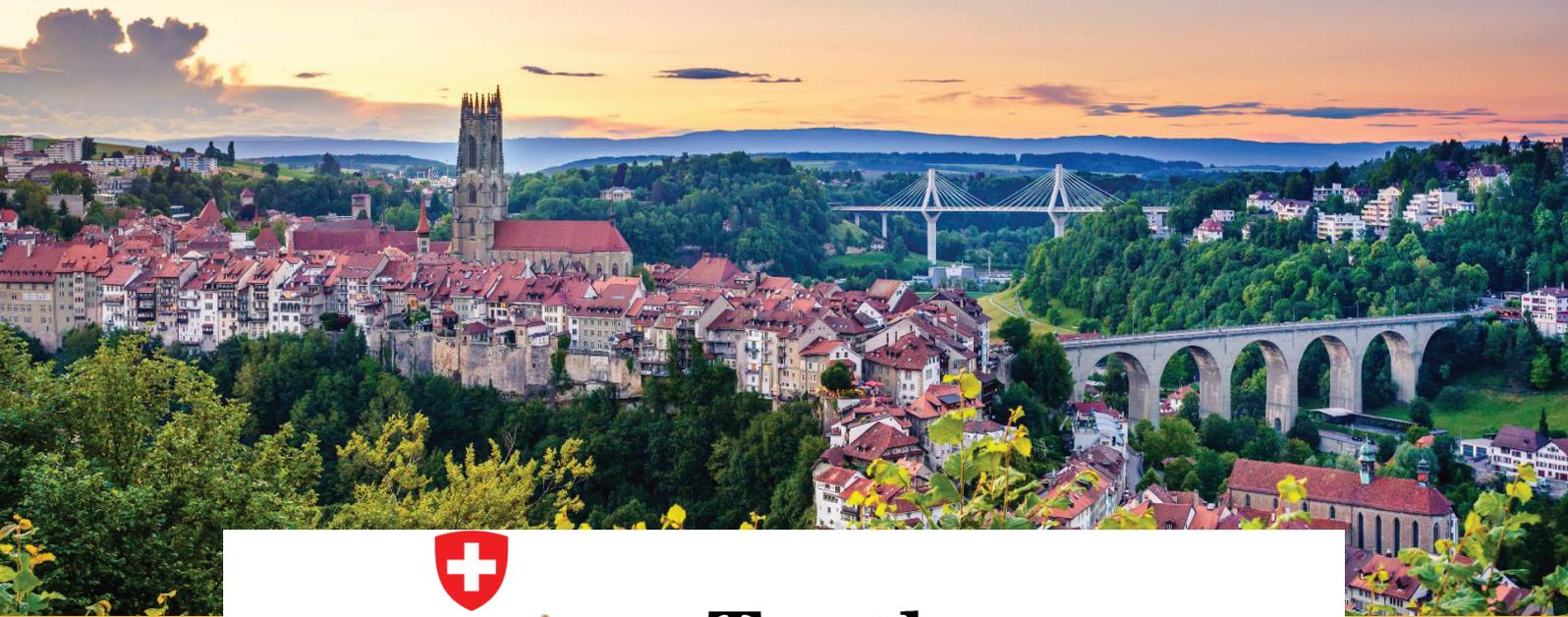


# Abstracts



## Turtle Evolution Symposium **2024**

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UNIVERSITÉ DE FRIBOURG  
UNIVERSITÄT FREIBURG

JURASSICA

**JUNE 26–29, 2024**

**FRIBOURG, SWITZERLAND**

**EDITORS**

Serjoscha W. Evers, Walter G. Joyce, Yann Rollot



**Turtle Evolutionary Symposium**  
**June 26-29 2024, Fribourg, Switzerland**

**Organizing Institutions**

Department of Geosciences, University of Fribourg, Switzerland (host institution)

JURASSICA Museum, Porrentruy, Switzerland (co-host)

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**Excursion**

Jérémy Anquetin (JURASSICA Museum & University of Fribourg)

**Financial Support**

Department of Geosciences, University of Fribourg, Switzerland

JURASSICA Museum

Swiss National Science Foundation

**Meeting Website**

<https://events.unifr.ch/tes2024/>

## **New chelonian cranial remains from Moghra: Early Miocene, Northwestern Desert, Egypt**

Mohamed K. **AbdelGawad**<sup>1</sup>, Martin **Pickford**<sup>2</sup>, Ahmed N. **El Barkooky**<sup>1</sup>, Mohamed A. **Hamdan**<sup>1</sup>

<sup>1</sup>Geology Department, Faculty of Science, Cairo University, Cairo, Egypt, mkabdelgawd@cu.edu.eg; <sup>2</sup>Sorbonne Université, Paris, France.

The Moghra Formation, Qattara Depression, Egypt, is one of the most important early Miocene fossil sites in Africa, especially North Africa. It is characterised by its high diversity and abundance of vertebrates, both mammalian and non-mammalian. The Moghra Formation consists of a series of interbedded shale-sandstone units with several ichnofossil assemblages comprising *Ophiomorpha*, *Thalassinoides* and root systems of mangrove trees and there are many silicified tree trunks. Invertebrates are also common. The currently known Moghra chelonian assemblage comprises two families represented by five genera. The two families are Podocnemididae, represented by *Erymnochelys*, *Mogharemys*, *Latenemys* and *Lemurchelys*, and the Trionychidae which includes *Trionyx*. These five chelonian genera show diverse biogeographic relations. Some genera are known from Eocene-Miocene deposits in Eurasia, some are unknown in Asia, some are immigrants to Africa and arrived by crossing the eastern Tethys while others are endemic to Africa. The five genera indicate the presence of fresh to brackish water palaeoenvironments. The specimen described in this presentation is curated at the Vertebrate Palaeontology Laboratory, Geology Department, Faculty of Science, Cairo University (CUWM) Egypt. The specimen is a well-preserved, complete skull with vertical orbits that face antero-laterally, the premaxilla forms the antero-medial part of the triturating surface and the labial ridge that is the edge of the triturating surface. Preliminary studies indicate that the specimen represents a new genus of Podocnemididae.

### **Identification of laminae in the cervical vertebrae of Pelomedusoides**

Dias C. **Andrade**<sup>1</sup>, Thiago F. **Mariani**<sup>1</sup>, Ingmar **Werneburg**<sup>2</sup>, Pedro S. R. **Romano**<sup>1</sup>

<sup>1</sup>Federal University of Viçosa, Viçosa, Brazil, dias.andrade@ufv.br; <sup>2</sup>Fachbereich Geowissenschaften & Senckenberg Center for Human Evolution and Palaeoenvironment an der Universität Tübingen, Tübingen, Germany.

The nomenclatural basis for identifying anatomical components of the cervical vertebrae in turtles is still non-standardized and incomplete. With that in mind, we propose a preliminary identification of laminae in the cervical vertebrae of Pelomedusoides derived from the well-established nomenclature used for sauropod dinosaurs. This approach is based on a serial analysis to examine the appearance of the laminae along the neck, i.e., identifying their presence or absence, and the changes in length, height, thickness, and orientation. We established the anatomical demarcations using traceable landmarks and were able to identify seven types of laminae. Three of them are developed from the transverse apophyses: (1) the cranial centroapophyseal (ending at the cranial portion of the neurocentral suture), (2) the caudal centroapophyseal (extending to the caudal portion of the neurocentral suture), and (3) the prezygapophyseal laminae (ending at the prezygapophyses). Two other laminae emerge from the neural spine: (4) the spinoprezygapophyseal (extending to the prezygapophyses) and (5) the spinopostzygapophyseal (which ends at the postzygapophyses). Finally, (6) the epipostzygapophyseal laminae connect the epipophyses to the postzygapophyses and (7) the centrohypapophyseal lamina is a link between the hypapophysis and the caudal portion of the vertebral centra. The application of such anatomical nomenclature in the future can improve phylogenetic assessments of turtle interrelationship and morphofunctional adaptations of both living and extinct taxa.

## A new mature specimen of the Late Jurassic thalassochelydian turtle *Jurassichelon oleronensis*

Jérémy Anquetin<sup>1</sup>, Renaud Bourgeois<sup>2</sup>, Dorine Pesquet<sup>3</sup>, Irena Raselli<sup>1</sup>

<sup>1</sup>JURASSICA Museum, Porrentruy, Switzerland, jeremy.anquetin@jurassica.ch; <sup>2</sup>Université PSL – Ecole Pratique des Hautes Etudes, Paris, France; <sup>3</sup>Géosciences Rennes – UMR 6118, Université de Rennes, Rennes, France.

The holotype and hitherto only known specimen of the Late Jurassic turtle *Jurassichelon oleronensis* figures prominently in most global phylogenetic analyses of fossil turtles scoring several thalassochelydians as terminal taxa. This is mostly due to the exquisite preservation of the material consisting of a sub-complete cranium, the anterior half of a shell, and a series of four cervical vertebrae. Here, we describe a new specimen from the type locality (headland of Chassiron, Oléron Island, France) that is very similar to the holotype in terms of preservation. It consists of a nicely preserved cranium missing only the skull roof, the associated complete right mandibular ramus, a near-complete cervical series, a partial shell, and elements of the girdles and limbs. Not only does this new specimen allow us to complete the description of *Jurassichelon oleronensis*, but it also documents a more advanced ontogenetic stage revealing that this species retains juvenile characters late during ontogeny. Adults of *Jurassichelon oleronensis* are notably characterized by the closure of costo-peripheral and lateral plastral fontanelles, a sutural contact between the carapace and plastron and along the midline of the plastron, a quadrangular nasal, the presence of a vomer-pterygoid contact, a posteroventral covering of the basioccipital by the parabasisphenoid, and a more complete ossification of the condylus mandibularis of the quadrate and labial ridge of the maxilla. In addition, the mandible is remarkable in having a low labial ridge, a strong lingual ridge, and a wide, pennate-shaped triturating surface in between.

