-Alagoas Basin) and the oldest named crown-Pelomedusoides to date (ca. 125 Ma). The original description of the species, however, is very succinct and based on a partially prepared holotype (and only known specimen), although well preserved — including a nearly complete skeleton. After additional preparation of the holotype, including an almost complete preparation of the skull, we performed the description of the skull that enabled the proposition of an amendment to *A. lepida* diagnosis. Furthermore, we tested the phylogenetic position of *A. lepida* among Pelomedusoides by reanalyzing recent published character-matrices, performing exclusions, recombination, and semantic redescription of the characters previously used. The osteological redescription allowed encoding 25 new informative characters to *A. lepida* in our dataset that included almost all Pelomedusoides lineages (without Sahonachelyidae, but including *Sokatra antitra*). Thus, we tested the current phylogenetic hypothesis for internal relationships of Bothremydidae, as well as for Pelomedusoides in general. The cladistic analysis consistently recovered *A. lepida* in the first divergence node of Bothremydidae. Also, we clarified internal Family relationships with sustained monophyly for Bothremydini, Cearachelyini, Kurmademydini (without *Sankuchemys*) and Taphrosphyini. Although some authors question the placement of *A. lepida* inside Bothremydidae (recovering it as a stem-Podocnemidoidea), the species can be diagnosed as a representative of the Family by the presence of (1) wide prefrontals, in contrast to Pelomedusidae and Euraxemydidae; (2) triturating surfaces moderately wide; (3) large palatine contribution to triturating surfaces; (4) maxilla-quadratojugal contact present; (5) wide exoccipital-quadrate contact present; (6) fossa precollumelaris absent; (7) cavum pterygoidei absent; (8) prootic partially covered in ventral view; (9) foramen posterius canalis carotici interni not in prootic and (10) basisphenoid-quadrate contact present. The cranium of *A. lepida* can be diagnosed relative to all other named Pleurodira taxa by the presence of the following autapomorphies: (1) foramen palatinum posterior longitudinally elongated, drop-shaped; (2) quadrangular opistotic in ventral view; (3) triangular basioccipital, unequal, with enlarged rostral portion; (4) extensive supraoccipital and (5) long contact between parietal and squamosal. The last two features provide additional information that enrich the diagnosis of *A. lepida* and the 25 informative characters that could be scored for this species — along with the new cladistic analysis — provide stronger evidence to understand the early history of Pelomedusoides as well as the definition and diagnosis of Podocnemidoidea lineages.

* Project funded (scholarship) by: CAPES (Financial Code 001).

OLD TAXON, NEW BONES: NOVEL MATERIAL OF *BAURUEMYS ELEGANS* IN AN UNEXPECTED REPOSITORY

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Our understanding about Brazilian Late Cretaceous Testudines is mostly restricted to the Bauru Group, a continental unit in South-central Brazil. Even though its strata have been extensively explored, knowledge about the Bauru's turtles is hindered by large amounts of unpublished material. In this contribution, we present undescribed remains deposited in the Collection of Fossil Reptiles of the Departamento de Geologia, Universidade Federal do Rio de Janeiro (DEGEO/UFRJ). The material comprises 44 fragments catalogued under a single collection number – UFRJ-DG 73-R. Preserved elements comprise carapace, plastron and indeterminate shell plates, parts of the shoulder and pelvic girdles, a zeugopodial bone, two femora, a ceratohyal and several unidentified bones. Repeated elements and the disparity in size between some fragments reveal that UFRJ-DG 73-R includes remains of at least four different individuals. All information about the origins of the specimen was extracted from its collection tag, as collection staff were unaware of this material and had no additional information about it. According to the tag, the fossils were collected in 1981 by late geologist Marco Aurélio Vicalvi, in rocks attributed to the "Marília Formation" at Ramal Dourados, Presidente Prudente, São Paulo state. Ramal Dourados is a deactivated railway, which passes through the famous "Tartaruguito" site, where hundreds of skeletons of the podocnemidoid *Bauruemys elegans* were found in close association. UFRJ-DG 73-R includes peripherals with deeply incised pleuro-marginal sulci, a first costal with a cranio-laterally constricted axillary buttress, shell elements ornamented with radial and concentric furrows and scapulae with flattened acromia, characteristics which indicate that this material can be attributed to *B. elegans*, known exclusively from the "Tartaruguito". The "Tartaruguito" exposes rocks attributable to the Adamantina Formation (Turonian–early Maastrichtian), contradicting the tag's statement that the fossils originate from the Marília Formation (Maastrichtian). However, this information is most likely mistaken, as the Marília Formation only crops out in the eastern portion of São Paulo. Knowledge about the lithostratigraphy of the Bauru Group was limited at the beginning of the 1980's, which explains the misunderstanding. We thus conclude that UFRJ-DG 73-R is a sample of *Bauruemys elegans* from the "Tartaruguito" site. The presence of pelvic girdles, a zeugopodial element and a ceratohyal is noteworthy, as a proper description of these bones of *B. elegans* has never been published. Novel material of *B. elegans* is particularly relevant today, as our best sampling of this taxon was unfortunately affected by the fire in the Museu Nacional (MN-RJ).

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TURTLES IN A LAND OF SHRIMP-EATERS: FOSSIL TESTUDINES OF THE POTIGUAR BASIN

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The Potiguar Basin is a sedimentary unit located in Northeastern Brazil, with strata ranging from the Lower Cretaceous to the Quaternary. Fossil finds are mostly restricted to the Albian–Cenomanian Açu Formation and the Turonian–Campanian Jandaíra Formation, both poor in tetrapod remains. We address the Testudines of the Potiguar Basin, presenting the first turtles from the Açu Formation and reanalysing the pelomedusoid *Apodichelys lucianoi*, the only tetrapod known from the Jandaíra Formation. The record from the Açu Formation consists of fragmentary shell remains collected by the team of the Laboratório de Macrofósseis over the course of several years of fieldwork in the state of Ceará. All material is deposited in the Fossil Reptiles Collection of the Departamento de Geologia, Universidade Federal do Rio de Janeiro (DEGEO/UFRJ). These fossils, considerably scarcer than the dinosaur and fish remains found at the same locality, belonged to small freshwater turtles. All specimens lack the pitted shell texture typical of araripemydids, the most abundant turtles in the Aptian–Albian of Northeastern Brazil, and some of them show prominent bridge elements. The absence of ornamentation pits and the presence of a strongly developed bridge lead us to tentatively assign some specimens to the Pan-Podocnemididae, a group known to have inhabited South America throughout the Cretaceous, and that is represented in many Cretaceous basins in Northeastern Brazil. The material from the Jandaíra Formation comprises a single specimen – MCT.R.418, the holotype of *Apodichelys lucianoi*, housed in the Fossil Reptiles Collection of the Museu de Ciências da Terra (MCT). The fossil is a steinkern with some bone fragments still preserved, but mostly concealed by matrix. Since its description in the 1950's, this turtle has received little attention, and a reappraisal is desired. We submitted the specimen to an X-ray microtomography, and preliminary results have revealed previously unknown anatomical features hidden within the carbonate concretion. The yet unprocessed images show the full extent of the axillary and inguinal processes, dorsal vertebrae, pelvic girdles and rib heads, which were previously known only partially from the few parts exposed outside of the concretion. The Testudines of the Potiguar Basin contribute to fill an important gap in our knowledge about South American turtle faunas during the Cretaceous Period. The material from the Açu Formation represents the first occurrence of Cenomanian turtles in Northeastern Brazil, and *Apodichelys* is the only fossil turtle in marine rocks from the Upper Cretaceous of the entire country.

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THE OLDEST EVIDENCE OF *TESTUDO GRAECA* IN THE IBERIAN PENINSULA

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The *Testudo graeca* (i.e., Greek tortoise or spur-thighed tortoise) origin in Western Europe is a subject of debate within the scientific community. The species is part of the current Spanish biodiversity, with three isolated populations, located in the south-eastern (Almeria and Murcia, Spain) and south-western (Doñana National Park, Spain) areas of the Iberian Peninsula, and in the Mallorca Island (Balearic Islands, Spain). Over the last two decades, mitochondrial DNA sequencing studies of Iberian and North African populations of the species have offered results that point to the area of Oran, in northern Algeria, as the area where the Iberian lineage originated. This data, combined with coalescence-based demographic analysis and revisions of the Iberian paleontological and archaeozoological record, have led researchers to propose the arrival of the species to the south-eastern region of the Iberian Peninsula at the end of the last glacial process (Würm), approximately 20,000 years ago. Throughout the 19th and 20th centuries, putative references to the presence of *Testudo graeca* in the Iberian palaeontological and archaeozoological records were relatively common. However, many of them were refuted in subsequent papers and, those that were not, are now considered doubtful. The aim of this work is to present and describe the oldest indisputable remains of *Testudo graeca* in the Iberian Peninsula. They correspond to several individuals, hitherto unpublished, found in Plaza Marqués de Busianos 5, a site in Valencia (eastern Spain) dated between the 1st and 2nd centuries AD. We assess whether these finds support the presence of *Testudo graeca* in the Iberian biodiversity of the 1st or 2nd centuries AD or if, on the contrary, the analysed remains correspond to specimens brought from abroad to the Iberian Peninsula by the Romans.

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A NEW SMALL SMOOTH-SHELLED KINOSTERNOID FROM THE LATE MAASTRICHTIAN FRENCHMAN FORMATION OF SASKATCHEWAN REPRESENTED BY AN ARTICULATED SKELETON

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A new specimen of a small smooth-shelled kinosternoid from the late Maastrichtian Frenchman Formation of Saskatchewan, Canada, provides the first articulated skeleton of a member of this group. The shell is similar to the previously described taxon, *Yelmochelys rosarioae* from the late Campanian Cerro del Pueblo Formation of Coahuila, Mexico, in being smooth and having a reduced plastron. However, the presence of a triangular posterior lobe of the plastron, rather than one that is broad and rounded, indicates that the Frenchman Formation specimen is taxonomically distinct. The carapace has eleven peripherals, rather than ten as shown in the composite reconstruction of *Y. rosarioae*. Thus, the reconstruction of the carapace of *Y. rosarioae* is likely incorrect in this feature, and the presence of ten peripherals can no longer be considered a character uniting *Y. rosarioae* with kionsternids. Micro-CT scans of the specimen provide detailed information on the morphology of the skull, neck and limbs. The skull is generally similar to other kinosternoids in proportions but differs in that the quadratojugal is small and does not form part of the margin of the upper temporal opening. Also in contrast with the condition in other kinosternoids, the stapedial canal is larger than the canalis caroticus internus. All cervical vertebrae are present, although C2 and C3 are represented only by part of the neural arch and C7 is missing part of the centrum. The cervical vertebrae are similar to those of extant kinosternids in proportions but differ in that C8 has a single rather than doubled ventral flange. Limbs are preserved inside the shell and one foot is partially articulated. The proportions of the limbs are similar to those of kinosternids. The presence of unexpected plesiomorphic features, particularly the small quadratojugal and large stapedial canal, plus the revised interpretation of the number of peripherals in *Y. rosarioae*, brings into question the conclusion that *Y. rosarioae* is a stem kinosternid. A preliminary PAUP analysis shows that the relationships of *Y. rosarioae* and the Frenchman Formation taxon are unresolved.

A NEW FOSSIL COULD END THE CONTROVERSY ON THE OCCURRENCE OF THE EXTANT GENUS *PODOCNEMIS* DURING THE MIOCENE IN NORTHERN SOUTH AMERICA

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At present, the oldest undisputable record for the extant genus *Podocnemis* is *P. bassleri* from the Neogene (Miocene–Pliocene) of Peru, despite molecular data suggests that the genus evolved during the late Eocene (~36.86 Ma). Fossils older than *P. bassleri* potentially belonging to this genus are still highly controversial because the absence of skull-shell associated material, and because of the lack of unique diagnostic shell features for this genus. The mentioned older fossils include the Miocene shell material of '*Podocnemis*' *pritchardi* and '*Podocnemis*' *medemi* from La Tatacoa desert, Colombia (La Venta Fauna). Here we present a new fossil turtle represented by a nearly complete articulated shell from the middle Miocene of La Tatacoa, and discuss the value of musk foramina as one of the most remarkable diagnostic features to identify the shell of taxa belonging to *Podocnemis*; based on the examination and comparisons of a robust number of extant specimens. Our data supports previous hypotheses that have proposed the relevance of these morphological features for taxonomic identification of fossils. We also ran a preliminary phylogenetic analysis adding new characters to a current taxon-character matrix, finding the new specimen from La Tatacoa inside a clade that includes the extant *P. unifilis*. The evidence that we present here supports the occurrence of the *Podocnemis* genus during the Miocene in northern South America, and the specimen described herein constitutes its potential oldest fossil record.