## Cranial osteology of the Campanian (Late Cretaceous) baenid turtle *Plesiobaena antiqua*

Scott Bellotti<sup>1</sup>, Donald B. Brinkman<sup>2</sup>, Walter G. Joyce<sup>1</sup>, Serjoscha W. Evers<sup>1</sup>

<sup>1</sup>Department of Geosciences, University of Fribourg, Switzerland, scott.bellotti@unifr.ch; <sup>2</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, don.brinkman@gov.ab.ca; <sup>2</sup>Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.

The fossil record of the turtle clade *Baenidae* ranges from the Early Cretaceous to the Eocene. While initially widespread across North America during the Early Cretaceous, baenids later became confined to the western regions of the continent during the Late Cretaceous and Paleogene. Most late baenids form the clade *Baenodda*, which is characterized by a modified pygal region consisting of a broadened pygal and contribution of the fifth vertebral to the posterior margin of the carapace. Much effort has been invested into resolving phylogenetic relationships within this clade, but results were often inconsistent with each other or with external data, such as stratigraphic fit. The detailed description of the cranial anatomy of a select number of baenodda taxa based on micro computed tomography scans ( $\mu$ CT) more recently provided invaluable data that helped further resolve and stabilize the phylogeny of the group. The main aim of this contribution is to document and describe the cranial osteology of the baenid *Plesiobaena antiqua* based on  $\mu$ CT scans. The sample is unusually large, consisting of four crania and three mandibles collected from the Late Cretaceous (middle to late Campanian) Dinosaur Park Formation of Alberta, Canada. The detailed study of *Plesiobaena antiqua* is expected to yield particularly meaningful phylogenetic insights, as this taxon is currently thought to be the earliest known unambiguous representative of the baenodda subclade *Palatobaeninae*.

# **An imperfect watercolour: reassessing the enigmatic Brazilian pelomedusoid “*Podocnemis*” *brasiliensis***

Joaquin P. **Bogado**<sup>1</sup>, André E. P. **Pinheiro**<sup>2</sup>, Pedro S. R. **Romano**<sup>1</sup>

<sup>1</sup>Federal University of Viçosa, Viçosa, Brazil, jpbogadodiniz@gmail.com; <sup>2</sup>Rio de Janeiro State University, São Gonçalo, Brazil.

*Podocnemis brasiliensis* is an enigmatic species from the Upper Cretaceous Bauru Group of South-Central Brazil. Known only from an incomplete plastron (specimen MCT.R.214), it has been regarded as a *nomen dubium* by most authors, though some consider it a valid (albeit poorly defined) species, tentatively assigned to the genus *Bauruemys*. A new incomplete plastron (specimen FFP PG 218) is very similar to the type specimen, but preserves additional parts. Its discovery prompted us to revise the validity of the species. We investigated the characteristics that had been used to identify *P. brasiliensis* in the past, and ran morphometric analyses to quantitatively assess the variation of some key characteristics that were supposedly diagnostic. We scored a new terminal in a recent cladistic matrix focused on Pelomedusoides, based on the new specimen and the type. We found that many of the characteristics that had been used to identify “*Podocnemis*” *brasiliensis* (e.g., entoplastron size, abdominal/femoral length, anal notch shape) are irrelevant for a proper diagnosis. However, other features (e.g., narrow gular, long interhumeral sulcus, “pelomedusoid” ornamentation) could be coded as character states, and are useful to create a combination of diagnostic characteristics identifying “*Podocnemis*” *brasiliensis*. While the species has no clear autapomorphies and was recovered as a wildcard taxon in the phylogenetic analyses, it can be clearly distinguished from other, well-established taxa, particularly other Bauru Group species with known shells. We find the assignment of the species to *Bauruemys* unfounded, and consider it as a Pelomedusoides *incertae sedis* (and not a *nomen dubium*).

## **Questions regarding the diversity of trionychid turtles in the Dinosaur Park Formation of Alberta, Canada**

Donald B. **Brinkman**<sup>1,2</sup>

<sup>1</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, don.brinkman@gov.ab.ca; <sup>2</sup>Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.

One of the characteristic aspects of the turtle assemblage of the late Campanian Dinosaur Park Formation of Alberta, Canada, is the abundance and diversity of members of the Trionychidae. In the most recent review of the group, four well defined taxa are recognized: the small bodied *Aspideretoides foveatus*, the large *Axestemys splendidus*, and two taxa of moderate size, *Aspideretoides alleni* and “*Apalone*” *latus*. The presence of additional taxa is suggested by isolated elements. Among these are fused hyo-hyoplastra that have been suggested to be from a plastomenine. However, the possibility that fusion of the hyo-hyoplastra is an ontogenetic feature of *A. foveatus* could not be ruled out. Recent study of a trionychid specimen from the Dinosaur Park Formation in the collections of the Natural History Museum of the United Kingdom have provided additional evidence that a plastomenine distinct form *A. foveatus* is present in the assemblage. This specimen consists of a complete carapace and partial plastron. The carapace is like that of *A. foveatus*, and the specimen has been placed in that species. However, the entoplastron differs from that of *A. foveatus* in having a more rounded lateral edge and in being narrower at the midline, and the hypoplastron differs in having a notch for the entoplastron and in having fewer medial processes. Since the hyo- and hypoplastron are not fused, this individual is interpreted as a subadult. Thus, this specimen is interpreted as being taxonomically distinct from *A. foveatus* and, along with the fused hyo-hyoplastra previously identified as plastomenine, is referred to the genus *Atoposemys*. With this identification, a minimum of five taxa can be recognized in the Dinosaur Park Formation.

## **A turtle paleomeeting in Switzerland; a fossil from Colombia represents the youngest record of thalassochelydians**

Edwin-Alberto **Cadena**<sup>1,2,3</sup>, Torsten M. **Scheyer**<sup>4</sup>, Dylan **Bastiaans**<sup>4</sup>, Loïc **Costeur**<sup>5</sup>, Jorge D. **Carrillo-Briceño**<sup>4</sup>

<sup>1</sup>Facultad de Ciencias Naturales, Grupo de Paleontología Neotropical Tradicional y Molecular, Uni. del Rosario, Bogotá, Colombia, edwin.cadena@urosario.edu.co; <sup>2</sup> Smithsonian Tropical Research Institute, Panama City, Panama; <sup>3</sup> Field Museum, Chicago, USA; <sup>4</sup> Paläontologisches Institut, Zurich, Switzerland. <sup>5</sup> Naturhistorisches Mus. Basel, Switzerland.

The fossil record of traditional thalassochelydians, including "Eurysternidae," "Plesiochelyidae," and "Thalassemydidae," is almost exclusively restricted to the Late Jurassic of Europe, with only one species known from South America—*Neusticemys neuquina* from the Tithonian of Argentina. Here, we present a new species of thalassochelydian turtle based on a remarkable fossil shell and parts of its postcranial bones. The specimen was collected in the Guajira Peninsula, northeast Colombia. It belongs to Thalassochelydia by the following characteristics non-exclusive to the group: (1) absence of mesoplastron; (2) V-shaped posterior plastral lobe, reduced in length and without anal notch; (3) completely ossified carapace and bridge to the plastron; (4) an indentation of the sutural contact between the hypoplastra and xiphiplastra. It is a member of "Plesiochelyidae" by: (1) the occurrence of an "intermediate" bone between the last neural (neural 8) and suprapygals 1; and (2) lack of carapacial fontanelles. This discovery represents the youngest record for thalassochelydians worldwide, dating back to the Hauterivian, and is the second record of the group outside of Europe. We tell a unique story of how we rediscovered this fossil in the collections of the Natural History Museum of Basel, Switzerland, after it was brought there half a century ago by the Swiss geologist Otto Renz. This South American fossil now connects with its European relatives in a literal turtle paleomeeting. We also provide preliminary discussions on systematic paleontology, phylogenetic position, paleobiogeographical implications, and bone anatomy using CT-scan analysis for this new fossil, which belongs to the *Craspedochelys* genus.

## **A preliminary database of fossil turtles from Czechia and Poland**

Milan **Chroust**<sup>1</sup>, Tomasz **Szczygielski**<sup>1</sup>

<sup>1</sup>Institute of Paleobiology of the Polish Academy of Sciences, chroust@twarda.pan.pl.

One of the key aspects of current research is easy access to information. In palaeontology, very powerful tools are databases with information about locations, ages, and a brief description of the material with its taxonomic identification and related references. With increasing data, the demand for visual content is essential. Here, we want to meet the demand and propose the creation of a new database, including photographs of fossil turtle material from Central Europe. Therefore, the most important information would be included on the first click, which drives the scientific progress rapidly. In the first stage of the project, we revise fossil turtles from Czechia and Poland. Much of the historical fossil turtle material from these countries has not been revised since its discovery, and many original publications are difficult to access. Progress in the understanding of fossil turtle phylogeny and taxonomy renders many original identifications dubious or invalid. Even worse, many specimens were never figured or poorly documented, which virtually excluded them from the current scientific discourse. Therefore, the actual total diversity of turtles in Central Europe and its changes over time since the Mesozoic remains unknown, and the territories of those countries frequently remain blank spots on the palaeobiogeographical maps. Researchers worldwide will be most welcome to contribute.

# Phylogenetic uncertainty and the taxonomy of fossil turtles

Julien Claude<sup>1,2</sup>, Haiyan Tong<sup>3</sup>

<sup>1</sup>Institut des Sciences de l'Evolution de Montpellier, Univ Montpellier, CNRS, IRD, Montpellier, France, julien.claude@umontpellier.fr; <sup>2</sup>Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand; <sup>3</sup>Palaeontological Research and Education Centre, Maharakham University, Maha Sarakham, Thailand.

Phylogenetic methods are being used more and more to justify supraspecific taxonomy, replacing the old-style systematic assessment. Despite the ever-increasing character datasets, the taxonomic delineation of fossil groups, especially when they branch deep into the tree, remains largely controversial among authors. With the help of phylogenetic methods, most of us have opted for a blind approach, challenging anterior taxonomic delineations and building their systematic assessment. However, fossil and morphological datasets are embedded with uncertainties: appreciation of character states may differ among authors, some characters can be missing, included characters and taxa vary among authors, and there might be simply not enough variation among characters to define unambiguous synapomorphies. A side-effect of phylogenetically blind taxonomy when uncertainty is present is over-classification on the basis of little scientific justifications. Although rarely done, parsimony does allow to estimate uncertainties due to the method and the data set. Using examples of basal turtle phylogenetic reconstructions, we show that several clades have highly variable contents and that intraclade relationships are rarely consistent. When phylogenetic hypotheses are used as guide for drawing taxonomic conclusions, we suggest that phylogenetic uncertainty should be discussed and evaluated, that true parsimony scores and indicators of uncertainty should be provided more frequently in publications to nuance conclusions (Bremer indices, consensus trees + 1 more step). At the generic level, we recommend the use of lumping rather than splitting when there is uncertainty (or when uncertainty has not been estimated). We hope that this essay will influence authors, editors and referees.

## Further notes on the turtle fauna from Langebaanweg (Early Pliocene, South Africa) with a revision of “*Geochelone*” *stromeri*

Massimo Delfino<sup>1,2</sup>, Loredana Macaluso<sup>3</sup>, Romala Govender<sup>4,5</sup>, Marco Pavia<sup>1,4</sup>

<sup>1</sup>University of Turin, Torino, Italy, massimo.delfino@unito.it; <sup>2</sup>Institut Català de Paleontologia Miquel Crusafont, Cerdanyola del Vallès, Spain; <sup>3</sup>Natural Sciences, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany; <sup>4</sup>Research and Exhibitions, Iziko Museums of South Africa, Cape Town, South Africa; <sup>5</sup>Biological Sciences, University Cape Town, South Africa.

The study of the turtle remains from the Early Pliocene of Langebaanweg (South Africa), hosted at the Iziko Museums of South Africa (Cape Town), represents a difficult task due to huge amount of remains (several tens of thousands) that so far discouraged any comprehensive research initiative, even if the material has been collected since the late '60s of the last century thanks to the pioneering work of Q.B. Hendey. The study is currently developing along the following priority lines: 1) description of a new species of *Chersina*; 2) redescription of “*Geochelone*” *stromeri* Meylan & Auffenberg, 1986; 3) identification of the less common taxa of the turtle assemblage. The description of the new species of *Chersina*, preliminary reported at TES 2021, can be now considered completed. This taxon, representing by far the most common tortoise of the assemblage, will be based on the most complete shell remains from Langebaanweg (including the nearly complete shell, SAM PQL 20734, and several partial shells). The revision of the type-material of “*G.*” *stromeri* (SAM PQL 13721) allows to confirm the validity of this large sized taxon and to exclude that it belongs to the genus *Geochelone*. The fossil remains of *Pelomedusa* identified so far (several dozens of shell and appendicular remains) could be the most abundant remains of this genus ever recorded. The rarest genus of the assemblage appears to be *Kinixys* that has been confidently identified thanks to the single xiphiplastron SAM PQL 12754d.

## Ecomorphology of stylopodial compactness in turtles

Serjoscha W. Evers<sup>1</sup>, Jérémy Anquetin<sup>1,2</sup>, Roger B. J. Benson<sup>3,4</sup>, Elias Hamann<sup>5</sup>, Nicole Klein<sup>6,7</sup>, Yann Rollot<sup>1</sup>, Torsten M. Scheyer<sup>6</sup>, Justyna Słowiak<sup>8</sup>, Tomasz Szczygielski<sup>8</sup>, Laura E. Wilson<sup>9</sup>, Marcus Zuber<sup>5</sup>, Guilherme Hermanson<sup>1</sup>

<sup>1</sup>Dep. Geosciences, Uni. Fribourg, Switzerland, serjoscha.evers@gmail.com; <sup>2</sup>JURASSICA, Porrentruy, Switzerland; <sup>3</sup>American Museum of Nat. History, NYC, USA; <sup>4</sup>Institute for Photon Science and Synchrotron Radiation, KIT, Eggenstein-Leopoldshafen, Germany; <sup>5</sup>Paläontologisches Institut, Uni Zurich, Switzerland; <sup>6</sup>Rheinische Friedrich-Wilhelms-Uni. Bonn, Germany; <sup>7</sup>Institute of Paleobiology, Polish Acad. of Sciences, Warsaw, Poland; <sup>8</sup>Sternberg Museum of Nat. History, Fort Hays State University, Hay, USA.

Bone compactness has been used to distinguish aquatic and terrestrial lifestyles in amniotes. We use turtle humerus and femur bone compactness derived from histological and micro-computed tomography midshaft cross sections to test this ecological proxy on turtles. Our dataset comprises 115/73 (humerus/femur) extant turtle species as well as 15/8 fossil taxa. Humerus and femur compactness are significantly and strongly correlated. When added to a global amniote femur compactness dataset, shelled (*Proganochelys quenstedtii*, *Proterochersis porebensis*) and non-shelled stem turtles (*Pappochelys rosinae*) are predicted as aquatic based on high compactness, suggesting an early onset of aquatic evolution on the turtle stem lineage or inherited aquatic habits. However, adding extant turtles lowers the predictive power of the dataset, because unlike in other amniotes, aquatic and terrestrial turtles have broadly overlapping ranges of compactness values. This is likely because terrestriality among crown turtles is secondarily evolved, suggesting phylogenetic inertia or exaptation of high bone compactness. The exception are extremely aquatic turtles (chelonioids, *Carettochelys insculpta*), which show significantly lower bone compactness, similar to reduced compactness in whales. Phylogenetic discriminant analysis shows that terrestriality/freshwater aquaticness cannot be predicted correctly for extant turtles, whereas flippered lifestyles indicating pelagic habits among marine taxa can be predicted. Despite the limited ecological predictive power of limb bone compactness for turtles, our data offer some preliminary insights into secondarily marine turtle groups. Among thalassochelydians, *Plesiochelys bigleri* is predicted to be marine based on low compactness also observed in extant chelonioids, protostegids, and the stem sea turtle *Toxochelys latiremis*. *Eurysternum wagleri* is unexpectedly predicted to be non-flippered.

## Lower jaw functional morphology of the largest freshwater turtle, *Stupendemys geographica*, suggests an herbivorous diet

Gabriel S. Ferreira<sup>1,2</sup>, Edwin-Alberto Cadena<sup>3,4</sup>

<sup>1</sup>Senckenberg Centre for Human Evolution and Palaeoenvironment at the University of Tübingen, Germany, gabriel.ferreira@senckenberg.de; <sup>2</sup>Geosciences Department, University of Tübingen, Germany; <sup>3</sup>Universidad del Rosario, Facultad de Ciencias Naturales, Grupo de Investigación Paleontología Neotropical Tradicional y Molecular (PaleoNeo), Bogotá, Colombia; <sup>4</sup>Smithsonian Tropical Research Institute, Panama, Panama.

The Miocene of Northern South America witnessed the largest freshwater turtle ever, *Stupendemys geographica*. This podocnemidid was known only from fragmentary postcranial remains, but recent discoveries of a rich fossil record from the Tatacoa Desert (Colombia) offer new opportunities to explore the paleobiology of this incredible turtle. Here we report the first attempt to understand the feeding behavior of *Stupendemys* using functional morphology. A complete and mostly undeformed mandible (VPPLT-979) shows an upturned symphyseal hook and an almost flat but relatively broad triturating surface, lacking rugosities and including a long midline ridge. The coronoid process and adductor fossa are greatly developed, suggesting powerful external adductors. We digitalized that specimen with photogrammetry and modelled the adductor muscles to simulate biting scenarios using Finite Element Analysis. We tested three models: the original-sized (jaw length = 24 cm, carapace length = 134 cm), an upscaled (JL = 54 cm, CL = 280 cm), and a downscaled (JL = 12 cm, CL = 72 cm). The maximum bite force obtained from the largest to smallest models were 6700, 1200, and 142 N. Although the bite force of the largest *Stupendemys* proved to be comparable to similar-sized crocodiles, it is lower than expected for biter turtles, but match nicely those expected for herbivorous species when upscaled to CL = 280 cm. Thus, together with the triturating surface anatomy, the biomechanical analyses suggest that *Stupendemys* was herbivorous, similar to its extant podocnemidid relatives.

## An insular testudinid from the Miocene palaeo-island of Gargano, Italy

Georgios L. **Georgalis**<sup>1</sup>, Evangelos **Vlachos**<sup>2</sup>, Andrea **Villa**<sup>3</sup>, Marco **Pavia**<sup>4</sup>, Lars W. **van den Hoek Ostende**<sup>5</sup>, Massimo **Delfino**<sup>3,4</sup>

<sup>1</sup>Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland, dimetrodon82@gmail.com; <sup>2</sup>CONICET and Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; <sup>3</sup>Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain; <sup>4</sup>Dipartimento di Scienze della Terra, Università di Torino, Italy; <sup>5</sup>Naturalis Biodiversity Center, Leiden, The Netherlands.

The Late Miocene (Messinian) Gargano “Terre Rosse” in southern Italy has yielded a diverse and peculiar insular vertebrate fauna, comprising an array of endemic taxa, including forms characterized by extreme sizes and unique morphologies. We here present a new testudinid from this insular assemblage. The material comprises few shell remains (both carapace and plastral elements, isolated and in most cases incomplete), appendicular elements (humeri, one femur, and one pubis), and one caudal vertebra hosted in the collections of the Museo di Geologia e Paleontologia dell’Università degli Studi di Torino (Turin, Italy) and Naturalis Biodiversity Center (Leiden, The Netherlands). Based on the femur morphology, we tentatively allocate the Gargano form to *Solitudo*, a late Neogene and Quaternary insular genus, otherwise known from a few Mediterranean islands. Unfortunately, the incomplete preservation of the trochanters hinders observation of the main diagnostic character of *Solitudo*, however, the similarities in the femoral head and diaphysis allow an open identification as cf. *Solitudo* sp. Still, the Gargano tortoise offers new anatomical information on the Mediterranean insular tortoises. An interesting feature of the few preserved plastral elements is the presence of sulci as distinct raised ridges, a character that has been reported in other insular extant and extinct tortoises as well. The preserved hyoplastron has a medially straight and laterally concave humeropectoral sulcus and a wide inguinal scute. If our identification is correct, the Gargano form would correspond to the earliest occurrence of this genus, denoting that this insular testudinid already radiated during the Late Miocene. An overview of the diversity and taxonomy of the Mediterranean insular testudinids is provided.