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NEW EVIDENCE OF A GIGANTIC ADVANCED CHELONIOID (TESTUDINES: CRYPTODIRA) FROM THE MIDDLE CAMPANIAN (LATE CRETACEOUS) OF THE SOUTHERN PYRENEES (NORTH-EASTERN SPAIN)

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Marine turtles (Testudines, Chelonioidea) were common in the subtropical Upper Cretaceous epicontinental seas that once washed the coasts of the ancient European archipelago. Dermochelyids, protostegids, and cheloniids achieved a remarkable diversity during the Cretaceous period, becoming one of the most successful turtle groups. However, the available fossil record of sea turtle remains is extremely scarce and fragmentary in the Upper Cretaceous record of the Iberian Peninsula, being limited to a handful of scattered shell and postcranial remains. Here, we report the preliminary results of newly discovered remains of a gigantic chelonioid from the Middle Campanian of the Southern Pyrenees, which was originally discovered in 2016 but fully excavated in 2021. The single individual was recovered from the Cal Torrades locality (Alt Urgell County, Lleida Province, Catalonia) that is mainly formed by pelagic marl deposits of the Perles Formation. The specimen is currently housed in the Museu de la Conca Dellà-Parc Cretaci (Isona, Pallars Jussà County, Lleida Province, Catalonia) under the repository number MCD-9884. MCD-9884 consists of an almost complete pelvic girdle and a partial neural plate. The pelvis is made up by the two strongly fused pubes to each other (being characterized by showing moderately expanded lateral pubic process), both left and right ilia, and a partial left ischium. Preliminary phylogenetic results suggest basal placement of the studied specimen within the superfamily Chelonioidea, but such affinity must be corroborated in future studies. As for the size of the pelvic elements, it is likely that MCD-9884 was as large as the famed *Archelon ischyros*, thus becoming one of the largest sea turtles worldwide. The discovery of this specimen in the Late Cretaceous Cal Torrades locality represents one of the best and more complete records of giant Mesozoic marine turtles in the Iberian Peninsula. As a summary, the revision of the new remains has abled to re-identify and recognize the Cal Torrades elements as a possible chelonioid with a big body size and represents one of the most complete records of a Mesozoic chelonioid testudine in the Iberian Peninsula.

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COMPSEMYDID AND HELOCHELYDRID TURTLES FROM THE LATE CRETACEOUS OF FRANCE

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Recent discoveries of turtle specimens from the Late Cretaceous of France allow us to better understand the diversity of turtles from Campanian–Maastrichtian deposits and their systematics. The first skull of *Solemys* (Testudines: Helochelydridae) is reported from the Late Cretaceous (Rognacian) Bastide Neuve locality, Fox Amphoux, Var, France. It is assigned to *Solemys gaudryi* (Matheron, 1869) on the basis of associated shell elements. Our study provides new insights on the skull morphology of the family Helochelydridae and suggests that *Helochelydra* from England and *Naomichelys* from North America are closer to one another than to *Solemys*. In addition, a new genus and species of turtle is described on the basis of a skull and shell elements from the Late Cretaceous of Pourrières-Jas Neuf Autoroute 1 locality in Var (southern France). This new taxon is assigned to the family Compsemydidae and characterized by a thick-boned robust skull, a shallow temporal emargination, a crista supraoccipitalis not extending beyond the posterior edge of the skull roof, large nasals meeting along the midline for their full length, frontals retracted from the orbital margin, absence of a cheek emargination, a large jugal forming a substantial part of the orbital margin, absence of a secondary palate and an uneven upper triturating surface; and a shell with the vertebral 1 clearly wider than the vertebrals 2–3, with the lateral margins strongly divergent towards the anterior border and wider than long vertebrals 2–3. The systematic position of this new turtle is confirmed by an updated parsimony analysis using a large updated taxa/character matrix. The phylogenetic relationships of compsemydids are discussed.

NEW PHYLOGENETIC HYPOTHESIS FOR EARLY TESTUDINOIDS BASED ON SHELL CHARACTERS

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The existing attempts of inclusion of early testudinoids of the Cretaceous (*Gravemys*, *Lindholmemys*, *Mongolemys*, etc.) and Paleocene (*Anhuichelys*, *Elkemys*, *Pseudochrysemys*, etc.) in the global phylogenetic analyses resulted either in their position on the stem of Testudinoidea or in polytomy with other testudinoids and other cryptodiran clades. Few phylogenetic hypotheses for testudinoids either consider these taxa as a paraphyletic assemblage at the base of Testudinoidea or distribute them among more advanced clades of testudinoids. The analyses of Tong and collaborators in 2016, based mostly on shell characters, places *Mongolemys* in Pan-Emydidae, *Gravemys* and *Lindholmemys* either in Pan-Testuguria or Pan-Emydidae, *Elkemys* and *Pseudochrysemys* either in Pan-Testuguria or in polytomy with Pan-Emydidae (or Emysternia) and Pan-Testuguria, *Anhuichelys* in Pan-Testudinidae or Platysternidae. The analysis of Vlachos and Rabi in 2018, based on a complete set of morphological and molecular characters, places *Anhuichelys* in polytomy with non-pan-testudinid testudinoids or in Emydidae. Such equivocal results are due to poor knowledge on morphology of early testudinoids (known mostly by shells), numerous homoplasies, and, probably, wrong outgroup choice. A new hypothesis for early testudinoids, presented herein, is based on shell characters only, and it shows the position of these taxa in better concordance with their morphology and age. The outgroup is represented by the pan-cryptodiran *Annemys*. The ingroup includes an undescribed Testudinoidea from the Neocomian of Japan (herein Testudinoid B), all early testudinoid genera mentioned above, *Tsaotanemys*/*Jastmelchyi*, an undescribed testudinoid from the Paleocene of Mongolia ("*Tsaganemys*"), *Platysternon*, *Planiplastron*, *Paramongolemys*, "*Mongolemys*" *trufanensis*, pan-testudinids (*Hadrianus*, *Testudo*), geoemydids (*Mauremys*, *Echmatemys*), and emydids (*Trachemys*, *Baicalemys*, and *Emys*). The final matrix contains 21 taxa and 30 characters. A single analysis was performed in TNT 1.5 using traditional search and resulted in four most parsimonious trees. The strict consensus tree is the following: *Annemys* (Testudinoid B (*Gravemys* ((*Hadrianus* + *Testudo*) (*Echmatemys* + *Mauremys*) (*Anhuichelys* + *Elkemys*))) (*Tsaotanemys*/*Jastmelchyi* (("*Tsaganemys*" (*Planiplastron* + *Platysternon*)) ((*Mongolemys* ("*M.*" *trufanensis* + *Paramongolemys*)) (*Lindholmemys* (*Pseudochrysemys* + *Trachemys* + (*Baicalemys* + *Emys*)))))))). Thus, *Gravemys*, *Elkemys* and *Anhuichelys* are pan-testugurians, *Elkemys* and *Anhuichelys* form a new clade. *Tsaotanemys*/*Jastmelchyi* is a pan-emysternian. "*Tsaganemys*" and *Planiplastron* are platysternids. *Mongolemys*, "*M.*" *trufanensis*, *Paramongolemys*, and *Lindholmemys* are pan-emydids, of them the first three taxa form a new clade.

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CRETACEOUS TURTLES OF BELGOROD PROVINCE (EUROPEAN RUSSIA): PREVIOUS RECORDS AND NEW FINDINGS

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The first report of Cretaceous turtles of Belgorod Province (European Russia) was made by Nessov and collaborators in 1988, who described fragmentary skeletal remains of a new genus and species of a chelosphargine protostegid *Teguliscapha rossica* from the Albian-Cenomanian deposits of Lebedinskii and Stoylenskii quarries near the cities of Gubkin and Staryi Oskol, respectively. Since then additional turtle material from there, represented mostly by isolated bones and collected by different collectors, was accumulated in the Zoological Institute (St. Petersburg). This material was only briefly mentioned in the literature as belonging to protostegids and dermochelyids. In 2019, an incomplete turtle skeleton (consisting of a partial shell, scapula and pelvic bones) was collected *in situ* from Stoylenskii quarry. This new finding allows better understanding of the fossil turtle diversity of these localities. The incomplete skeleton, along with an isolated entoplastron, maxilla and a short dentary symphysis, as well as most remains previously attributed to *Teguliscapha rossica*, are referred to a new taxon of protostegids characterized by the following characters: triturating surface of maxilla with pronounced labial and lingual ridges; lingual ridge extending farther ventrally than the labial ridge; sagittal ridge on triturating surface of mandible; nine neurals; neural keel poorly developed; eight pairs of costals; costal plates extend about a half the length of the ribs; last pair of costals not meeting along midline; distal end of ribs fit into pits on posterior peripherals; two suprapygals; entoplastron T-shaped, not sutured to other bones; hyoplastron and hypoplastron stellate in outline; scapula with acromial tubercle; ischium lacks posterior process. Inclusion of the new taxon to the phylogenetic analysis of protostegids by Hooks in 1998 (??????????1100100000011???1) resulted in its position as sister to the clade uniting *Microstega copei*, *Protostega gigas*, and *Archelon ischyros*. A pygal with a deep posterior notch, a keeled bridge peripheral, and a proximal humerus are referred to as ?*Rhinochelys* sp. Material of *Teguliscapha rossica* is here restricted to the holotype (long dentary symphysis), but may also include a hypoplastron with a short bridge part, previously attributed to macrobaenids. If this is correct, then *Teguliscapha rossica* is a stem-chelonioid. Large peripherals with deep emargination of the medial border are referred to as ?Dermochelyidae gen. et sp. indet. based on their similarity with *Mesodermochelys undulatus*. A moderately long dentary symphysis belongs to an undetermined chelonioid. Thus, the Albian–Cenomanian turtle assemblage of Lebedinskii and Stoylenskii quarries includes at least five taxa of sea turtles, instead of three reported previously.

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PALEOGENE PELOMEDUSOID TURTLES FROM NORTHWESTERN ARGENTINA: A PRELIMINARY APPROACH

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The record of the Paleogene fossil pelomedusoid turtles in northwestern Argentina is scarce, with only one named species ("*Podocnemis*" *argentinensis*). These pelomedusoids have been discovered in several Paleocene, Eocene and Oligocene formations and localities of La Rioja (Puesto La Flecha Formation), Jujuy (Maíz Gordo, Lumbrera Formations), Tucumán (Río Loro Formation) and Salta (Geste and Lumbrera Formations) provinces. Among the Paleogene specimens the plastron-based "*Podocnemis*" *argentinensis* from Maíz Gordo Formation at Quebrada Queñoal (Jujuy Province) was reconstructed by Cattoi and Freiberg in 1958 on the basis of a partial preserved plastron (holotype MACN 17988) and a referred specimen represented by a partial right epiplastron (MACN 16553) showing a simple gular-extragular scale pattern and a relatively narrow anterior plastral lobe. Two different pelomedusoid turtles in Casa Grande Area (Jujuy Province) were recovered. One of them found in outcrops of Maíz Gordo Formation at Quebrada del Puesto is assigned to an unnamed taxon of pelomedusoid characterized by a large sized, pit-decorated carapace. The other discovery is represented by several shell specimens (AMNH 3005, 9690, 9694, 9696–9698, 25571–25573, 25575) from outcrops of the Maíz Gordo Formation exposed at Quebrada del Agujero (Jujuy Province) showing a plastral morphology similar to that of "*Podocnemis*" *argentinensis*, although they are smaller than the holotype. Among them, one skull associated with these small shells is preserved. This specimen (AMNH 9700) is characterized by a short beak, lateral orbits, interorbital groove absent, high maxilla, large vomer, pterygoid flange extended posterolaterally covering most of the pterygoid fossa, and a posterior roof elevation of the skull. These skull morphologies suggest that "*Podocnemis*" *argentinensis* from the Maíz Gordo Formation, is a podocnemidid species belonging to a different genus from *Podocnemis*. A skull and two shells (IBIGEO-P 107-108) represent a different taxon of Podocnemididae recently discovered from the Geste Formation (Eocene) in the proximity of San Antonio de Los Cobres (Salta Province). This new genus and species presents a different plastral and cranial morphology than "*Podocnemis*" *argentinensis*. Among these characters we can list: a short and subquadrangular anterior plastral lobe two times wider than long, a gular-extragular scheme showing a punctual contact between the gular scute and humero-pectoral sulcus preventing midline contact of humeral scutes, a huge foramen palatinum posterius, and a short pterygoid flange that cover partially the cavum pterygoidei. These discoveries suggest a greater diversity than expected in the Paleogene pelomedusoid assemblage of northwestern Argentina.