## New perspectives on the evolution of pan-trionychids based on the study of plastomenid skulls

Léa C. **Girard**<sup>1</sup>, Tyler R. **Lyson**<sup>2</sup>, Walter G. **Joyce**<sup>1</sup>

<sup>1</sup>Department of Geosciences, University of Fribourg, Switzerland, lea.girard@unifr.ch; <sup>2</sup>Department of Earth Sciences, Denver Museum of Nature & Science, Denver, Colorado, USA.

Soft shell turtles (Pan-Trionychidae) can be recognized by the unique morphology of their shell, which is highly reduced and covered with a thick leathery skin, rather than scales. This aquatic clade likely originated during the Early Cretaceous in Asia and today is spread across parts of Africa, Asia, Australasia, and North America. Extant representatives of the group closely resemble their earliest relatives, leading to difficulties in discerning phylogenetic relationships. In addition, the detailed cranial anatomy is only known for few fossil taxa. The evolutionary history of the group is, therefore, still poorly understood. Plastomenidae is an extinct North American subclade of Pan-Trionychidae characterized, among others, by a secondary reossification of the plastron and a prolonged midline contact between the maxillae that forms a secondary palate. Until recently, the skulls of plastomenids were barely figured and described in the literature. We examined the cranial morphology of *Hutchemys rememidium*, a potential plastomenid, based on micro-computed tomography ( $\mu$ CT) scans of undescribed skulls and jaws from the Paleocene of North Dakota. A phylogenetic analysis following the inclusion of the new material supports the identity of *Hutchemys rememidium* as a plastomenid, but still supports the somewhat questionable placement of Plastomenidae as sister to Cyclanorbinae. Our current work aims to expand our data set through the study of additional  $\mu$ CT scans obtained from other potential Late Cretaceous and Paleogene plastomenids, including those of *Atoposemys superstes*, *Aspideretoides foveatus*, and “*Trionyx*” *allani*.

## **Cranial morphogeometric analysis of pan-cryptodiran sea turtles**

Isabella V. **Goulart**<sup>1,2</sup>, Márton **Rabi**<sup>2</sup>, Jorge Domingo **Carrillo Briceño**<sup>3</sup>, Marcelo R. **Sánchez-Villagra**<sup>3</sup>, Torsten M. **Scheyer**<sup>3</sup>, Benjamin P. **Kear**<sup>4</sup>, Pedro S. R. **Romano**<sup>5</sup>

<sup>1</sup>Universidade Federal de Viçosa, Viçosa-MG, Brazil; <sup>2</sup>Eberhard Karls Universität Tübingen, Tübingen, Germany, isabellachelys@gmail.com; <sup>3</sup>University of Zürich, Institute of Paleontology, Zürich, Switzerland; <sup>4</sup>University of Uppsala, Museum of Evolution, Paleontology and Mineralogy, Sweden; <sup>5</sup>Universidade Federal de Viçosa, Viçosa-MG, Brazil.

This ongoing 2D geometric morphogeometric study was designed to quantify select osteological correlates of marine adaptation in the skull of pan-cryptodiran sea turtles. We performed a landmark analysis of 41 species, including stem-chelonioids, cheloniids, dermochelyids, protostegids, and thalassochelydians, in dorsal and lateral views. The configurations are aimed to capture orbit lateralization, the deepening of the skull, the supraoccipital process extension, and the development of the upper and lower temporal emarginations. The absence of the latter is known to correlate with secondary loss of neck retraction, likely representing a hydrodynamic advantage. With the exception of Late Cretaceous chelonioids, most structures observed in the principal component analyses exhibit a clear (but not tested) phylogenetic signal. The overlap of clades onto the morphospace (PC1xPC2) is mostly seen involving Mesozoic cheloniids, which retain PC scores closer to protostegids and thalassochelydians. Overall, Mesozoic sea turtles are characterized by a deep temporal emargination and dorsally faced orbits, although these traits may not always co-occur. Cenozoic cheloniids are clearly distinct from the remaining species and the Late Cretaceous cheloniids are indistinguishable from the other Mesozoic turtles clades. Unexpectedly, pelagic protostegids and nearshore-marine thalassochelydians are closely positioned in both lateral and dorsal view to the exclusion of pelagic crown-chelonioids. In general, our results suggest independent evolution of temporal emarginations and orbit lateralization in crown-chelonioid and protostegid sea turtles. This is due to the seemingly ancestral condition shared by protostegids and thalassochelydians, with more pronounced upper temporal emarginations, narrower interorbital spaces, and shallower skulls.

## **Pathological anomalies in Cretaceous and Paleogene pleurodiran turtles of Spain: an update**

Andrea **Guerrero**<sup>1</sup>, Adán **Pérez-García**<sup>1</sup>

<sup>1</sup>Grupo de Biología Evolutiva, Facultad de Ciencias, UNED, Madrid, Spain, guerbach@gmail.com.

Fossilized turtle shells often display anomalies of pathological origin. This provides tangible evidence that, like their current representatives, extinct turtles were also exposed to various external agents capable of compromising the shell integrity. Accurate interpretation of the shell pathologies is crucial for several purposes. Specifically, it allows to understand the paleoecology of extinct turtle species, providing insights into the diseases that have affected this lineage over time, as well as the subsequent healing stages experienced throughout the lives of these extinct organisms. In this context, our study synthesizes the main cases of pathological anomalies in the fossilized remains of different exclusively freshwater to inhabitants of brackish to marine coastal waters turtle taxa from the Spanish Upper Cretaceous and Eocene records, all of them belonging to Pan-Pleurodira (i.e., several representatives of Dortokidae, Bothremydidae, and Podocnemididae). Through this analysis, we identify diverse typologies of anomalies of pathological origin evaluating their corresponding etiologies, contributing to a deeper understanding of the various causative agents associated with prevalent shell anomalies. Likewise, we discuss previously proposed hypothetical clinical diagnoses by other authors for some specimens, refuting them by justifying different causal agents. As a result, the integration of data on anomalies of pathological origin affecting multiple taxa provides a comprehensive perspective on the diverse external factors influencing the shells of pan-pleurodiran turtles in the Spanish record, offering a better understanding of their lifestyle.

# **Preliminary morphological study of the appendicular skeleton of the Spanish Bartonian (middle Eocene) *Neochelys salmanticensis* (Pleurodira; Podocnemididae)**

María **Gutiérrez-Gálvez**<sup>1</sup>, Francisco **Ortega**<sup>1</sup>, Santiago **Martín de Jesús**<sup>2</sup>, Adán **Pérez-García**<sup>1</sup>

<sup>1</sup>Grupo de Biología Evolutiva, Dpto. de Física Matemática y de Fluidos, Facultad de Ciencias, UNED, Madrid, Spain, maria.gutierrezgalvez@gmail.com; <sup>2</sup>Colección de Vertebrados Fósiles de la Cuenca del Duero (Sala de las Tortugas), Departamento de Geología, Facultad de Ciencias, Universidad de Salamanca, Salamanca, Spain.

The Eocene record of vertebrates from the Duero Basin (northwestern Spain) is abundant and diverse. Several clades of turtles are recognized, highlighting, for their abundance and diversity, the podocnemidids. Two species of the European genus *Neochelys* have been identified. The first species described was *Neochelys salmanticensis*, exclusive from the Bartonian (middle Eocene) of the Salamanca Province. It is the youngest known representative of this diverse genus. For more than 50 years *Neochelys salmanticensis* was based on scarce material, which did not allow an adequate diagnosis. Recently, hundreds of remains (including articulated and relatively complete shells) were analysed, allowing a detailed shell characterization. Although the shell is the only element recognized in all *Neochelys* representatives, such a large collection has never been documented for any other species. All published information on this Spanish species is restricted to its shell. Abundant and well-preserved appendicular remains of *Neochelys salmanticensis* have been identified, both from the type locality and at other sites, including more than one hundred bones. As with the shell remains, the collection of appendicular bones is much larger than in any other documented representative of the genus and includes elements unknown in most other species. We present a preliminary study of the morphology of the appendicular elements of this species, based on both remains of relatively complete skeletons and isolated bones from different ontogenetic stages. Since *Neochelys salmanticensis* is the largest representative of the genus, morphological differences from other *Neochelys* species with documented appendicular bones are to be expected.

## **Ecomorphology and disparity of the turtle shell through time**

Guilherme **Hermanson**<sup>1</sup>, Serjoscha W. **Evers**<sup>1</sup>

<sup>1</sup>University of Fribourg, Fribourg, Switzerland, guilhermehermanson@gmail.com.

The shell is the defining feature of turtles, and evolved on the turtle stem lineage about 230 Ma. Turtle shells vary considerably across taxonomy and ecological gradients, for instance in the aspect ratios of carapace and plastron. However, questions remain about whether ecology is the primary factor driving shell shape evolution, what other factors may play a role, and how the shell influences turtle evolution more generally, for example by imposing constraints on morphological evolution. Using a newly collected 3D landmark dataset comprising 161 extant species and fossil taxa of various lineages, we investigate turtle shell shape ecomorphology across their phylogenetic and ecological diversity with phylogenetic comparative methods, as well as patterns of morphological disparity through time. Turtle shell morphospace indicates phylogenetic constraints on shell shape and overlap of distinct ecological groups. Primary habitats (terrestrial, freshwater, marine) do not explain shape variation and ecology predictions based on shell shape have low success rates in phylogenetic discriminant analysis, although finer ecological classifications return significant correlations in phylogenetic regressions. We corroborate previous palaeoecological hypotheses for some fossils, while others remain ambiguous due to convergences that weaken clear cut ecology-shape associations. Our disparity through time analyses show an initial disparity peak during an ‘experimental phase’ of shell evolution during the Triassic, and a steady increase during the Jurassic and the Early Cretaceous, when most crown groups and ecologically diverse fossil groups evolved. Turtle shell shape disparity was unaffected by the K/Pg event, contradicting expectations of ecological extinction selectivity.

# Fossil marine turtles (Cheloniodea) from the Kuji Group in Iwate Prefecture and a systematic review of Cretaceous marine turtles from Japan

Ren HIRAYAMA<sup>1</sup>, Seishiro TADA<sup>2</sup>

<sup>1</sup>Waseda University, Shinjuku-ku, Japan, renhirayama@gmail.com; <sup>2</sup>Fukui Prefectural University, Eihei-ji, Japan.

The Kunitan Formation of Noda Village in Kuji City of Iwate Prefecture of northeastern Japan is a geological unit bearing the rich Coniacian marine vertebrate fossils. Among them are marine turtle remains which represent at least 23 skeletons, including partial shells, limb bones, a cervical, and a pterygoid, possibly of a single individual. The carapace is estimated as about 60 cm long. Its peripherals have serrated medial margins, hitherto only known in *Mesodermochelys*, an endemic chelonoid turtle from the Late Cretaceous (Santonian to Maastrichtian) of Japan (Hokkaido, Hyogo, Kagawa, and Wakayama Prefectures). Scute sulci of the carapace are more clearly preserved than in *Mesodermochelys*. Thus, this marine turtle from the Kunitan Formation is likely a more basal taxon of the *Mesodermochelys* group. Its radius shows outward bending, an apomorphic feature of the Protostegidae. A newly found skull of *Mesodermochelys* from the Santonian stratum in Hokkaido Prefecture shows the following derived characters: (1) jugal expanding posteriorly; (2) medial meeting of palatines; (3) pterygoid reaching to the articular facet of quadrate; (4) foramen of the internal carotid artery located between basisphenoid and pterygoid in ventral view. The above characters suggest that *Mesodermochelys* belongs to the Protostegidae or another monophyletic group and is not an ancestral taxon of the Dermochelyidae as hitherto proposed. A *Mesodermochelys*-like peripheral was also collected from the upper part of the Tamagawa Formation (about 90 mya). Thus, a monophyletic endemic *Mesodermochelys* group might have existed from the latest Turonian to Maastrichtian as a dominant marine turtle in Japan.

## Taxonomic richness in middle Eocene turtles of the Washakie Formation

Patricia A. HOLROYD<sup>1</sup>, Susumu TOMIYA<sup>2</sup>

<sup>1</sup>University of California Museum of Paleontology, Berkeley, USA, pholroyd@berkeley.edu; <sup>2</sup>Center for International Collaboration and Advanced Studies in Primatology, Center for the Evolutionary Origins of Human Behavior, Kyoto University, Inuyama, Japan.

The Kinney Rim and Adobe Town members of the Washakie Formation, southwestern Wyoming, USA, preserve a series of successive early middle Eocene non-marine faunas of Bridgerian and Uintan age that overlap with and also span the gap between the better-known faunas of the Bridger and Uinta Formations. Laid down on the floodplain northeast of the shrinking ancient Lake Gosiute, the channels and mudstones of the Washakie Formation preserve a diverse but under-studied fauna. To date, only 5 turtle specimens have been described from this formation. Here we present an initial survey of the taxonomic richness and turnover of turtles from more than 700 previously undescribed occurrences tied to the published stratigraphy. Trionychids (represented by at least 2 taxa) are the most common throughout the section, followed by the testudinoid *Echmatemys* and the carettochelyid *Anosteira*. Rarer tortoises (two taxa) and a kinosternid are also present. Some taxa appear only in the Bridgerian portion of the section, notably the dermatemydid *Baptemys*, and the baenids *Chisternon* and *Baena*. This absence may reflect facies changes and local extirpation as the lake recedes but may also reflect sampling differences through time due to differences in available outcrop.

## **Estimating 3D shell asymmetry of Testudines from preserved specimens**

Merin Joji<sup>1</sup>

<sup>1</sup>Department of Biology, University of Copenhagen, Copenhagen, Denmark, merin.joji@bio.ku.dk.

Turtles are a unique group of vertebrate animals that diversified over 220 million years into aquatic, semi-aquatic, and marine habitats. Despite their ecological importance, over half of the ~360 living turtle and tortoise species are threatened with extinction due to human activities. My project aims to monitor turtle health based on fluctuating asymmetry (FA), a sensitive biomarker to environmental stress that can lead to shell deformation. To develop a baseline of shell FA across Testudines, I landmarked 3D scans of 120 preserved specimens from 92 species, representing all turtle families and ecological types (see models on Sketchfab; <https://sketchfab.com/search?q=merin+joji&type=models>). Shell shape varied by ecology, ranging from the hard dome-shaped carapace and wide plastron of terrestrial tortoises to the flat carapace and narrow plastron of aquatic softshell turtles. Shell shape was only weakly predicted by shell size and phylogeny, indicating that environment poses a strong selective pressure likely related to locomotion. FA was not detected in whole shell or plastron landmark configurations, although the carapace exhibited significant variability in left-right landmark differences among individuals and ecologies, with marine species being most asymmetrical and aquatic being least. Environmental factors are difficult to detect in preserved specimens, results suggest that sea turtles may experience greater disturbance in carapace development, possibly due to fluctuations in nest incubation temperature that can destabilize scute formation. These results demonstrate that FA is a sensitive tool for detecting subtle deformations in shell shape, which may help to inform turtle conservation efforts.

## **Inferring the phylogeny of pan-trionychid turtles using postcranial characters**

Walter G. Joyce<sup>1</sup>

<sup>1</sup>University of Fribourg, Fribourg, Switzerland, walter.joyce@unifr.ch.

Soft-shells (*Pan-Trionychidae*) are a highly distinct clade of turtles with a near worldwide current or past distribution. Although the group has an excellent fossil record, particularly in Europe and North America, current phylogenies are unable to identify with confidence the deep time ancestral lineages of any extant species. This is partially a result of high levels of skeletal polymorphism caused by ontogenetic changes or variable growth that obscure any phylogenetic signal when using traditional polymorphic coding. To address this issue, I developed 66 new or revised shell characters that I scored separately for more than 600 extant trionychids representing nearly all extant species. 41 characters are multistate characters that form morphoclines. 11 characters utilize morphometric measurements of lengths, surfaces, or angles obtained from photographs. While individuals with intermediate morphologies were liberally scored polymorphic, specimens displaying abnormalities were disregarded for the affected characters. Species were scored by reference to the most adult morphology for characters with a demonstrable ontogenetic signal. Species were otherwise only scored polymorphic if more than 20% of regular individuals display a particular character state. A preliminary analysis of the resulting species level matrix using equal weights parsimony retrieves a tree that almost fully parallels the results of recent molecular analyses. This suggests on the one side high levels of morphological conservatism to the shell of trionychids, but also highlights the potential utility of shell characters in resolving pan-trionychid relationships.

# The first pan-trionychids specimen (Reptilia: Testudines) from the Upper Cretaceous of Southern China

Yuzheng **Ke**<sup>1</sup>, Fenglu **Han**<sup>1</sup>

<sup>1</sup>School of Earth Science, China University of Geosciences (Wuhan), Wuhan, China, key1480@163.com.

Pan-trionychids are a group of typical aquatic turtles that lived from the Early Cretaceous to the present. Abundant fossil specimens of pan-trionychids have been found in Asia, but there is no fossil record from the Late Cretaceous of southern China. Here, we report a small pan-trionychid specimen (CUGW VH245) from the Zhoutian Formation of Ganzhou Basin, China, which only includes an incomplete carapace (preserved length of ~7.3 cm). CUGW VH245 has eight neurals and eight pairs of costals, and both the eighth neural and eighth costals are reduced in size. Only the eighth costals contact their counterparts at the midline. Overall, the skeletal features of CUGW VH245 are comparable with the other Asian pan-trionychids during the Cretaceous. Because the specimen is a juvenile with a poorly preserved condition, we temporarily assign it to be within Pan-Trionychidae indet. CUGW VH245 represents the first record of pan-trionychids from the Upper Cretaceous of southern China. Moreover, the turtle population in the Upper Cretaceous of the Ganzhou Basin shows an obvious succession from pan-trionychids to lindholmemydids to nanhsiungchelyids, which may be caused by environmental change.

## Paleobiogeographic review of Early Cretaceous trionychians

Do Hyeon **Kim**<sup>1</sup>, Teppei **Sonoda**<sup>2</sup>, Yuong-Nam **Lee**<sup>1</sup>, Jin Young **Park**<sup>1</sup>

<sup>1</sup> Seoul National University, Seoul, South Korea, ehgus5590@snu.ac.kr; <sup>2</sup> Fukui Prefectural Dinosaur Museum, Fukui, Japan.

Based on the fossil records from the Lower Cretaceous formations of Japan and SE Asia, it is suggested that the trionychians originated from Asia. They diversified into two groups later, the carettochelyids and pantrionychids. Most carettochelyids occurred in Southeast Asia during the Early Cretaceous, whereas all the pantrionychids were limited to Central and East Asia. It has been suggested that there was a geographical isolation between SE Asia and the mainland during the Neocomian, and this physical barrier may have caused the allopatric speciation among the earliest members of the Pan-Trionychia, corresponding to the common ancestors of the carettochelyids and the pantrionychids. This hypothesis is supported by the similar distributional aspects of other turtles during the Early Cretaceous in Asia, including adocids, macrobaenids, sinemydids. The carettochelyid materials from the Lower Cretaceous Tatsukawa and Kitadani formations (Barremian ~ Aptian) of Japan, which represents the only record of Early Cretaceous carettochelyid outside the SE Asia, suggests that the dispersal of carettochelyids were somewhat more flexible than pantrionychids. The most influential factor that made this possible is inferred to be dispersal by marine routes bypassing the physical barrier. However, such inference requires further discussions, since both carettochelyids and pantrionychids are known for having tolerance in saline environments.

# The missing giant: a gigantic softshell turtle (Trionychidae) from the Pleistocene of Taiwan

Yi-Lu Liaw<sup>1</sup>, Cheng-Hsiu Tsai<sup>1</sup>

<sup>1</sup>National Taiwan University, Taipei, Taiwan, liawlulu@gmail.com.