THE TURTLE FAUNA FROM THE EARLY PLIOCENE OF LANGEBAANWEG (SOUTH AFRICA)

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Langebaanweg is an early Pliocene site renowned for its abundant and diverse mammalian assemblage, including species no longer found in sub-Saharan Africa. The presence of turtle remains in the vertebrate assemblage is known since the early '70s of the last century when Hendy reported the retrieval of *Chersina* sp. remains, later stating that, "*remains of this animal were sometimes present in astonishing quantity, and they occasionally occurred where no other fossils were obvious*". Later on, Meylan and Auffenberg confirmed the common occurrence of fossil *Chersina*, but limited their systematic study to very rare remains of another tortoise, on which they based a new species, *Geochelone stromeri*. More recently, in her preliminary catalogue of African chelonians, de Lapparent de Broin listed for Langebaanweg "Testudininei ? incl. first *Chersina*" or simply "*Chersina* sp.". Despite the abundance of fossils, and the fact that they represented the geologically oldest remains directly testifying for the evolutionary history of the extant angulate tortoise, *Chersina angulata*, none of these authors provided information on the morphology of the fossils. In the frame of the project "Evolution of West Coast ecosystems" we started the identification and the description of the entire turtle collection at Iziko Museums of South Africa (Cape Town), a collection of tens of thousands of fossil remains, hosted in nearly 100 boxes. The type material of "*Geochelone*" *stromeri* is still available, and we have detected the possible presence of a third tortoise species, as well as rare remains of *Pelomedusa* sp. Here we focus on the description of the extremely abundant remains of *Chersina*, including a nearly complete shell (SAM PQL 20734), that we refer to a candidate new species and evaluate its phylogenetic relationships in the context of African extant and extinct tortoises. All the epiplastra exhibit a long, to very long, anterior protrusion and testify for the fusion of the gular shields in a single unit as in *C. angulata*, but the new candidate species is diagnosable thanks to a well-defined set of characters, including the morphology of the nuchal, the epiplastra and the entoplastron. The result of the phylogenetic analysis, based on a recent data matrix developed by Vlachos and Rabi for a total evidence analysis of extant and extinct tortoises, confirms the referral to *Chersina*.

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TURTLE LABYRINTH SHAPE AND SIZE VARIATION AND EVOLUTION THROUGH TIME

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The vestibular organ (= labyrinth) of vertebrates governs stabilization of the visual field, and is thus central for balance and coordination. The morphology and size of the semicircular canals of the vestibular organ have predictable effects on sensitivity to rotational accelerations. This led to widespread hypotheses of universal form-function relationships, linking labyrinth morphology to ecological, and specifically, locomotor specializations among vertebrates. These hypotheses received general empirical support from mammals, but have recently been challenged in non-mammalian vertebrates, particularly archosaurs. Turtles offer 230 million years of evolution, a well-preserved fossil record, and ecological transitions during their evolution that provide the chance to further scrutinize labyrinth ecomorphology in reptiles. We study this system using 3D geometric morphometrics and comparative phylogenetic regression models of 168 digital specimens, covering one fourth of extant turtle diversity and fossil representatives of all major extinct lineages, as well as stem taxa of extant lineages. Our results show that turtles, including their testudinatan stem-lineage, have a conserved labyrinth morphology. Labyrinth shape variation cannot be accounted for by variables of habitat ecology or differences in neck structure and retraction mode. Instead, allometry and the spatial dimensions of the braincase are important in explaining shape variation. High residual variation from regression models hints at additional unknown factors that affect labyrinth morphology. Turtles ancestrally have small labyrinths relative to head size, but evolve unexpectedly large relative labyrinth sizes that rival those of birds. The size increase is observed early on the stem lineage, coinciding with the conquest of aquatic habitats. Statistical models support an effect of active swimming ecologies on large labyrinth size. Ecological explanations of labyrinth size are also found in secondary labyrinth size reductions in terrestrial taxa, particularly testudinids, receiving significant model support. We hypothesize that labyrinth size increase drives a corresponding size increase of the otic capsule, thereby triggering modifications that led to the jaw adductor re-direction system. The independent origin of large labyrinth sizes in turtles with respect to other amniote lineages challenge current models of labyrinth form-function relationships, as variation in locomotor agility is insufficient in explaining why turtle labyrinths should be as large as those of birds.

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BODY SIZE IN TURTLES: A DEEP-TIME ODYSSEY

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Previous studies have attempted to explain the processes underlying the extensive body size variation observed in Testudinata. However, these often neglected the extensive fossil record of the group, which could potentially reveal important patterns. Here, we characterize the patterns of body size evolution in Testudinata and explore the influence of biotic and abiotic factors, such as ecological habitats and paleotemperature. Time-scaled supertrees based on alternative phylogenetic hypotheses were constructed, including 846 turtle species from the Triassic to present. As a proxy for body size, we collected dorsal midline carapace length, and also gathered chronostratigraphic and habitat information — assigning taxa to freshwater, marine, and terrestrial habitat categories. We assessed significant differences in mean body size across time intervals and for each habitat category. We use linear and non-linear regressions to assess the influence of paleotemperature on body size and also fitted different macroevolutionary models to test if Cope's rule can explain body size evolution in turtles. Our findings suggest that each habitat category shows different patterns of body size through time. Freshwater turtles present a constant range of body size and higher disparity than terrestrial or marine turtles, possibly related to their higher ecological diversity. Terrestrial turtles reached their highest body size disparity during the Cenozoic, which might be explained by the high diversity of Testudinidae, including the ability of oceanic dispersal of giant tortoises. Highest mean body size is found in marine turtles, possibly related to the pelagic lifestyle acquired by chelonioids. Body size evolution in turtles does not follow a trend-like process as described by Cope's rule, and larger sizes evolved through other evolutionary processes (*e.g.*, adaptive zones). Mean body size and paleotemperature are not correlated, but we found a significant relationship between body size disparity and paleotemperature, suggesting that higher temperatures might be linked to increased body size variation, possibly due to increased niche availability.

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WHAT'S IN THE BOX? ARE BRAINCASE ENDOCASTS GOOD PREDICTORS OF TURTLE NEUROANATOMY?

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The rich fossil record and repeated habitat transitions make turtles one of the best case studies for investigating morphological evolution associated with different functions and ecologies. Growing interest has been given to different aspects of neuroanatomy — brain cavity, endosseous labyrinth, nasal cavities — due to their potential to infer paleobiology. The link between anatomy and function/ecology is already loose but how good the cavities represent their respective soft tissue organs — brain, membranous labyrinth and nasal organ — is even more contentious. The brains of birds and mammals fill almost the entire cavity, but in crocodilians and squamates large epi- and subdural spaces are commonly found. Although this is believed to be the case of turtles as well, the lack of representative samples and quantitative data hampered any critical assessment of the issue. Here, we digitally reconstructed the brain tissue and braincase of eleven extant taxa based on contrast-enhanced µCT scans and took total volume and linear measurements from the olfactory bulbs, cerebral hemispheres, and otic region, to evaluate how good the brain cavity is as a proxy for the brain in turtles. The otic region is not well-represented in the endocast, but the anterior parts of the brain are. Large sub- and epidural spaces surround the turtle brain, especially in the mid- and hindbrain. Volumetric comparisons also indicate that brain to endocast correspondence is weak, but brain volume (BV) is clearly correlated to endocast volume (EV; $R^2 = 0.97$, $p<0.001$). For all variables, the measurement disparity is lower in younger than in older individuals; BV~EV regression shows that larger turtles have proportionally smaller brains (slope = 0.92; SE = 0.08). Since endocast volume was found to be a reliable proxy for brain volume, we used a dataset of EV corrected by skull box volume of 27 extant and extinct turtles to reconstruct ancestral BVs and further explore brain size evolution. Our results reveal an increase in brain size towards the origin of Testudines. Considering the brain is relatively larger in young individuals than in adults and that paedomorphic changes have been suggested to act on other parts of the body during the origin of Testudines, we hypothesize that heterochronic processes might have driven brain size evolution in turtles. More data on ontogenetic series and a large sample of adult endocasts are needed to further explore this hypothesis, but our results highlight the caveats and usefulness of analyzing endocast morphology in turtles.

THE NEW OUTFIT OF *NEUSTICEMYS NEUQUINA*: HOW RECENT FINDINGS AND TECHNIQUES HELPED CLARIFYING ITS PHYLOGENETIC AFFINITIES

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Neusticemys neuquina is one of the two known turtles from the Upper Jurassic of the Vaca Muerta Formation. Since its initial description in 1988 its taxonomic affinities have been unstable because all known specimens are postcranial elements, which seem to lack phylogenetic relevance. Initially referred, putatively, to the genus *Eurysternum*, it has also been considered a protostegid or a basal cryptodire. Recently, the discovery and descriptions of three skulls (MOZ 064, MACN-PV 105, MHNSR-PV-1195) and their study using computed tomography helped establish it as a member of Thalassochelydia. The new skulls have in common with Thalassochelydia: the articular process of the quadrate posteriorly oriented; the presence of a prominent, ventrally infolding ridge of the posterior surface of the processus articularis of the quadrate; a long interpterygoid contact; the presence of a pterygoid contact with the articular surfaces of the quadrate; an anterolateral recess of the anterior surface of the quadrate lateral to the processus trochlearis oticum; the presence of a fossa on the supraoccipital-opisthotic-exoccipital contact area; the foramina anterius caroticus cerebralis close together but as independent foramina in the basisphenoid; and the presence of a splenial bone in the mandible. Some of the features that distinguish it from other Thalassochelydia are the presence of a depression on the ventral surface of the basisphenoid, a relatively larger foramen nervi trigemini and reduced and steepened triturating surfaces in both the mandible and maxilla. The mandibular morphology resembles that of *Dermochelys coriacea* rather than that of other thalassochelydians and panchelonioids, which might indicate similarities in the feeding preferences between these species. New research has shown that thalassochelydians might have been better adapted to marine environments than previously thought and *Neusticemys neuquina* is not the exception.

EVALUATION OF PAN-CHELONIOIDEA (TESTUDINES: CRYPTODIRA) RELATIONSHIPS BASED ON PHYLOGENETIC MORPHOMETRICS

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This study presents a cladistic analysis based on landmark data, known as Phylogenetic Morphometrics. The analysis was conducted investigating 11 landmark configurations (carapace, coracoid, humerus, ilium, ischium, jaw, plastron, pubis and skull – dorsal, ventral and lateral views) of 31 species of sea turtles (Pan-Chelonioidea). These configurations represent a set of anatomical landmarks that retain the general shape of above-mentioned structures whose morphological minimum distances can be measured between taxa with less subjectivity than with discrete characters. These data were incorporated into recently published morphological character-taxa matrix and molecular constraints were not assumed a priori. Although some inconsistencies persist, such as internal relationships and the phylogenetic placement of Cheloniidae, the results help to enlighten some aspects about the evolution of Pan-Chelonioidea. *Ctenochelys procax* and *Toxochelys latiremis* were recovered as, respectively, the first two divergent nodes of the tree. Despite being positioned outside Dermochelyidae, the results are not conclusive in supporting *Mesodermochelys undulatus* as a stem-Chelonioidea. The Cretaceous stem-cheloniid *Euclastes wielandi* was nested into a monophyletic group with *Ctenochelys* spp. and *Prionochelys matutina*, while the Paleogene stem-cheloniids, *Eochelone*, *Procolpochelys*, *Carolinochelys*, *Puppigerus* and *Erquelinnesia*, were placed in two strongly supported groups. Our results confirm that the durophagous stem-cheloniids *Euclastes*, *Erquelinnesia* and *Ctenochelys* have different origins and therefore are independent lineages. The composition of Dermochelyoidea *sensu* Evers and Benson, 2019 is supported by our data and *Allopleuron* was recovered as sister-taxon to this group. *Ocepechelon bouyai* was recovered in Protostegidae, which was recovered within the Chelonioidea crown-group, implying an extensive ghost lineage for most Cheloniidae. Therefore, it is possible that such positioning of Protostegidae is the result of evolutionary convergence, probably comprising morphological specializations in some configurations associated to pelagic ecology that masked part of the phylogenetic signal in the analysed data. To our knowledge, this is the first attempt to perform a Phylogenetic Morphometrics analysis of Pan-Chelonioidea and, even preliminarily, the results seem promising and contribute to improving the knowledge about the phylogenetic relationships of this highly specialized group of turtles.

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PRELIMINARY ANALYSIS OF SHELL ANOMALIES IN THE SPANISH UPPER CRETACEOUS BASAL PLEURODIRE *DORTOKA VASCONICA* (DORTOKIDAE)

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Paleopathological studies have been key to understanding injuries and diseases in extinct organisms. They provide knowledge about the categories of skeletal damage present in extinct populations, their causes, and by inference, aspects of their paleoecology and behaviour. Paleopathologies have long been reported among fossil vertebrates, mostly in dinosaurs and other archosaurs. However, pathologies in extinct turtles are poorly documented, usually integrated into morphological descriptions without detailed analysis. Shell damage remains a controversial area of study, with pathology variously associated with infection, trauma, or metabolic disease. Likewise, it is generally unclear which agents may be responsible for certain types of shell lesions recognized in the fossil record. Thus, in extinct but also in extant turtle taxa, shell pathology continues to be a source of confusion. In this context, the aim of this study is to analyse pathological conditions recognized for the shell of the Spanish freshwater basal pleurodiran turtle *Dortoka vasconica*. This study is based on the first-hand revision of all material from its type locality (Laño, Treviño County, Burgos). Two pathological plates have been identified, both corresponding to the plastron. These pathologies have been analysed through macroscopic examination and also using Computerized Axial Tomography. The discussion has been established through a differential diagnosis procedure, which constitutes one of the methodological tools of paleopathology. As a result, two types of shell irregularities have been identified here for *Dortoka vasconica*. This study provides the first detailed pathological analysis of a stem-pleurodire turtle and contributes to our understanding of pathologies in turtle taxa.