The extinction of large Pleistocene reptiles is less well-known than that of large mammalian species. Here, we describe a newly discovered and well-preserved fossil skull and revise “*Trionyx*” *liupani*, whose holotype is also a well-preserved skull. Both specimens show broad and short snouts, large orbits (twice as long as the postorbital bar), a narrow triturating area of the maxilla, and a wide anterior margin of the basisphenoid, indicating their affinity to *Rafetus swinhoei*. We also test the phylogenetic position of the fossils, using a dataset that includes 116 characters and 41 operational taxonomic units with Bayesian tip-dating analysis and maximum parsimony. Our phylogenetic results support that the fossil materials from the Pleistocene of Taiwan belong to the genus *Rafetus*, likely to be *R. swinhoei*. Given the geographical location (Taiwan), both fossils are more likely to be *Rafetus swinhoei*, although the morphological differences of the *Rafetus* species remain uncertain and unclear. The newly-discovered fossil skull is large (length: 208 mm and width: 176 mm), and this dimension indicates its body size: reaching 1.5 meters long and one hundred kilograms, similar to the extant gigantic *Rafetus swinhoei*. Our discovery represents the rare fossil record of giant softshell turtles globally and shows the easternmost distribution of the gigantic genus *Rafetus*. This study should then invite more in-depth research to describe more hidden reptilian diversity and to assess the lost ecosystem structure and the megafaunal extinction of reptiles in the Pleistocene.

## Earliest Vallesian fossil turtle remains from Creu de Conill 20 (Vallès-Penedès Basin, NE Iberian Peninsula)

Àngel H. Luján<sup>1</sup>, Kelly A. Vega-Pagán<sup>1</sup>, Alessandro Urciuoli<sup>2</sup>, Juan Abella<sup>3</sup>, Daniel DeMiguel<sup>4</sup>, Sergio Almécija<sup>5</sup>, David M. Alba<sup>1</sup>, Marta Pina<sup>1</sup>

<sup>1</sup>Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain, angel.lujan@icp.cat; <sup>2</sup>Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Spain; <sup>3</sup>Grup d'Investigació en Paleontologia de Vertebrats del Cenozoic, Departament de Botànica i Geologia, Universitat de València, Burjassot, Spain; <sup>4</sup>Fundación Agencia Aragonesa para la Investigación y el Desarrollo at Departamento de Ciencias de la Tierra, Universidad de Zaragoza, Zaragoza, Spain; <sup>5</sup>Division of Anthropology, American Museum of Natural History, New York, USA.

The earliest Vallesian (11.2 Ma, MN9) site of Creu de Conill 20 (CCN20), located in the Vallès-Penedès Basin (NE Iberian Peninsula), has yielded abundant vertebrate fossil remains since excavations were reopened in 2016. However, taxonomic studies have so far focused on large and small mammals. We describe more than 200 unpublished turtle remains from CCN20, mostly consisting of isolated plates and a few postcranial bones. More than three-quarters of the specimens are medium-size testudinids (some of them with semiarticulated shells), mostly attributable to a medium-sized tortoise (*Testudo* aff. *burgenlandica*), which is characteristic of the Vallesian, and otherwise assigned to *T. catalaunica* (originally described from the MN7+8 site of Sant Quirze in the same basin). Only seven specimens (a distal phalanx and shell fragments) belong to the large testudinid *Titanochelon* sp. Freshwater turtles are represented by moderately abundant geoemydids remains (carapace and plastron plates) here referred to *Clemmydopsis* sp. and scarcer remains (carapace plates and postcranial bones) of Trionychidae indet. The tortoise remains confirm the sympatric co-occurrence of two medium-sized testudinids during the earliest MN9, which has important implications (potentially being a biochronological marker of the earliest Vallesian). In turn, the geoemydid material represents the first record of *Clemmydopsis* in the Vallès-Penedès Basin, while the trionychid remains are the youngest record so far documented for this family in the Vallès-Penedès Basin.

## Origin and early evolution of the turtle body plan

Tyler R. Lyson<sup>1</sup>

<sup>1</sup>Denver Museum of Nature & Science, Denver, CO, USA, tyler.lyson@dmns.org.

The origin of turtles and their uniquely shelled body plan is one of the longest standing problems in vertebrate biology. Historically, answers to these questions have been elusive largely due to the lack of a clear transitional fossil record. However, the last 20 years has witnessed a wealth of paleontological discoveries that have shed unprecedented light on the timing, tempo, and structural nature of fundamental transformations in the turtle body plan. This period was initiated by the recovery of the late Triassic *Odontochelys semitestacea*, whose T-shaped ribs and lack of osteoderms served as an important guide for what morphologies could be expected in the deeper reaches of the turtle stem lineage. This led to the re-examination of the middle Permian reptile *Eumotosaurus africanus*, which shares numerous developmental and morphological synapomorphies with other stem turtles. Additional discoveries of new stem turtles, as well as novel insights into known stem turtles, now provide an integrated, time-calibrated model of the morphological, developmental, and ecological transformations responsible for the modern turtle body plan. This evolutionary trajectory was initiated in the Permian when a turtle ancestor with a diapsid skull evolved a novel mechanism for lung ventilation. This key innovation permitted the torso to become apomorphically stiff, most likely as an adaptation for digging and a fossorial ecology. The construction of the modern turtle body plan then proceeded over the next 100 million years following a largely stepwise model of osteological innovation.

### Cervical variation and shape similarities in the neck of Pleurodira

Thiago F. Mariani<sup>1</sup>, Gabriel S. Ferreira<sup>2</sup>, Ingmar Werneburg<sup>2</sup>, Pedro S. R. Romano<sup>1</sup>

<sup>1</sup>Universidade Federal de Viçosa, Viçosa, Brazil, tmariani.bio@gmail.com; <sup>2</sup>Senckenberg and University of Tübingen, Tübingen, Germany.

This is an ongoing project on turtle neck evolution addressed through 3D geometric morphometrics and multivariate analyses. Here we preliminary address how the neck might have evolved in Pleurodira by exploring shape variation (35 landmarks) of the cervical vertebrae (C2-C8) of seven pleurodire species (two chelids, five pelomedusoids) and ordinate cervical shape differences/similarities. The ordination analysis (PCA) partitioned most of the variance into three RWs (ca. 68%). Variation explained by PC1 was consistent with the phylogeny, with most Pelomedusoides and Chelidae spp. retaining, respectively, positive and negative scores. The structure found along PC2 is consistent with shape similarity of three cervicals subsets: anteriormost (C2), middle (C3-C5), and posteriormost (C7-C8). The morphospace of C6 spanned between the two latter subsets. Phylogenetic structure is expected given the particular central articulations of each clade. As expected, C2 shape outstands as the most distinguished vertebra, possibly for being the closest to the head and playing more constrained functions. Shape variation in the middle region may be due to specific neck functions in different lineages, as indicated by the heterocoely in *Podocnemis* species. Shape variation of the posteriormost region seems to be partitioned in Chelidae but not in Pelomedusoides. C7-C8 are, respectively, biconcave, and biconvex in chelids but procoelous in pelomedusoids. This partition is possibly related to their unique articulation that plays different functions in neck movements. In sum, the cervical morphological variation in pleurodires seems to be related to both phylogenetic and function-related reasons.

## Neuroanatomy of the Paleocene bothremydid turtle *Taphrosphys* (Pleurodira, Taphrosphyini), based on a skull from Morocco

Marcos **Martín-Jiménez**<sup>1</sup>, Javier **Catalá Montolio**<sup>2</sup>, and Adán **Pérez-García**<sup>1</sup>

<sup>1</sup>Grupo de Biología Evolutiva, UNED, Madrid, Spain, mmartinjimenez@gmail.com; <sup>2</sup>Gran Via Corts Catalanes, 460, 4<sup>o</sup> 2<sup>o</sup> A, 08015, Barcelona, Spain.

Taphrosphyini was a successful lineage within Bothremydidae that inhabited several Laurasian and Gondwanan areas, from the Late Cretaceous to the Eocene. *Taphrosphys* is identified as the most diverse genus within Taphrosphyini, being represented by three Paleocene species, corresponding to a North American and two African forms. The cranial anatomy of all of them is relatively well-known. Although some neuroanatomical elements of several representatives of Taphrosphyini were described and figured (not for *Taphrosphys*, but some aspects of the endosseous labyrinth of *Taphrosphys ippolitoi* were considered in comparative framework), the detailed study of the neuroanatomy of no member of this clade was carried out. This contribution presents the first complete neuroanatomical study of a representative of Taphrosphyini. This is based on the analysis of an unpublished almost complete skull of *Taphrosphys* from Morocco, *a priori* attributable to *Taphrosphys ippolitoi* based on knowledge about the paleobiogeographic distribution of the members of this genus. It was scanned through a high-resolution micro-CT. The obtained archives were processed, generating the three-dimensional models of both the skull and the inner cavities related with neuroanatomical structures. The study of cranial characters will allow us to evaluate its specific attribution. The comparison of the endocranial and labyrinthic cavities, and the circulatory and nerve canals of this specimen with those of the representatives of Taphrosphyini in which these structures are known, but also with other bothremydids, will allow us recognizing neuroanatomical features shared by all bothremydids and, potentially, exclusive for Taphrosphyini or not shared with other representatives within this lineage.

## A new “eurysternid” turtle from the Late Jurassic Solnhofen Formation and the paleoecology of thalassochelydians

Chloé **Mazier**<sup>1</sup>, Jillian **Degagne**<sup>2</sup>, Walter G. **Joyce**<sup>3</sup>, Jérémy **Anquetin**<sup>1</sup>

<sup>1</sup>JURASSICA Museum, Porrentruy, Switzerland, chloemazier@gmail.com; <sup>2</sup>Geosciences, University of Rennes, Rennes, France; <sup>3</sup>Department of Geosciences, University of Fribourg, Fribourg, Switzerland.