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ECOMORPHOLOGICAL PATTERNS OF SKULL SHAPE IN TURTLES

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The evolutionary history of turtles documents great diversity of habitat and feeding ecologies, which are hypothesised to correlate with the morphological disparity seen in skulls of both extinct and living taxa. Likewise, functional aspects related to their cervical mobility are also suggested to influence their cranial shape, especially in the temporal region. In this sense, the skull of turtles can possibly be regarded as a decoupled module from the rest of their body: together with the neck, the skull is the primary tool of interaction with the environment, and key to understanding the ecological feeding specialisations we observe among them. Here, we use a three-dimensional geometric morphometrics approach to explore shape aspects of the turtle skull. We developed a new landmark concept that includes single-point, sliding and surface landmarks that capture the dimensions but also curves and surface details of their cranial structure. We analyse ecological and functional traits altogether under a phylogenetic framework to assess what are the main factors that structure turtle skull shape. We find that form-function relationships of their skulls involve allometry, habitat and diet preferences, feeding strategy as well as the ability to hide their necks. Turtles that feed underwater exhibit longer skulls and more flattened palates than terrestrial species, and the use of suction-feeding implies a slight lengthening of posterior skull parts in aquatic feeders. Furthermore, we show that prey type is associated with changes in skull height, width of the triturating surfaces and position of the orbits, and that lack of neck retraction correlates with extreme reduction of both emarginations simultaneously, in addition to changes in overall skull dimensions. Our results can be applied to predict such traits to fossils, recognising that several unrelated extinct turtles could not retract their necks, as well as that distinct marine groups evolved similar ecological diversity compared to extant sea turtles. These include independent origins of durophagy, suction-feeding and preference for more sedentary preys, illustrating remarkable ecomorphological convergence in these ecosystems throughout turtle evolution.

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FOSSIL TURTLES FROM THE LATE CRETACEOUS TAMAGAWA FORMATION OF KUJI CITY, IWATE PREFECTURE, EASTERN JAPAN

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The Tamagawa Formation in the Kuji Group of the Kuji City, Iwate Prefecture of northeastern Japan is the richest geological unit bearing Late Cretaceous terrestrial vertebrates as well as numerous ambers in this country. More than two thousand vertebrate fossils, including dinosaurs and crocodiles, have been found from about the 20 cm thick coaly mudstone layer and overlying 1 m thick marine sandstone bed of the Tamagawa Formation since 2005. Fission track dating carried about the volcanic tuff layer inter-bedded between the mudstone and marine sandstone units indicates the Turonian age of the Late Cretaceous (90.51 Ma). Turtles (Order Testudines) are the most abundant vertebrates (1012 specimens in total) from the Tamagawa Formation, identified as the genus *Adocus kohaku* (Adocidae), Trionychidae, Carettochelyidae, Nanhsiungchelyidae, and Lindholmemydidae. Most of the turtle remains are isolated shell elements, whereas few cranial and appendicular materials were collected. *Adocus kohaku* seems to be the most derived species of this genus in the possession of extremely wide marginal scales and the complete loss of cervical scale of carapace. The largest specimen of *Adocus* in this locality suggests an individual with a 70 cm long shell. Trionychids from the Tamagawa Formation are about 40 cm long in shell length, intermediate size between the Early Cretaceous and more advanced soft-shelled turtles. They are also characterized by reduced eighth costals and rather weak sculptures of the plastron. Carettochelyids are represented by at least two taxa based on size and sculpture differences. The largest specimen (entoplastron) shows this individual was about 70 cm long (shell length). Nanhsiungchelyids are found as shell fragments such as a right hyoplastron and few limb bones. They suggest individuals of about 40 cm long shell. Lindholmemydids are about 30 cm long in maximum shell length, characterized by its linear sculptures and deeper scute sulci. All terrestrial vertebrate fossils from the bone bed inter-bedded by marine sandstone layers, except three partially articulated turtle shells of *A. kohaku*, are isolated and fragmentary. This occurrence suggests they were transported by river stream near the mouth. The fauna and flora of the Kuji Group is one of the most expectable examples of both non-marine and marine vertebrates of the Late Cretaceous in Japan. This excavation will continue for coming years for more plentiful results.

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A SNAPPING TURTLE (*PAN-CHELYDRIDAE*) FROM THE MIDDLE EOCENE OF FRANCE

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Snapping turtles (*Pan-Chelydridae*) are a species-poor clade of cryptodires that play a prominent role in extant ecosystems. The group has a particularly fragmentary fossil record, in part likely due to the fact that their shells disarticulate easily after death, but also a bias against collecting fragmentary turtle remains. As published, the record suggests that the clade originated in North America during the Late Cretaceous but dispersed to Asia and Europe no later than the late Oligocene and to South America no later than the Pleistocene. While a Neogene arrival in South America correlates well with the Great American Biotic Interchange, an Oligocene dispersal to Asia and Europe does not correlate well with other known turtle dispersal events, in particular the global dispersal event that took part across the Northern Hemisphere in concert with the Paleocene–Eocene Thermal Maximum (PETM) that led to the complete replacement of the European turtle fauna. A collection of 100 three-dimensionally-preserved pan-chelydrid shell fragments was collected near the turn of the millennium from a sandpit located near Chéry-Chartreuve, Department of Aisne, northern France. All fragments originate from a laterally constrained lens of sediments consisting of aeolian sands and clays that were deposited at the base of continental sediments that overlay marine sediments in this region. The rich, but poorly described mammalian fauna from this lens suggests an early Bartonian (MP15, middle Eocene) age. The available material, which represents at least three different individuals, documents nearly the full plastron and peripheral series, but only aspects of the neurals and costals. Initial analysis of the material suggests close morphological affinities with *Tullochelys montana* from the early Paleocene of Montana, U.S.A. and *Chelydropsis decheni* (also known as *Chelydropsis santihenrici*) from the late Oligocene of France. This is consistent with the arrival of the *Chelydropsis* lineage in Europe, perhaps directly from North America, no later than the middle Eocene. The previously unanticipated arrival of pan-chelydrids in Europe by the middle Eocene raises the possibility that pan-chelydrids may have arrived in Europe during the early Eocene following the PETM, but remain undetected due to the above-mentioned collecting bias.

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ORTHOGRAPHIA LINGUÆ LATINÆ: NOMENCLATURAL DETAILS TO BE CONSIDERED

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The *I*nternational Code of Zoological Nomenclature regulates the system of names, and provisions for their formation and use, their priorities and implications of the taxonomic operations in question and not the operations themselves. It asks for the usage of Latin, which includes both Ancient and Mediaeval Latin. Greek names are widely accepted but restricted to Ancient Greek. Genus-group names transliterated from Greek into Latin *without* changes take the Greek gender (Art. 30.1.2), otherwise if it is a latinized Greek word, it takes the gender appropriate for Latin (Art. 30.1.3). As examples, the Greek word χέλυς is transliterated as *chélys* following the former article, and latinized as *chelus* following the latter. So, *Chelys* Oppel, 1811, has feminine gender, and *Chelus* Duméril, 1805, has masculine gender. Although *Chelys* Oppel, 1811, is a junior synonym of *Chelus* Duméril, 1805, the feminine gender also applies to any name ending with -*chelys* (*e.g.*, *Erymnochelys*, *Platychelys*, *Peltochelys*, *Eochelys*). In a genus name transliterated from Greek, the family-group name is formed by the stem which is found by deleting the case ending of the appropriate genitive singular (Art. 29.3.1). The genitive singular of χέλυς is χέλυος (chélyos). But there is also the Latin word chĕlys with feminine gender and genitive singular *chelўis*. As both *chélyos* and *chelўis* have the same stem (*chely-*), the family name with a type-genus ending with -*chelys* will be -chelyidae. *Chĕlys*, and its genitive singular *chelўis* was source of past mistakes ("Chelydidae"). Another detail to be considered is the usage of the prefix Pan-. It comes from Greek πας (pas, entire, all) and it flexes as παμ- (pam-) before any Greek name started with Β, Μ, Π, Φ and Ψ, and as παν- (pan-) before the remaining letters. This orthographic trait, which appeared in inscriptions after the 86th Olympiad (432 BCE), turned to be a Greek rule and was inherited by Latin, as well as by modern Romance languages. As the usage of hyphen is not allowed by the Code (Art. 11.2) in family-group names (and also in class-group names, Art. 1.2.2), any name starting with B, M and P should be written using Pam- (*e.g.*, Pampleurodira, Pampelomedusidae, Pampodocnemididae). We also express our opinion that the authorships of those newly formed names with Pan- and Pam- should follow the Principle of Coordination and authorship (Art. 36) because these names are only inflations of those old pre-existed ones (*i.e.*, a group of a type-genus also including something else).

CREATING A 3D MORPHOSPACE OF POND TURTLE (FAMILY: EMYDIDAE) SKULL VARIATION TO BRIDGE MORPHOLOGICAL AND MOLECULAR TAXONOMIC ASSESSMENTS

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Fossil and modern turtles of the genera *Pseudemys*, *Trachemys*, and *Chrysemys* (Family: Emydidae) have been the subject of frequent taxonomic revision for over 150 years. Some resolution has recently been achieved through the application of molecular-based techniques but this leaves the morphological status of the genera, and the position of fossil taxa, unresolved. Bony anatomical differences can be revealed only within a comparative morphological framework that maps with phylogenetic relationships, facilitating the taxonomic identification of fossil specimens. To test the hypothesis that these three genera can be distinguished by morphology and that fossil skulls share similarities with extant analogues, I assembled a dataset of six fossil specimens, representing extinct and extant taxa, and 91 skeletonized, modern specimens from across their range and housed in paleontological and zoological collections across California, Texas, and Florida. These three genera are the focus of my investigation because three-dimensional geometric morphometric studies of turtle skulls have been infrequent and not focused on this part of the clade. Specimens in this dataset were scanned using high resolution computed tomography (μCT) to attain high fidelity of the resultant 3D surface models. I used automated three-dimensional geometric morphometric analysis (auto3dGM) to establish pseudolandmarks, quantify the variation between these specimens using principal components analysis, and develop a turtle skull morphospace. Preliminary results indicate that these genera occupy different regions of the skull morphospace and can be distinguished from each other. Along PC1, *Pseudemys* largely separates from space occupied by *Trachemys* and *Chrysemys*, with this variation driven by changes to the region caudal to the orbits (*i.e.*, the postorbitals, jugals, and squamosals). *Pseudemys* variation is primarily along PC2, whereas the *Trachemys* + *Chrysemys* variation is relatively confined along the PC2 axis. Fossil specimens plotted with their extant congeners with one exception. Fossil *Trachemys* from the Pleistocene of Florida appear at the extreme end of the extant range in morphospace, overlapping with extant *Chrysemys*. At the species-level, *P. concinna floridana* clusters separately from the members of *P. concinna* along PC1, indicating that it may warrant separate species designation from *concinna*. Supporting the hypothesis that *P. suwanniensis* is a subspecies of *P. concinna*, *suwanniensis* clusters with *concinna* along PC2. For scientists interested in the phylogenetic placement of fossil turtles, this study demonstrates how morphology can be combined with molecular phylogenetics to identify taxonomically relevant cranial variation in turtles.

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LUDWIG HEINRICH BOJANUS AND THE ANATOMY OF THE EUROPEAN POND TURTLE: FACTS, FICTION, AND FUTURE

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Detailed anatomical knowledge is a prerequisite for studying a variety of biological questions. This holds true particularly for the evolutionary realm in which fossils play an important role. Extinct organisms usually can mainly only contribute with their morphology to such discussions, in fact frequently even only with parts of it (*e.g.*, hard tissues such as bones). Putting these data in perspective consequently requires a profound knowledge of the corresponding structures of the extant representatives of a given lineage as well. Numerous morphological studies have contributed to our understanding of chelonian anatomy over the past centuries, but one of the earliest ones — whose completion celebrates its bicentenary this year — still stands out among all of them: *Anatome Testudinis Europaeae*, published by Ludwig Heinrich Bojanus (1776–1827) in two installments in 1819 and 1821. The Alsacian-born scientist delivered a masterpiece on the complete anatomy of the European pond turtle, *Emys orbicularis*, while working in the provincial Vilnius. Although important and influential contemporary peers of Bojanus, such as Lorenz Oken (1779–1851) and Georges Cuvier (1769–1832), immediately praised the work and already prophesied that it will set the standard for generations to come, it never experienced a broad distribution. This may have been related to the high price, which was simply necessary, also because of the 40 folio-sized plates, which were executed as impressive copper engravings by Friedrich Lehmann (1787–?1832) and partly by Bojanus himself. However, it led to a situation in which the famous antiquarian book dealer Wilhelm Junk (1866–1942) gave it the predicate of being one of the rarest of all zoological works already at the turn of the 20th century. Numerous myths around this publication have evolved ever since. With this presentation, I intend to set the record straight for some of them, and based on the personal inspection of multiple copies, I will discuss currently unrecognized aspects about the existence of exceptional variant editions. Finally, I will make a proposal for how this work can be used even more effectively in its upcoming third century of existence. Last but not least and despite considerable controversies related to its bibliographical aspects, one fact remains an unchallenged reality: *Anatome Testudinis Europaeae*, even 200 years after its first publication, still is among the by far most detailed and accurate anatomical works on a single chelonian species ever produced and has lost absolutely none of its value for modern-day science.

TAXONOMIC REVISION OF *CHINEMYS PANI* (TESTUDINES: GEOEMYDIDAE) FROM THE PLEISTOCENE OF TAIWAN

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Proper taxonomic identification is critical to our understanding of biodiversity and the underlying evolutionary history as problematic interpretations lead to wrong and confusing conclusions. Here we re-examine the taxonomic status of *Chinemys pani*, a Pleistocene geoemydid turtle dredged from the sea bottom between Penghu and Taiwan. The geological age remains uncertain, but the locality that produces *Chinemys pani* and other abundant vertebrate fossils is broadly dated Middle to Late Pleistocene. *Chinemys pani* has been synonymized with *Mauremys reevesii* in various publications without re-examination of the holotype. Our study here represents the very first attempt that examined the specimen in detail, showing that the original diagnostic features for *Chinemys pani* are not valid and the morphology of *Chinemys pani* falls in the range of intraspecific variation of extant *Mauremys reevesii*. The actual fossil was not curated appropriately after the original publication and was most likely lost; we found a plaster cast deposited in the collection of Chang Jung Senior High School, and the accession number is CJSHS-911001. The replica, though not ideal, preserves various morphological features that allow reliable taxonomic identification to *Mauremys reevesii*, including the presence of three longitudinal keels on the carapace, the second to sixth neural bones anteriorly short-sided, and the lack of movable plastral hinge. In addition, we also confirm that the original diagnostic features that established the new taxon: *Chinemys pani* – are polymorphic characters of *Mauremys reevesii*. For example, the relative length among abdominal, femoral, and anal scutes was originally considered a critical character to diagnose *Chinemys pani* (the femoral scute longer than abdominal and anal scutes), but this feature proves to fall within the intraspecific variation of *Mauremys reevesii*, making *Chinemys pani* unidentifiable. Our results then provide solid evidence to show that *Chinemys pani* should be identified as *Mauremys reevesii*. This taxonomic revision of a Pleistocene geoemydid turtle from Taiwan resolves the debate on whether *Mauremys reevesii* should be a native or an introduced invasive species as the presence of a Pleistocene *Mauremys reevesii* in Taiwan demonstrates the arrival of *Mauremys reevesii* prior the human introduction. More importantly, our study offers new insights into the origin of modern biodiversity in Taiwan and gives a straightforward example of how fossils can be applied to conservation policies.

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ESTIMATION OF THE NATURAL MORTALITY AND ECOLOGICAL FACTS OF *CARETTA CARETTA* THROUGH AN ECOLOGICAL MODELING AT THE GULF OF ULLOA

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The loggerhead turtle *Caretta caretta*, migrates 12,000 km approximately to feed and congregate on the Gulf of Ulloa, within which find a Biological Active Center (BACs). BACs are oceanographic regions that have high biological productivity and make a distinctive faunal assemblage, allowing the presence of species both ecological and economically important. Further of this, in the zone are fishing communities which give social importance because this activity is the main source of income. On the other hand, in this area have been strandings of *C. caretta*, reaching its historical maximum in 2012, however, the main hypothesis about those events is the interaction of the sea turtle with riparian fishing, nevertheless, the study of the ecological aspects of the species such as natural mortality has been left aside. A previous study showed that the natural mortality rate "M" is close to the biomass production ratio (P/B) of the population, under this assumption, the construction of an Ecopath with Ecosim (EwE) model allows us to simulate scenarios which may help begin to know the ecological facts of *C. caretta*, in order to understand the factors that could impact this species in this critical area. The scenarios were made with two forcing factors: fishing effort (f) and sea surface temperature (SST). The scenarios allowed estimating ecological facts of the species such as its biomass (0.100 t/km^2), ecotrophic efficiency (0.5), trophic level (3.37) and production/biomass (1.023 biomass/year). On the other hand, the scenarios proved the hypothesis of the study by showing that the temperature got a greater influence on the organism in comparison with the incidental catch resulting from the fishing effort (f) of the zone, by showing higher values of "M" in cold temperatures, even in the scenario with the absence of f (1.11). The model also allowed us to estimate with certainty the values of the system corroborating its production capacity with a total primary production of 1405.415 t/km^2/year. These results indicate that the warm temperatures are beneficial for the species, therefore, the information of this work could provide a new approach for the study and conservation of this sea turtle species, emphasizing these efforts in the knowledge of the ecological attributes of the sea turtle like so the climatological and oceanographic factors in which it develops.

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NEW SKULL REMAINS OF *PROCHELIDELLA BUITRERAENSIS* FROM THE CANDELEROS FORMATION (CENOMANIAN) OF NEUQUÉN BASIN, PATAGONIA, ARGENTINA SHEDS LIGHT ON THE ANTERIOR ROSTRAL EVOLUTION IN CHELIDAE

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New skull remains of *Prochelidella buitreraensis* were recovered from the Candeleros Formation (Cenomanian) exposed in the "La Buitrera" locality (Río Negro Province, Argentina). These materials were sampled from the same level and outcrops as the holotype. The new specimen (MPCA PV 658) consists of an almost complete skull, a right lower jaw, four articulated cervical vertebrae, some hyoid apparatus bones, and several shell remains. The size of the new materials is similar to the holotype, with a 4 cm skull length. The skull is more complete than the holotype and allows us to describe and compare the rostral area, absent in the *Prochelidella buitreraensis* holotype. Besides, cervical vertebrae and carapace remains allow us to increase our knowledge about the anatomy of this species. MPCA PV 658 can be referred to *Prochelidella* sp. after a well-developed retropterygoideum foramen and a big area for muscle attachment over the basisphenoid. Additionally, the presence of nasals and prefrontals improve the knowledge of skull holotype (MPCA PV 307). The prefrontals in the new specimen of *Prochelidella buitreraensis* do not contact each other in the midline. A similar condition is observed in some South American extant chelids such as *Mesoclemmys nasuta*, *Phrynops geoffroanus* and *Platemys platycephala*. The nasal is a small bone that contacts the prefrontals posterolaterally and forms the dorsal portion of the apertura narium externa. The contact between nasal and prefrontal is also recognized in some extant South American chelids (*e.g.*, *Acanthochelys macrocephala*, *Phrynops geoffroanus*, and *Platemys platycephala*) but not in *Mesoclemmys nasuta*. Also, the size of the nasal bone differs from that observed in *Platemys platycephala* where it is bigger. The posterior margin of the carapace is preserved as in other *Prochelidella* species. The eight costals contact each other along the dorsal and visceral surfaces, not allowing the visceral contact of the last neural with the suprapygal, contrary to the situation in *Prochelidella cerrobarcinae*. The cervical vertebrae exhibit the typical morphology of Chelidae centra (atlas biconcave, 2nd, 3rd, and 4th opisthocoelous). These new features improve the diagnosis of *Prochelidella buitreraensis* and provide a better understanding of the morphology of this key genus on the evolution of Chelidae.

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NEW REMAINS OF *PROCHELIDELLA* IN THE ANACLETO FORMATION (CAMPANIAN LEVELS) OF NEUQUÉN BASIN, PATAGONIA, ARGENTINA

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The new turtle remains presented here were recovered from the Anacleto Formation (Campanian) exposed in the Aguada Grande site. This area is located 10 km south of Rincón de Los Sauces city, in the north of the province of Neuquén, Patagonia, Argentina. The specimen (MAU-Pv-AG-452) consists of a partially preserved skull, carapace remains, an almost complete plastron, and a left ilium. The new specimen is assigned to Pleurodira because its ilium is sutured to the carapace. Both parietals, the posterior part of frontals and postorbitals, the dorsal region of the supraoccipital, both pterygoids, the basisphenoid, and part of the prootics are recognized in the skull. The carapace remains are represented by a left first costal bone in articulation with a peripheral bone, a left paired costal bone, and another fragmented costal. The plastron is represented by both epiplastra, the entoplastron, left hyoplastron, both hypoplastra, and the left xiphiplastron. The skull shows some characters that allow its referral to *Prochelidella* spp. (*e.g.*, a developed retropterygoid foramen, and a big muscle attachment area over the basisphenoid). The visceral view of the first costal bone exhibits long axillary buttresses that extend 2/3 of the costal width. This condition is also observed in the costal bone of *Prochelidella buitreraensis* from the Candeleros Formation (Cenomanian). The scute pattern observed in the anterior lobe of the plastron shows a large gular that extends along the entoplastral length and small extragulars over the epiplastra. In contrast, on the scheme observed in *Prochelidella cerrobarcinae* and *Prochelidella portezuelae*, the gular does not extend beyond the first third of the entoplastron. The material recovered from the Anacleto Formation represents the most complete specimen outside the *Prochelidella* peak of diversity range (Albian–Cenomanian) and the second skull recognized in this genus.

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MECHANICAL DIFFERENCES IN CERVICAL ARTICULAR FORMULAE OF CROWN-PLEURODIRA LINEAGES INDICATE RELATION BETWEEN CERVICAL LENGTH, NECK ELONGATION, AND ARTICULAR MORPHOLOGY

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Concave-convex and convex-concave joints supposedly own different biomechanical properties that impose limits to movement. The first is mechanically stronger than the second, which may constrain articular morphological diversity since there would be no need to overcome the mechanical limits of movement. Both joints occur on the cervical series of crown pleurodiran species, which are distinguished by different articular formulae: (2(3(4(5)6)7(8) in Chelidae and (2)3)4)5)6)7)8) in Pelomedusoides. Influence of joints on neck elongation and variation across Crown-Pleurodira was addressed through morphometry and exploratory Principal Component Analysis on cervical vertebrae (C) proportion followed by Linear Discriminant Analyses (LDA) to test if there is only one type of long and short neck in pleurodires. The sample included all living lineages of Pleurodira (18 Chelidae and twelve Pelomedusoides) with three fossil species: *Araripemys barretoi* and *Euraxemys essweini* from the Early Cretaceous of Araripe Basin, Brazil, and *Turkanemys pattersoni* from the Miocene of Nawata Formation, Kenya. Long-necked species varied in C2, with *Araripemys* adding variation in C8. Short-neckeds varied in C2, C7, and C8. Chelidae had a high variation in C2, whereas Pelomedusoides varied mostly in C7–C8. Pelomedusoides was structured by 'families', which also reflects the articular shape that each 'family' shows. It represented a major part of total variation in the sample. Concave-convex posterior articulation occurs in opisthocoelous cervicals of the anteriormost neck region in chelids. It is supposedly mechanically stronger, allowing elongation, notably in C2, which represented most of the variation in long-neckeds and chelids. Posteriorly, convex-concave articulation occurs in procoelous cervicals of Pelomedusoides and is supposedly mechanically weaker. It may have had less constraint on the evolution of the clade, however. That way, it had permitted articular morphological differentiation across Pelomedusoides to overcome the potential mechanical weakness. *Araripemys* apparently bypassed the mechanical joint fragility by evolving a specific cervical morphology to achieve a long neck. The same joints also occur in C5–C6 and C8 of chelids and may have been related to specializations of C5 and C8 proportions (*i.e.*, lengths) of *Chelus* to trawling-feeding. LDAs found nine neck types that encompass subtypes of both pleurodiran clades and morphotypes (*e.g.*, short-necked chelid and saddle-shaped). We hypothesize that due to these phylogenetic and mechanical constraints, neck elongation events were more frequent in Chelidae than in Pelomedusoides, which have undergone morphological differentiations to achieve other neck types such as *A. barretoi*. The same mechanical constraints allowed the evolution of different types of long-neckeds and short-neckeds.

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THE NEUROANATOMY OF THE PLEURODIRAN TURTLE *GALIANEMYS* (BOTHREMYDIDAE), FROM THE LATE CRETACEOUS (CENOMANIAN) OF MOROCCO

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Bothremydidae was a diverse lineage of pleurodiran turtles, well represented from the Early Cretaceous to the Paleogene in both Laurasian and Gondwanan areas. The Cearachelyini bothremydid genus *Galianemys* was described from several skulls found in the Cenomanian Kem Kem beds of Morocco. The genus is represented by two species, *Galianemys whitei* and *Galianemys emringeri*, whose holotypes are housed in the American Museum of Natural History of New York. Both are exclusively represented by cranial material. Despite the circulatory cranial system of *G. whitei* was described and figured, the complete neuroanatomy of no representative of this genus has so far been reconstructed. Two well-preserved fossil skulls attributable to *Galianemys*, housed at the Muséum national d'Histoire naturelle of Paris, were scanned and subsequently segmented to generate the three-dimensional reconstruction of each of the bones that compose them. These skulls were compared with those of the so far described species to establish their accurate systematic determination. The internal cranial cavities were also reconstructed, including the endocast of the cranial cavity and nerves, nasal cavities, inner ears, and carotid canals. The comparison of the neuroanatomical structures observed for *Galianemys* with those of other previously studied bothremydid turtles is performed. It allows us to recognize some common neuroanatomical features between *Galianemys* and all other members of Bothremydidae, but also other characters that allow us to characterize the neuroanatomical structure of this genus. As a result, inferences related to the lifestyle of *Galianemys* are proposed.