The cranial anatomy of thalassochelydians is known only for a few species. This is particularly true for “eurysternids,” whose existing skulls are often inaccessible, because they are embedded into slabs of lithographic limestone. Here, we present a new specimen from the Solnhofen Formation in Zandt (Germany) for which we mechanically extracted the skull for further description and CT scan. This new specimen offers new data on the little-known cranial anatomy of “eurysternids” and is assigned to a new species based on cranial and postcranial characters. Two other specimens from the Solnhofen Formation are also reassigned to this new species, including one previously referred to *Palaeomedusa testa*. The question of the validity of the latter species and its potential synonymy with *Eurysternum wagneri* is therefore reopened. Based on depositional environment and the putative presence of hypertrophied salt glands (large foramen interorbitale), thalassochelydians are traditionally regarded as coastal marine dwellers. However, their taxonomic and morphological diversity suggests that they probably inhabited a multitude of environments from the open sea to brackish lagoons, and possibly freshwater ecosystems. As a preliminary study to test this hypothesis, we measured limb bone proportions in a number of thalassochelydians to assess their paleoecology. Our results indicate that some species, including the new “eurysternid” presented here, appear to be more adapted to living in small or stagnant bodies of water, whereas others, notably *Thalassemys bruntrutana* and *Idiochelys fitzingeri*, were more efficient swimmers. However, these paleoecological inferences based on modern species should be regarded with caution.

## **New perspectives on fossil sea-turtles from the Cretaceous to the Neogene**

Juliette C. L. **Menon**<sup>1</sup>, Walter G. **Joyce**<sup>1</sup>, Serjoscha W. **Evers**<sup>1</sup>, Donald B. **Brinkman**<sup>2,3</sup>

<sup>1</sup>University of Fribourg, Fribourg, Switzerland, juliette.menon@unifr.ch; <sup>2</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; <sup>3</sup>Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.

“Sea-turtles” are an assemblage of fossil and recent testudinales with uncertain interrelationships, including Protostegidae, Chelonioida, Sandownidae, Thalassochelydia, and Bothremydidae. They document secondary transitions to the marine realm and include the last surviving fully marine amniote clade from the Cretaceous-Paleogene extinction. Fossil sea turtles have received little attention and their early morphological evolution is therefore poorly understood. Indeed, hundreds of fossils still await primary evaluation or secondary redescription, while the group as a whole is in need of taxonomic revision. We here present new work on fossil sea turtles targeting to improve our understanding of this fascinating group. We first present the results of the redescription of *Nichollsemys baieri* (Campanian, Alberta), based on a micro-computed tomography scan of the holotype skull, which is notable for being preserved without crushing. Morphological analysis of this specimen documents similarities with *Toxochelys latiremis* while highlight the early acquisition of derived characters in stem chelonioids. We also present work in progress on the redescription of two nearly complete shells of the enigmatic, but nearly forgotten taxon *Glyptochelone suykerbuykii* from the Maastrichtian of Limbourg (Netherlands). In order to shed new light on the alpha-taxonomy of fossil sea-turtles, we also provide early results regarding our taxonomic revision of cryptodiran lineages of sea-turtles, spanning from the Cretaceous to the Recent.

### **Fossil turtles of the Iberian Peninsula (Southwestern Europe): new finds and ongoing research**

Adán **Pérez-García**<sup>1</sup>

<sup>1</sup>Grupo de Biología Evolutiva, UNED, Madrid, Spain, a.perez.garcia@ccia.uned.es.

The fossil record of turtles of the Iberian Peninsula is recognized as one of the most abundant and diverse for the European continent. The relative geographical position of the Iberian Peninsula over time has been strategic for the diachronic dispersion of numerous lineages of turtles to and from different geographical areas, not only considering other European regions, but also other continents (i.e., Africa, Asia, and North America). Numerous turtle lineages have been recognized in the Iberian context, including both stem taxa and, especially, pan-pleurodiran and pan-cryptodiran representatives. This record is well represented for almost all geological series, from the Upper Jurassic to the Holocene (with the sole exception corresponding to the Paleocene). Knowledge about the extinct turtles that lived in this region has improved significantly in the last two decades, through both the review of the previously documented specimens and the discovery and study of numerous new finds. The main objectives of this keynote talk are to show some of the latest finds carried out as a result of recent prospecting and excavation campaigns, as well as others previously performed but that remained unpublished until now; and to present some of the main research on the fossil record of Iberian turtles currently underway. Thus, not only aspects linked to the systematics of these taxa will be shown, but also new data related to other research disciplines, such as, among others, those linked to the paleobiogeography, temporal distributions, variability, or neuroanatomy.

## Pelagization in turtles: single or parallel origins?

Márton **Rabi**<sup>1</sup>, Benjamin P. **Kear**<sup>2</sup>, Jorge Domingo **Carrillo Briceño**<sup>3</sup>, Marcelo R. **Sánchez-Villagra**<sup>3</sup>, Torsten M. **Scheyer**<sup>3</sup>

<sup>1</sup>University of Tübingen, Department of Geosciences, marton.rabi@uni-tuebingen.de; <sup>2</sup>University of Uppsala, Museum of Evolution, Paleontology and Mineralogy; <sup>3</sup>University of Zürich, Institute of Paleontology, Zürich, Switzerland.

Phylogenies keep reinforcing that the full set of pelagic marine adaptations, including enlarged, rigid fore-paddles for an underwater flight-style locomotion and lateralized orbits for a wider field of vision evolved only once during the history of turtles in a group that includes extant chelonoid sea turtles. Protostegidae, an extinct Cretaceous clade, is hypothesized to be part of this marine invasion even though their plesiomorphic morphology and spatiotemporal distribution is more compatible with a relationship with Late Jurassic stem-cryptodiran turtles that already show advanced marine adaptations. Part of the issue is that fossils of early protostegids are globally rare and no taxa with transitional specializations are known. We report on a new early protostegid from the Early Cretaceous (Aptian) of Venezuela, based on a three-dimensionally preserved skull, characterized by plesiomorphies absent in all other protostegids but present in shallow-marine or freshwater pancryptodires, including a narrow interorbital space, dorsolaterally oriented and relatively small-sized orbits, an anteriorly sloping skull roof, and relatively deep lower and upper temporal emarginations. We discuss the implications of this taxon for the evolution of key pelagic adaptations in Protostegidae and critically review the evidence from the fossil record and previous phylogenies for a single pelagization in turtles.

## New insights into the anatomy and evolution of Carettochelyidae

Yann **Rollot**<sup>1</sup>, Serjoscha W. **Evers**<sup>1</sup>, Gabriel **Ferreira**<sup>2</sup>, Léa C. **Girard**<sup>1</sup>, Ingmar **Werneburg**<sup>2</sup>, Marcus **Zuber**<sup>3</sup>, Elias **Hamann**<sup>3</sup>, Walter G. **Joyce**<sup>1</sup>

<sup>1</sup>Department of Geosciences, University of Fribourg, Fribourg, Switzerland, yann.rollot@unifr.ch; <sup>2</sup>Fachbereich Geowissenschaften, Universität Tübingen, Tübingen, Germany; <sup>3</sup>Institute for Photon Science and Synchrotron Radiation, Karlsruhe Institute of Technology, Eggenstein-Leopoldshafen, Germany.

Carettochelyidae is a clade of aquatic hidden-neck turtles, of which the pig-nosed turtle *Carettochelys insculpta* lives as a relict in New Guinea and Australia as the only extant representative. The fossil record of this clade is relatively poor with only 14 valid species that range from the Early Cretaceous to the Miocene. The known material remains overall scarce and generally consists of partial and sometimes isolated skulls or shells. As part of a project that aims to reinvestigate the evolutionary history of trionychians, we here present several advances into our understanding of the anatomy and evolution of carettochelyid turtles using microcomputed tomography. We provide a description of the head of *Carettochelys insculpta*, including insights into osteological ontogenetic variation and jaw-related myology, and describe a new cranial arterial pattern unique to the pig-nosed turtle. We also focus on the anatomy of several extinct members of the *Allaeochelys* lineage. We redescribe the cranium of *Allaeochelys libyca* from the Middle Miocene of Libya, correcting past interpretations about its anatomy and proposing new phylogenetic characters. We also report new cranial and shell material from the Early Miocene of Egypt that represents remains of one of the largest carettochelyid turtles known to date. Last, we reinvestigate the anatomy of the emblematic *Allaeochelys crassesculpta* from the Eocene Messel pit of Germany. Despite the remarkable richness of the material recovered, this taxon still lacks a detailed description, which we have undertaken using a still rarely employed imaging method, X-ray computed laminography.

## **First vertebrate reported from the Maastrichtian Neylandville Marl Formation of Texas is a novel marine turtle (Chelonioidea: Ctenochelyidae)**

Heather F. Smith<sup>1,2\*</sup>, Brent Adrian<sup>2</sup>, Patrick Kline<sup>3</sup>

<sup>1</sup>Midwestern University, Glendale, USA, hsmith@midwestern.edu; <sup>2</sup>Arizona State University, Tempe, USA; <sup>3</sup>Heard Natural Science Museum & Wildlife Sanctuary, McKinney, USA.

The marine turtle family Ctenochelyidae was a Late Cretaceous North American radiation of Pan-Chelonioidea, broadly distributed along the coastlines of the Atlantic Coastal Plain and Mississippi Embayment. Here, we describe a large carapace representing a novel ctenochelyid taxon from the Maastrichtian Neylandville Marl Formation in northeastern Texas. It represents the first vertebrate reported from the unit, although a rich assemblage of marine invertebrates is previously known. The specimen is recognized as a ctenochelyid by its large carapace with a prominent midline ridge of epineural ossifications and it is reduced by fontanelles between the peripherals and costals. It has a unique combination of characters: large, cordiform carapace (~120 cm); epineurals between neurals N1/2, N3/4, N5/6, and N7/8; complete articulation of costal 1 and peripherals 1-2; lack of postnuchal fontanelles; broad nuchal embayment including a pronounced anterior projection of peripheral 1; preneural present; smooth shell texture; weakly serrated lateral peripheral edges. A maximum parsimony phylogenetic analysis was conducted in TNT v1.6, and in the resulting majority-rule consensus tree, the specimen was positioned at the base of Ctenochelyidae in an unresolved polytomy with *Asmodochelys parhami* and the unresolved clade (*Peritresius ornatus* + *Prionochelys matutina* + *Ctenochelys acris* + *Ctenochelys stenoporus*). The presence of a new Maastrichtian ctenochelyid from the western end of the Gulf of Mexico expands the known diversity and geographical distribution of Ctenochelyidae. The Neylandville Marl lies within the faunal zone of the marine oyster *Exogyra cancellata*, providing a particular marine ecological context that extends from Mexico to New Jersey.