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A DEVELOPMENTAL PERSPECTIVE ON THE ORIGIN AND EVOLUTION OF THE SCUTES OF THE TURTLE SHELL

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The scutes of the turtle shell are epidermal shields that begin their formation during the early stages of shell development. The scutes are patterned by reaction-diffusion systems characteristic of mechanisms used by other skin appendages. We have previously established *ex vivo* and *in silico* systems to study these mechanisms experimentally, and we have further shown that mathematical models can explain the dynamics of the induction of turtle scute primordia and the generation of final scute architecture. Using these foundations, we expanded our current knowledge of the molecular signaling pathways and mechanisms that may produce variation in the scute patterns on the turtle shell. Specifically, we differentiate the timing of scute patterning events relative to other events of morphogenesis and consider the roles of molecules during these events and in the evolution of the turtle shell.

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EVOLUTIONARY TRENDS AND HOMOLOGY OF BASICRANIAL STRUCTURES IN MESOZOIC TURTLES

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The vast majority of basicranial structures found in Mesozoic turtles can be interpreted, homologized, and put in a series of transitional forms, assuming that the basicranium was exposed to two independent transformation processes, which were continuously active from Triassic turtles up to the early crown. These processes are: 1) dorsoventral flattening of basicranial elements and substructures, and 2) widening of dermal palatal elements (except vomer). The vomer is the only dermal palatal element that does not expand but narrows. Together with the flattening of the posterior part of the fossa nasalis and widening of the vomer-palatine contact, it transforms a flat and wide ventral portion of a primitive vomer seen in basal turtles into a "thin sagittal ventral septum" separating the meatus choanae in derived turtles. The interpterygoid vacuity disappears as a result of a combination of both widening of bony sheets on the medial edge of pterygoids, and dorsoventral convergence of pterygoids and basisphenoid. Heterochrony of these two processes may produce a variety of forms: a) widening of medial sheets without dorsoventral convergence transforms interpterygoid vacuity into interpterygoid slit, b) dorsoventral convergence without growth of the medial sheets may result in a condition seen in Pleurosternidae; c) simultaneous medial widening of pterygoids and dorsoventral convergence of pterygoids and basisphenoid produce a "classical" transitional series with gradually narrowing interpterygoid vacuity and reinforcing akinetic palate, in which "early basal" turtles, "advanced basal" turtles (such as *Heckerochelys romani*), "early Cryptodira" (such as Xinjiangchelyidae) and "advanced Cryptodira" are successive stages. The growth of the bony sheet on the medial edge of the posterior part of the pterygoid forms a flooring under the canalis caroticus internus and under the cavum acustico-jugulare in Cryptodira. The foramen carotico-pharyngealis forms when the two sheets (anterior and posterior) do not meet each other, leaving a gap at the level of a branching point of the internal carotid artery. Prominent basisphenoid tubercules, considered an autapomorphy of *Proganochelys quenstedti*, can be homologized to "basisphenoid pits" of more derived Mesozoic turtles through a simple flattening of the basisphenoid. In the same way, a single basioccipital tubercule corresponds to a nameless bulge on the ventral surface of basioccipital of more derived Mesozoic turtles, but not to a paired tuberculum basioccipitale.

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INTRASKELETAL HISTOVARIABILITY OF *CHELYDRA SERPENTINA*

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Chelydra serpentina is a large, extant freshwater snapping turtle native to North America. It grows rapidly during the first two years after hatching, then undergoes slow, protracted growth thereafter. Large adults exhibit a reduced plastron which aids in parasagittal terrestrial walking. Here we aim to describe the limb and girdle intraskeletal histovariability of one wild *Chelydra serpentina* and propose osteohistological correlates that reflect the organism's rapid growth and life history. Medullary remodeling of primary tissue obscures the highest proportional cross sectional area of girdle elements like the ischium, pubis, coracoid, and scapula. Compact coarse cancellous bone (CCCB) is present adjacent to the medullary cavity in stylopodial elements, suggesting that they underwent substantial morphological change during ontogeny. Zeugopodial elements, like radii and fibulae, exhibit the highest relative proportion of primary cortical tissue due to a lower proportional degree of medullary enlargement. Five to six growth marks are present throughout most appendicular elements, and the largely unremodeled zeugopodial elements show a seventh mark deep within the cortex, interpreted as a neonatal hatching line. The innermost primary cortical tissue of stylopodial elements exhibit loosely organized lamellar bone that locally grades into woven bone. The relatively rapid cortical deposition implied by this disorganized tissue is consistent with what is known of *C. serpentina*'s rapid initial posthatching growth. From mid to outer cortex, the tissue gradually transitions to organized lamellar bone with sparse primary osteons, again consistent with *C. serpentina*'s late- ontogeny reduction in growth rate. Regions adjacent to the glenoid and acetabular fossae consistently exhibit notable changes in the orientation and density of Sharpey's Fibers from inner to outer cortex. These changes coincide with the aforementioned period of rapid growth, suggesting that they may reflect a mass-dependent shift from sprawling to semi-erect posture. The outermost regions of all elements consist of nearly avascular lamellar tissue, making it difficult to identify the distinct outer cortical layer (OCL) typically used to interpret end-ontogeny growth cessation. These findings demonstrate that rapid testudine growth and its biomechanical accommodations impart osteohistological correlates that could readily fossilize, allowing for their study over geologic time.

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QUANTIFYING SHELL PATTERNING HELPS IDENTIFY SPECIES OF TRIONYCHIDAE

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Soft-shelled turtles (Trionychidae) display characteristic pits and ridges, or "sculpturing", on the bony carapace. Variation in the pattern of sculpturing may be useful in classifying fossilized shell fragments. However, while past attempts were able to discern qualitative differences in certain best-case scenarios, most early uses of sculpturing traits have been reevaluated as unreliable in the face of intraspecific variation. The potential of sculpturing to contain consistently reliable, quantitative, taxonomically informative traits remains underexplored. Here, we revisit this idea by quantifying trionychid shell patterning with topographic measurement techniques more commonly applied to nonhomologous quantification of mammalian teeth. We assess potential sources of variation and accuracy of these metrics for species identification. Carapaces of extant specimens used in this study included members of the species *Apalone ferox*, *Apalone spinifera*, and *Amyda cartilaginea* and were obtained from the herpetology collections of the Florida Museum of Natural History. *Amyda cartilaginea* and *Apalone* spp. were chosen to represent a relatively easy test of discriminatory power between two distantly related genera likely to have evolved detectable differences in sculpturing. In contrast, the congeners *A. ferox* and *A. spinifera* have qualitatively similar sculpturing and were used to explore the limits of our approach. 3D scans of shells were systematically sampled to create digital "fragments" of consistent size, known identity, and known position on the carapace. The external surface of each fragment was quantified using three topographic measurements from the molaR package in RStudio: the Dirichlet Normal Energy (DNE), Relief Index (RFI), and Occlusal Patch Count Rotated (OPCR). A nested MANOVA suggests there is significant variation at the species, individual, and carapace location levels of analysis. Additionally, linear discriminant analysis (LDA) correctly predicts a sample's species identity from DNE, RFI, and OPCR approximately 75% of the time. This result suggests there is measurable and differing variation in shell sculpturing patterns among species and individuals. These promising results indicate that topographic measures may provide a method for identifying shell fragments that are currently identifiable only as Trionychidae indet. Future work should further explore the utility of this approach in additional species, as well as accounting for ontogenetic changes in sculpture pattern.

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A NEW SKELETON OF *CHELYDROPSIS* (CHELYDRIDAE) FROM THE UPPER MIOCENE OF HÖWENEGG (SOUTH GERMANY)

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Höwenegg is a late Miocene fossil Lagerstätte site in South Germany. Its faunal assemblage is considered to be of Vallesian age (MN9 biozone). Numerous remains of vertebrates, invertebrates and plants have been excavated from the site during the past decades. The vertebrate remains include numerous chelonian skeletal remains as well. At least four cryptodiran clades (Trionychidae, Chelydridae, Geoemydidae, Testudinidae) of tortoises and freshwater turtles have been reported from the Höwenegg assemblage, representing one of the most diverse Neogene chelonian fauna of Central and Northern Europe. Among the remains of chelydrid freshwater turtles an almost complete skeleton is found. As the contact between the postorbital and the maxilla excludes the jugal from the orbit, the specimen can be attributed to the genus *Chelydropsis*. The specimen is exposed ventrally, showing the skull, the plastron, the limbs and the tail in a nearly anatomical position, suggesting minimal transportation after the ground contact of the carcass. The completeness and excellent preservation of this specimen provides new information on the taxonomic composition of the genus *Chelydropsis*. The Höwenegg *Chelydropsis* specimen revealed characters referable to other described species of chelydrids from the middle and upper Miocene of Eastern and Central Europe, including *Chelydropsis murchisoni*, as well as its included invalid taxa (*Chelydra allingensis*, *Chelydropsis carinata*, *Chelydropsis murchisoni staeschei*, *Macrocephalochelys pontica*, and *Trionyx sansaniensis*). Based on the broad anterior lobe and entoplastron, the Höwenegg specimen can be provisionally referred to *C. murchisoni*, a conclusion that is consistent with the known chronostratigraphic middle Miocene–Early Pliocene distribution of this taxon.

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THE ERYMNOCHELYINI (PLEURODIRA, PODOCNEMIDIDAE) FOSSIL RECORD OF THE DEMOCRATIC REPUBLIC OF CONGO

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The lineage of the podocnemidid pleurodiran turtles Erymnochelyini, of African origin, is known from the Late Cretaceous. However, no member of this group has been defined at pre-Eocene levels. The extant *Erymnochelys madagascariensis* is the only representative of Erymnochelyini that is part of the current biodiversity. Knowledge about many of the Erymnochelyini representatives has improved remarkably throughout the last decade, through the description of new species, as well as new genera. On the one hand, the genus *Eocenochelus*, which groups three species identified in the Eocene record of Europe (the early Eocene *Eocenochelus lacombiana*, the middle Eocene *Eocenochelus eremberti*, and the late Eocene *Eocenochelus farresi*), was established in 2007. On the other hand, the oldest genera of Erymnochelyini currently defined for the African record have been proposed in 2021: the early Oligocene *Shetwemys* (known through the Egyptian species *Shetwemys fajumensis*) and the early Miocene *Apeshemys* (known through the Egyptian species *Apeshemys aegyptiaca*). Two other species are identified for Erymnochelyini, both defined at late Miocene sites: *Kenyemys williamsi* and *Turkanemys pattersoni*. Both species are recognized at both late Miocene and Pliocene levels, being exclusive to the Kenyan fossil record. Erymnochelyini material with uncertain systematic attribution is identified in several Neogene areas of Africa. Among them, this lineage is represented in the Democratic Republic of Congo. However, only the presence of *Erymnochelys* sp. has been referred to in the fossil record of that country, based on scarce material attributable to Erymnochelyini. Abundant specimens from the Democratic Republic of Congo, including well-preserved cranial material, belonging to several individuals, are recognized. All of them are compatible with a single species. Its attribution to the genus *Erymnochelys* cannot be supported. The Erymnochelyini material from the Democratic Republic of Congo is here analyzed in order to establish if the paleobiogeographic and/or biostratigraphic distribution of a previously defined taxon is increased, or if it is attributable to a new form.

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THE EXCEPTIONALLY WELL-PRESERVED FOSSIL REMAINS OF A NEW SPECIES OF *TESTUDO* FROM THE LATE MIOCENE OF ROMANIA

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Testudinidae is a successful clade with a wide global distribution. Its fossil record is known from the lower Eocene. These reptiles represent the only group of terrestrial turtles living today. The first defined testudinid was the extant *Testudo graeca* Linnaeus, 1758, a form of relatively small size that lives in southern Europe, northern Africa, and the Middle East. The genus *Testudo* Linnaeus, 1758 was employed, during more than two centuries, to group almost all members of Testudinidae. However, numerous extinct and extant genera are currently known. Today, the genus *Testudo* is generally identified as restricted to the lineage grouping *T. graeca* and the taxa closely related to it, and it is characterized by the presence of a hypo-xiphiplastral hinge. It is restricted to three extant species and to scarce extinct forms, being identified since the late Miocene. All the extinct taxa are exclusively known by postcranial elements, generally restricted to shell remains, several of them being identified by the partial shell of a single individual. Abundant remains of testudinids from the upper Miocene fossil site of Crețești 1, in the Vaslui County (Moldova, eastern Romania), are presented here. They are attributable to a single taxon. It corresponds to a member of *Testudo*, which differs from all the species defined up to now. A selection of seven well-preserved individuals is analyzed. These specimens not only preserve the shell, but also other axial and appendicular elements, some of them being articulated. Furthermore, the partial skulls and lower jaws of two of them are identified. The three-dimensional reconstruction of the cranial remains and of the neuroanatomy of this new form is presented.

REVISION OF THE LATE JURASSIC TURTLE *JURASSICHELON* (TESTUDINATA, THALASSOCHELYDIA) BASED ON NEW MATERIAL FROM NORTHWESTERN SWITZERLAND

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The thalassochelydian turtle *Jurassichelon* has a complex taxonomic history. The species *Thalassemys moseri* was initially coined for a few shell remains from the late Kimmeridgian of Solothurn (Switzerland). A specimen from the Tithonian of Oléron Island (western France) consisting of a cranium and anterior half of a shell was later referred to this species. This last specimen was subsequently scored in several phylogenetic analyses as '*Thalassemys*' *moseri*. However, both the validity of this species and the referral of the material from Oléron Island have been discussed by several authors in the past 30 years, including ourselves. One of the most recent studies on this question concluded that the material from Oléron Island should be assigned to a new genus and species, *Jurassichelon oleronensis*, without reconsidering the status of '*Thalassemys*' *moseri*. In a global review of thalassochelydian taxa, we concluded more recently that *Jurassichelon moseri* and *Jurassichelon oleronensis* were two closely related, but distinct taxa. Unfortunately, these studies failed to review the material from Oléron Island or to provide new fossil evidence to support their conclusions. In the present study, we provide a revision of the systematics of *Jurassichelon* based on a reassessment of the material from Oléron Island, including a CT scan of the cranium, and new material from the late Kimmeridgian of northwestern Switzerland, including sub-complete shells and a partial cranium. We confirm that *Jurassichelon moseri* and *Jurassichelon oleronensis* share cranial and shell features that distinguish them from other Thalassochelydia (*e.g.*, short and U-shaped triturating surface, well-developed lower temporal emargination, axillary process reaching peripheral 1). The new material provides new morphological evidence to clearly differentiate the two species of *Jurassichelon* (*e.g.*, morphology of the triturating surface, posterior extension of the vomer, outline of the foramen palatinum posterius, shape of lateral peripheral, absence of lateral plastral fontanelle) and documents part of the skeleton that were previously unknown. Finally, thanks to the CT scan, we can emend the original description of the Oléron Island cranium.

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RECENT ADVANCES IN MESOZOIC TURTLE PHYLOGENY

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New discoveries and detailed descriptions of key Mesozoic turtle taxa since the last Turtle Evolution Symposium held in Tokyo allow for novel insights into the global phylogeny of the group. I will provide a brief overview of these recent advancements in my presentation by reviewing the relevant literature as well as unpublished data. In addition, I attempted to integrate part of these data into published global datasets and expanded character/taxon sample by focusing particularly on Mesozoic stem turtles from Europe and Australia, as well as on pan-cryptodirans from Asia and South America. Unweighted parsimony analysis combined with a molecular backbone constraint yielded a generally well-resolved strict consensus tree. The topology has important implications for the contentious distribution of meiolaniforms and global turtle paleobiogeography. Sichuanchelyids are found more crown-ward than meiolaniforms, as are helochelydrids, which form a paraphyletic grade with Compsemydidae (notably including *Kallokibotion bajazidi*), Pleurosternidae, and baenids. Paracryptodira is, therefore, not recovered in its traditional sense, but missing data and minimally longer most parsimonious trees when monophyletic preclude drawing conclusions. Xinjiangchelyids and sinemydids are retrieved within pan-cryptodires, in contrast to some recent phylogenies placing them outside the crown-group of turtles. The morphology of their cervical vertebrae, among others, share unique features with cryptodires. The unique plastral morphology of *Manchurochelys manchoukuoensis* from the Early Cretaceous Jehol Biota, as revealed by a recently described specimen, places this species as the sister taxon of the bizarre clade of spiny turtles *Sinemys* spp. Sinemydidae furthermore includes *Dracochelys bicuspis* and *Ordosemys leios*. The sister group of this clade includes *Hangaiemys hoburensis*, *Judithemys sukhanovi*, and *Jeholochelys lingyuanensis*, among others. This dichotomy within Asian-North American Cretaceous stem-cryptodires corresponds to their pre-cladistic classification into "Macrobaenidae" and "Sinemydidae," which, however, has never been reproduced in phylogenies. Finally, the addition of new data resulted in a better stratigraphic fit for the phylogeny of protostegid marine turtles compared to previous works.

FROM LATE JURASSIC PLEUROSTERNIDAE TO EARLY CRETACEOUS BAENIDAE: A JOURNEY THROUGH CRANIAL ANATOMY AND PHYLOGENY OF PARACRYPTODIRAN TURTLES

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Paracryptodira is a clade of freshwater turtles that lived from the Late Jurassic to Eocene of North America and Western Europe. The clade was initially considered to be one of the three primary groups of turtles along with Pleurodira and Cryptodira and to consist of the North American and European Pleurosternidae and the North American Baenidae. While the phylogenetic placement of Paracryptodira within Testudinata is still under debate, recent phylogenies suggest the clade may include Compsemydidae, Helochelydridae, and *Kallokibotion bajazidi* as well. Although paracryptodiran fossils have been described since the 19th century, plenty of material remains poorly understood. Late Jurassic and Early Cretaceous pleurosternid shell material recently received greater attention, but the cranial anatomy of several taxa historically lacked detailed insights. Similarly, while about ten derived baenids skulls have been published over the last two decades, only one basal baenid benefited from a detailed study during that period. As a better understanding of paracryptodiran cranial anatomy is crucial for more confidently assessing the phylogenetic relationships of that clade, we have described a series of skulls over the course of the last two years using micro-computed tomography, in particular the putative pleurosternids *Uluops uluops* from the Tithonian of Wyoming and *Pleurosternon bullockii* from the Berriasian of the United Kingdom, and the putative basal baenids *Arundelemys dardeni* from the Aptian–Albian of Maryland, *Lakotemys australodakotensis* from the Berriasian–Valanginian of South Dakota, and *Trinitichelys hiatti* from the Aptian–Albian of Texas. Our initial analyses retrieve *Uluops uluops* as the most basal pleurosternid. The basipterygoid process is interpreted as a symplesiomorphy with *Pleurosternon bullockii*. The latter two taxa share with helochelydrids the presence of anterior tubercula basioccipitale on the parabasisphenoid. *Arundelemys dardeni*, *Lakotemys australodakotensis*, and *Trinitichelys hiatti* share an interesting combination of typical pleurosternid features, such as a relatively large exposure of the prefrontal on the skull roof and a well-developed external process of the pterygoids, and features typical of derived baenids, such as the presence of a posterior elongate contact of the pterygoid with the basioccipital and the absence of a basipterygoid process. *Uluops uluops* and *Lakotemys australodakotensis*, the most basal members of pleurosternids and baenids, respectively, possess a canal for the palatine artery, suggesting the independent loss of the palatine artery at the base of Pleurosternidae and Baenidae.

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THE LATEST MIOCENE TO PLIOCENE FOSSIL TURTLES, TESTUDINIDAE AND GEOEMYDIDAE, FROM MAKRYGIALOS, THERMAIKOS GULF, NORTHERN GREECE

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Although the fossil turtle fauna of Makrygialos, on the west side of the Thermaikos Gulf in Northern Greece, has been known for almost two decades, it has not been studied so far in detail. Over the last 5 years, we have conducted systematic fieldwork and exploration, focusing on the discovery and recovery of fossils in the coastal broader area of Makrygialos. There, fluvial deposits of late Miocene–Pliocene age of the Makrygialos Formation are exposed by tectonic uplift and sea erosion in coastal slopes several meters high, and they are correlated with the coeval fossiliferous deposits in the east side of the Gulf. The size and weight of the giant tortoise specimens and the coastal landscape pose important challenges in the discovery, excavation, transportation, and preparation of these fossils. Eleven fossil turtles have been found so far, eight of which have been collected, on the outcrops of the beaches of Makrygialos and Agiannis. Four of these specimens are terrestrial giant tortoises that we attribute to the species *Titanochelon* cf. *bacharidisi* (we describe three of these herein), two of them are small tortoises identified as *Testudo graeca* and *Chersine hermanni*, and the last two are freshwater turtles referred to the genus *Mauremys*. The fossil turtle fauna of Makrygialos is probably the richest and most diverse in Greece, as in no other Greek locality more than three species of turtles have been found. The occurrence of *Testudo graeca* is the first confirmed occurrence of this species on the west of Axios river, suggesting that the environmental conditions were different in the past. The information obtained by the giant tortoises of the study area, in combination with those found on the east side of Thermaikos Gulf, leads us to the conclusion that the bay in the past was a large plain with great diversity of turtles that occupied many different niches.

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THE TOPOGRAPHY OF DIET: USING MOLAR TO PREDICT TURTLE FEEDING HABITS

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Dental complexity is an important source of data for resolving the diets of extinct and extant animals. Software packages like MorphoTester and molaR utilize 3D models of extinct and extant animal dentitions to produce an Orientation Patch Count Rotated (OPCr) value, which measures the surface complexity of a particular 3D model. In general, higher OPCr values correlate with more herbivorous diets. OPCr has thus far only been used to predict the diets of animals with teeth, including primates and crocodilians. The 'beak' morphology of edentulous taxa, including monotremes and avian dinosaurs, has been examined to better understand the relationship between overall beak structure and diet, but no edentulous group has been analyzed using OPCr. Complicating matters is the fact that the actual triturating surface in most edentulous groups is keratinous, and keratin tends not to fossilize. In this study, we used OPCr to determine the complexity of keratinous rhinothecae and the underlying bones of the skull and mandible across nine extant turtle families and five dietary categories. We then compared these values to determine if the complexity of keratin and the complexity of bone correlate, as well as if correlations exist between bony rhamphotheca surface complexity and animal diet. Results indicate that the correlation between bony and keratinous rhamphothecae surface complexity varies across diet rather than clade. Additionally, we find that — much like the increased complexity of herbivore teeth — keratin OPCr increases with more herbivorous diets, and that herbivorous turtles from different clades (*e.g.*, Testudinidae, Emydidae) have convergently evolved increased beak complexity. These promising results suggest we can use OPCr to more confidently predict the morphology of keratinous rhinothecae in extinct turtles, as well as other extinct edentulous clades, such as dicynodont therapsids.

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HOW DID LARGE TEMPORAL CHANGES AFFECT THE EVOLUTION OF TORTOISES (TESTUDINIDAE)?

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Great environmental changes may affect directly or indirectly the survival capability of a variety of organisms. Testudinidae is, among living species, the most diverse family of terrestrial chelonians within the whole order (Testudines). However, it is interesting to highlight that the number of extinct species overcome the extant ones. In order to understand better how the diversification process of this family occurred, this work utilised the PyRate software, which estimates both the preservation and diversification processes in a continuous time interval. For such, the software used a list of fossil occurrences obtained from the Paleobiology Database in addition to a list of extant species obtained from Catalogue of Life. This way, the probability of the ancestral clade having resulted in these species during its evolutionary history was inferred. The resulting curve showed a great rise in the extinction rate starting 6 million years ago. This increase is likely to be related to the drop of atmospheric CO_2 all over the globe at the end of the Miocene, about 8 to 6 million years ago. It is believed that this event led to the turnover of the vegetation composition seen on the fossil record of low-latitude warmer areas of the planet, including North and South America, East Africa and Pakistan, with plants that used C3 metabolism giving way to C4 plants. In terms of landscape, grasses and herbal vegetation, such as savannas, started dominating from that point on. As a group composed mostly by herbivores, we believe that testudinids responded to these changes by suffering a great loss in diversity, where only the species that were capable of adapting to new food sources or that were not strict herbivores survived. This has been reported for other animal groups in that period, where grazers were more successful than browsers. Likewise, it would be interesting to take a closer look at the feeding habits of the late Miocene fossil tortoises to better understand if and how global vegetation changes may have shaped the macroevolution of this group.

A NEW BAENID CRANIUM FROM THE JUDITH RIVER FORMATION REVEALS THE INNER EAR MORPHOLOGY OF A CAMPANIAN BAENID

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A partial baenid cranium was recently recovered from an undescribed outcrop in the lower half of the Judith River Formation in Valley County, Montana. Turtle taxa from Judith River Fm. consist mainly of baenids, trionychids, and adocusians, while other reported taxa include a diverse vertebrate fauna of chondrostean and osteichthyan fishes, salamanders, lizards, champsosaurs, crocodiles, pterosaurs, chasmosaurine and centrosaurine ceratopsians, pachycephalosaurs, ankylosaurs, and several mammals. Badlands Dinosaur Museum (BDM) 004 is a well-preserved partial cranium including the posterior neurocranium, basicranium, and otic region. It is diagnosed as a baenid by the presence of basioccipital-pterygoid contact and foramen posterior caroticus canalis internus that is approximately halfway along the pterygoid-basisphenoid suture, and (symplesiomorphically) a small processus trochlearis oticum. It has a point contact between the pterygoids, prefrontals with small dorsal lappet, open sutures in the adult skull, parietals larger than frontals with a parieto-frontal suture that is concave posteriorly, with large orbits as in known *Stygiochelys estesi* from the Maastrichtian Hell Creek Formation. In a phylogenetic analysis, BDM 004 fell on the branch of *S. estesi* and did not differ in any character states, supporting a referral to this species. Microcomputed tomographic (microCT) scans revealed morphology of the middle and inner ear that has been minimally described in baenids. Semicircular canals of BDM 004 are consistent in dimensions to those of other aquatic turtle taxa, including anterior and posterior semicircular canals (ASC and PSC) that are shorter than the common crus and diverge from each other at an angle of less than 90°. The ASC and PSC are robust as in other aquatic turtles and relatively similar in shape and width, although the ASC is slightly wider. However, Principal Components Analysis (PCA) of labyrinthian dimensions separated BDM 004 from all other published Testudines in morphospace. The aspect ratio of the superior labyrinth to labyrinthian width is moderate, within the range of other aquatic turtle taxa. Medially, the intact columella begins with a posterodorsally flared basis columella before becoming more cylindrical and taller than it is wide. It courses across the middle ear in a slight arc that is concave anteriorly and terminates in an anteroposteriorly-flattened expansion. Its morphology is generally consistent with published descriptions of other baenid columellae. The incisura columella auris is spherical and closed. This study adds to the understanding of baenid middle and inner ear morphology and extends the temporal distribution of *Stygiochelys* into the Campanian fossil record.

TURTLE DIVERSITY AND EVOLUTION IN SOUTHERN SOUTH AMERICA

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Argentina has one of the most complete and continuous fossil records of turtles worldwide. In the present work we explored the diversity of turtles and tortoises of Chubut Province, Argentina, located in southern South America. Our analysis suggests that the fossil record of turtles of this territory is the richest, most diverse, and continuous not only from the country, but on a continental scale. More than 241 occurrences of extinct turtles are documented for Chubut spanning from the Toarcian (Early Jurassic) to the Tortonian (late Miocene). In this work we compiled all published and unpublished information about the extinct turtles from this territory and placed them in a comprehensive and detailed chronostratigraphic context. During this revision we were able to fill some gaps in the fossil record, to add new anatomical information about known taxa, to explore new geographical areas, and to present some important highlights such as the record of the oldest pan-chelid turtles of the world. Furthermore, we discuss the changes in the diversity and faunal turnovers of the various turtle clades in this region during the last 180 million years and across important events during the Cretaceous–Paleocene and Oligocene–Miocene boundaries.

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THE LIMB MUSCULATURE OF THE TRIASSIC TURTLE *PROTEROCHERSIS* (TESTUDINATA, PROTEROCHERSIDAE) SUGGESTS CHANGES IN HABITAT ADAPTATION IN THE ONTOGENY OF EARLY TESTUDINATES

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Proterochersidae belong to the oldest true turtles (Testudinata) as evidenced by their plesiomorphic features. Therefore, they are a good model for locomotory adaptation in the earliest turtles. Triassic turtles in general, proterochersids in particular, show a mosaic of characteristics suggesting either terrestrial or aquatic ecology which historically led to disagreements about their habitats. This is reflected by their limb morphology. The rigid structure of the turtle trunk involves the incorporation of most of the body axial skeleton into the shell, as a result of which the driving forces are generated almost exclusively by the limbs in any environment. We examined muscle scars on the shell and limb bones in order to reconstruct the locomotory musculature of *Proterochersis porebensis* (Norian of Poland, collection housed in the Institute of Paleobiology, Polish Academy of Sciences). We observed that the attachment sites for the forelimb muscles mm. latissimus dorsi, deltoideus, coracobrachialis, suprascapularis, supracoracoideus, pectoralis, triceps brachii, biceps, and brachialis inferior, as well as attachment sites for the hind limb muscles mm. iliofemoralis, puboischiofemoralis internus, puboischiofemoralis externus, flexor tibialis internus, flexor tibialis externus, ischitrochantericus, and femorotibialis expanded in respect to other turtles. We observed stronger and more developed protractors, which usually show more intense activity during swimming compared to walking. Among the extensors and retractors, the muscles used during swimming are also slightly stronger and more developed. This suggests a capability for efficient water locomotion by walking on the bottom but not exclusively aquatic or terrestrial behavior. However, the water adaptations are more pronounced in younger individuals. The older ones have similar adaptations to today's terrestrial turtles. As in other turtles, most of the forelimb muscles were likely involved in respiratory movements in association with the upper arm. Two posterior muscles, m. obliquus abdominis and m. rectus abdominis, preserved the ancestral condition and probably also were involved in respiration, despite the fusion of the pelvis with the shell (change of volume through isometric contraction). The pelvis is characterized by a particularly strong attachment to the plastron. The results of biomechanical research will be presented elsewhere.

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SHELL HISTOLOGY OF *PROTEROCHERSIS POREBENSIS*

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Shell histology of *Proterochersis porebensis* (Norian of Poręba, Poland) was studied based on specimens representing various individual sizes and shell elements (materials housed in the Institute of Paleobiology, PAS). Regardless of origin (endoskeletal-derived costals and neurals; gastralia-derived plastron; pectoral girdle-derived nuchal bone, epiplastra, and entoplastron; osteodermal peripherals and carapacial mosaic), the ossifications exhibit a rather homogenous microstructure — well developed spongiosa surrounded by external and visceral cortices. Unlike most turtles (but similar to that found in the costals of *Stupendemys geographicus* and *Trapalcochelys sulcata*, and the neurals of *Condorchelys antiqua*), the visceral cortex of carapacial bones incorporates interwoven structural fibers, even in large and thick specimens, suggesting an unusually thick integument. A larger variability is observed between specimens of different sizes, with porosity generally decreasing with size. However, in some larger specimens trabeculae have an osteoporotic appearance, either physiologically or due to taphonomic factors. In general, younger individuals exhibit shell microstructure resembling aquatic turtles (in agreement with the previous reports of turtle-like bromalites with fish remains from Poręba) while larger individuals appear more terrestrial; note, however, that the correspondence between the shell microstructure and habitat is not strict. Previous reports of varied occurrences of shell ankylosis (fusion) regardless of individual size are confirmed histologically: even in small individuals the sutures may become completely obliterated by remodeling, while in some large individuals normally-structured sutures are present. Likewise, the presence of a carapacial mosaic is confirmed, the elements are interconnected by normal sutures and are not an effect of fracturing. Although differences in the relative timing of ankylosis could be explained by sexual dimorphism or extreme intraspecific variability, the observed lack of bimodal distribution of terminal shell sizes or clear disjunction between the shell size and morphological maturity (owing to the significant impact of suture obliteration on growth efficiency in recent species) seem to render those hypotheses unsatisfactory. Because of that, another hypothesis is here considered: reformation of sutures via physiological bone fragmentation due to localized destruction and reossification of bone tissue. Similar processes of bone sequestration and reformation are employed in modern turtle taxa in cases of severe shell damage due to trampling or wildfires. In that context, the presence of irregular, asymmetric carapacial mosaic in *Proterochersis* spp. (and, possibly, *Chinlechelys tenertesta*) may thus either reflect initial shell composition, be an artifact of improper shell partitioning (as observed in some recent cases of shell damage regeneration), or a combination of both.

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FUNCTIONAL MORPHOLOGY OF THE STRIKE MODES OF THE *CHELODINA* (TESTUDINES: CHELIDAE) EXAMINING THE MUSCULAR AND SKELETAL MORPHOLOGY

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Over the past 20 years I have developed phylogenetically informative morphological characters related to feeding behavior within *Chelodina*. These characters in the *Chelodina* are largely novel, though there are some similarities with *Chelus*, *Hydromedusa* and several forms of softshell turtles. The *Chelodina* are currently divided into 3 subgenera — *Chelodina*, *Chelydera*, and *Macrochelodina* which differ in their method of feeding behavior. *Chelodina* (*Chelodina*) is not a strike-and-gape predator, but instead have long, highly dexterous necks to poke in among underwater debris for invertebrates. The cervical vertebrae have flattened platelike transverse processes allowing the attachment of enlarged inter cervical musculature for control of the head and neck movement. The *Macrochelodina* are phylogenetically closely related to *Chelodina* (*Chelodina*) but are a genuine strike-and-gape predator. Their necks have enlarged horizontally projecting transverse processes for stiffening the neck during the strike, they also have enlarged neurals and expanded rib heads/ neural arches permitting the passage of enlarged longissimus dorsi muscles, the primary muscle used for the strike. This is similar to, though not homologous with, that seen in *Chelus*. The *Chelydera* are also strike-and-gape predators and have similar, though larger, transverse process morphology to *Macrochelodina*. However, the neural/ rib arch is not enlarged, instead it is the longissimus colli muscles that are enlarged in combination with the retrahens captious collique muscles, the two primary muscle groups powering the strike. In addition, the longissimus colli muscles do not insert into the sacral vertebrae region, but are instead attached by tendons to the anterior of the pubis for a stronger anchor point, a feature not found in any other turtle. All *Chelodina* fall into one of these three patterns of neck/ shell morphology which is also phylogenetically supported. The oldest lineage in the *Chelodina* is the *Chelydera* with its oldest fossil *Chelydera alanrixi* at 52 myo, however its ghost lineage is twice that, leading to the possibility that the long neck is the ancestral condition of the Chelidae, a point that would suggest that the various short necked lineages evolved independently from a number of ancestral long necked forms.

A CHELONIOID SEA TURTLE FROM THE UPPER CRETACEOUS NON-MARINE DEPOSITS OF SOUTHERN FRANCE?

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The Upper Cretaceous non-marine deposits of southern France are rich in fossil turtles. This turtle fauna consists of the pleurodiran Bothremydidae and Dortokidae, and the basal testudines Helochelydridae and Paracryptodira. The Campanian–Maastrichtian Bastide Neuve locality, Fox Amphoux, Var is the type locality of the bothremydid turtle *Foxemys mechinorum*. Turtle remains are abundant and diverse in this locality; in addition to pleurodiran turtles, the helochelydrid *Solemys gaudryi*, and an eucryptodiran turtle are also present. This third taxon, previously mentioned as Eucryptodira indet. or Chelydroidea, consists of isolated shell elements (a nuchal with associated peripheral 1, a costal, several additional isolated peripherals and a hypoplastron). The morphology of the hypoplastron, with a short and wide bridge, a loose carapace/plastron connexion and medially connected right and left abdominal scutes, is reminiscent of some turtles with reduced plastron such as Macrobaenidae; whereas the bow-shaped nuchal with a large cervical emargination that is bordered by the peripherals 1, the presence of central and lateral fontanelles on the plastron and the hypoplastron not sutured to its counterpart more resemble some primitive Chelonioidea, such as *Toxochelys*. Importantly, the ventral surface of the nuchal bears a sagittal ridge, that probably serves as the pedestal for articulation with the 8th cervical vertebra. This character is considered a synapomorphic feature of chelonioids. To test the phylogenetic hypotheses, a parsimony analysis was performed that placed this turtle within Chelonioidea. The turtle remains from the Bastide Neuve locality are associated with a rich non-marine vertebrate fauna. The fossils occur in sandstones and siltstones of fluvial origin deposited in the floodplain. The vertebrate fauna consists of hybodont sharks, bony fishes (Lepisosteidae and coelacanth), squamates, crocodiles (*Acynodon* and *Allodaposuchus*), turtles, pterosaurs (azhdarchids), birds (enantiornithines and the giant flightless bird *Gargantuavis*) and various dinosaurs: theropods (*Variraptor mechinorum*), sauropods (titanosaurs), ornithopods (*Rhabdodon*) and ankylosaurs. The occurrence of a chelonioid turtle in a non-marine environment is unusual, some hypotheses are proposed and discussed.

VARIATION IN THE EMBRYONIC DEVELOPMENT OF *PELODISCUS* AS A MODEL TO UNDERSTAND PROGRESSIVE CHANGES IN TURTLE EVOLUTION

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Natural selection operates on within-population anatomical variation. It involves the differential survival and reproduction of individuals due to differences in phenotype. Developmental variation is a major source for natural selection as the general body form is established. Ontogenetic variation, as such, is a major contributor to evolutionary fitness. Traditional embryonic 'staging tables', however, were not able to trace character variation in detail, such that it could be used to inform hypotheses on evolutionary fitness. Here we study within-species variation of the Chinese soft-shelled turtle *Pelodiscus sinensis*, which is a model species in experimental biology and one of the most frequently examined turtle species in embryonic and anatomical studies. In total, 563 embryos of different ages were incubated at a stable temperature of 30°C. We recorded 16 metric measurements and the mass of each embryo. Moreover, by using the "Standard Event System to Study Vertebrate Embryos" (SES), we coded the developmental timing of 104 discrete external ontogenetic characters. We found a very fluent nature of character appearance through embryogenesis and describe a methodology on how to quantify developmental variation when establishing a traceable embryonic staging system in general. As for *P. sinensis*, this pattern clearly differs from the standardized 'staging table' used for this species in the literature. Moreover, we show that within *P. sinensis*, embryonic variation is even larger than variation among all other turtles previously examined with standardized 'staging tables'. These observations should be considered when drawing conclusions about embryonic changes and molecular development through turtle evolution. Finally, our documentation illustrates which metric or discrete embryonic characters vary the most. They are interpreted to be particularly prone to evolutionary selection and might provide a guide to choose for adult correspondences of these characters in phylogenetic analyses.

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