## **Updated cranial and mandibular description of the Late Cretaceous baenid turtle *Saxochelys gilberti* based on micro-computed tomography scans and new information on the holotype-shell association**

Gaël E. Spicher<sup>1,2</sup>, Tyler R. Lyson<sup>3</sup>, Serjoscha W. Evers<sup>2</sup>

<sup>1</sup>Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany, s84gspic@uni-bonn.de; <sup>2</sup>University of Fribourg, Fribourg, Switzerland; <sup>3</sup>Denver Museum of Nature & Science, Denver, Colorado, USA.

*Saxochelys gilberti* is a turtle from the clade Baenidae from the Late Cretaceous Hell Creek Formation of the United States of America. This species is known from numerous cranial, shell, and other postcranial material. Baenid turtles present a high taxonomic diversity and are common in the fossil record throughout the Late Cretaceous to the Eocene. Detailed anatomical knowledge is essential to understanding the systematics and morphological evolution of the group. This is particularly important as baenids represent an important group of continental vertebrates that survived the Cretaceous/Paleogene mass extinction. The use of high-resolution micro-computed tomography scanning on the holotype skull reveals additional anatomical details for the already well-known *Saxochelys gilberti*. This includes the revision of certain anatomical observations from the original description, but also detailed knowledge of internal anatomical features of the braincase and the description of a well-preserved axis (cervical vertebra 2). Our new detailed description of the skull, coupled with prior research on the shell and postcranial elements make *Saxochelys* one of the best documented nearly complete baenid turtles, which are often only known from either isolated shell or cranial material. A revised phylogenetic analysis confirms the position of *Saxochelys gilberti* as a derived baenid (Eubaeninae) more closely related to *Baena arenosa* than to *Eubaena cephalica*.

## **Trabecular long-bone ecomorphology in Testudines: insights into evolutionary adaptations**

Xenia **Steinmann**<sup>1</sup>, Gabriel S. **Ferreira**<sup>1,2</sup>

<sup>1</sup>Department of Evolution and Ecology, Geosciences Department, University of Tübingen, Tübingen, Germany, [xenia.steinmann@student.uni-tuebingen.de](mailto:xenia.steinmann@student.uni-tuebingen.de); <sup>2</sup>Senckenberg Centre for Human Evolution and Palaeoenvironment at the University of Tübingen, Tübingen, Germany.

The trabeculae in long bones are characterized by relatively higher metabolic activity and extensive remodelling rates, being particularly responsive to external loading conditions. As such, the trabecular morphology of long bones has been noted to be impacted by lifestyle across different vertebrates, with aquatic reptiles generally displaying thicker and more spaced trabeculae. Turtles, completely relying on their limbs for locomotion while occupying diverse habitats ranging from fully terrestrial to fully aquatic, offer an intriguing opportunity for studying osteological adaptations, but have been largely neglected in trabecular bone analyses. Most studies focus on the shell, with only one analysis of the 3D trabecular microstructure of long bones including turtles. In this study, we aim to analyse long bone trabecular structure in turtles using micro-CT data. A comprehensive examination of various trabecular parameters — e.g., trabecular spacing, bone volume and anisotropy — was conducted on extant Testudines with different ecologies. The sampling will encompass a diverse array of species to facilitate a meticulous analysis of the wide spectrum of lifestyles and body sizes within the group. Preliminary observations indicate that fully and semi-aquatic turtles exhibit more similar degrees of anisotropy and bone volume fraction in comparison to their terrestrial counterparts. Additionally, body size seems to influence trabecular thickness, with larger turtles displaying thicker and more spaced trabeculae. Although still preliminary, our results seem promising for revealing the relation between long bone microstructure and ecology in turtles and might prove to be a useful tool for palaeobiological inference.

## **Past, present, and future studies on southern Gondwanan turtles: a view from the South**

Juliana **Sterli**<sup>1,2</sup>

<sup>1</sup>Consejo Nacional de Investigaciones Científicas y Técnicas; <sup>2</sup>Museo Paleontológico Egidio Feruglio, Trelew, Argentina, [jsterli@mef.org.ar](mailto:jsterli@mef.org.ar).

Extinct turtles from Southern Gondwana are known from the XIX Century. However, two-thirds of the knowledge about them has been produced during the last 30 years, changing notably our understanding on the evolution of the cheloniofauna of this region. Nowadays, there are more than 500 occurrences of turtles in southern Gondwana spanning from the Lower Jurassic until the Holocene. Like South America, in southern Gondwana the Pangean and the Gondwanan phases in the evolution of continental turtles could be recognized. The Pangean phase (Early–Middle Jurassic) is characterized by basal forms belonging to non-perichelydian Mesochelydia. The Gondwanan phase (Early Cretaceous–middle Eocene) is dominated by pan-chelids and meiolaniforms. Since the middle Eocene, Australia+Zelandia and Patagonia underwent through different biogeographic histories. In South America, chelids and meiolaniids became extinct in Patagonia after the middle Eocene, and it was not until the late Oligocene that tortoises arrived at South America that turtles roamed again in that region. On the contrary, in Australia, chelids and meiolaniids diversified during the Neogene, reaching distant islands in the case of meiolaniids. The Neogene-Recent Australian cheloniofauna is completed by the arrival of trionychids and carettochelyids. The meiolaniids became extinct during the Pleistocene and there is no evidence of human interaction with these giant, terrestrial turtles. In this contribution, new findings from Southern Gondwana are briefly presented and their impact in the understanding on turtle evolution is discussed. Furthermore, I explore pending questions and future lines of research to provide a more complete view on the evolution of turtles from the South.

## Revision of ‘*Proganochelys*’ *ruchae* from the Late Triassic of Thailand

Tomasz **Szczygielski**<sup>1</sup>, Dawid **Drózdź**<sup>2</sup>, Phornphen **Chanhasit**<sup>3</sup>, Sita **Manitkoon**<sup>4</sup>, Pitaksit **Ditbanjong**<sup>5</sup>

<sup>1</sup>Institute of Paleobiology, Polish Acad. of Sciences, Warsaw, Poland, t.szczygielski@twarda.pan.pl; <sup>2</sup>Nalecz Institute of Biocybernetics and Biomedical Engineering, Polish Acad. of Sciences, Warsaw, Poland; <sup>3</sup>Sirindhorn Museum, Department of Mineral Resources, Kalasin, Thailand; <sup>4</sup>Palaeontological Research and Education Centre, Excellence Center in Basin Studies and Applied Palaeontology Mahasarakham University, Maha Sarakham, Thailand; <sup>5</sup>Department of Geotechnology, Khon Kaen University, Thailand.

The Triassic stem turtle genus *Proganochelys* was historically proposed to have an exceptionally wide geographic distribution, spanning modern-day Europe, Asia, and North America. However, most remains attributed to *Proganochelys* are fragmentary and difficult to interpret. Moreover, most of those referrals were made before the reassessment and/or discovery of other informative Triassic turtle species, representing different clades (Proterochersidae, Australochelyidae) and providing valuable data about the Triassic turtle diversity and anatomy. Therefore, they require validation. Remains of ‘*Proganochelys*’ *ruchae* include shell fragments from the Huai Hin Lat Formation (Thailand). Our review of the material also revealed a single ilium. Their original generic identification was based on the presence of large gular and extragular projections and dorsal epiplastral processes – characters since found to be common in the earliest testudinans. The uncertainty of that referral was admitted by the original authors, who more recently called the species either “*Proganochelys*” *ruchae* or aff. *Proganochelys* *ruchae*. Our revision revealed that some specimens (described in 1982) are lost but the holotype and other fragments show morphology more congruent with *Proterochersis* than *Proganochelys*: anteroposteriorly elongated, shelf-like pleural bosses, three supramarginals, shape and layout of bridge-level marginals, rounded gulars, position of gularohumeral sulcus, details of extragulars, location and shape of dorsal epiplastral processes, bridge geometry, two pairs of abdominal scutes, and morphology of the ilium. The main differences with *Proterochersis* concern the anterior plastral lobe, may represent plesiomorphies, and warrant a generic distinction. ‘*Proganochelys*’ *ruchae* is recovered as a proterochersid based on a phylogenetic analysis utilizing 22 new characters.

### Evolution of the rostral vasculature in turtles

Seishiro **Tada**<sup>1</sup>, Takanobu **Tsuihiji**<sup>2,3</sup>, Donald J. **Morgan**<sup>4</sup>, Lawrence M. **Witmer**<sup>4</sup>, Ingmar **Werneburg**<sup>5,6</sup>

<sup>1</sup>Fukui Prefectural University, Eiheiji, Japan, seishiro.tada.0809@gmail.com; <sup>2</sup>National Museum of Nature and Science, Tsukuba, Japan; <sup>3</sup>The University of Tokyo, Bunkyo-ku, Japan; <sup>4</sup>Ohio University, Athens, U.S.A.; <sup>5</sup>Senckenberg Centre for Human Evolution and Palaeoenvironment an der Universität Tübingen, Tübingen, Germany; <sup>6</sup>Paläontologische Sammlung, Eberhard Karls Universität, Tübingen, Germany.

Although turtles are characterized by numerous morphological features unique among diapsids, evolutionary origins and changes of such features along their fossil lineage have not been fully explored. For elucidating the evolutionary history of turtles within Diapsida, reconstruction of soft-tissue anatomy in early-diverging fossil forms is highly relevant, but such an endeavor requires detailed information on extant forms. We herein focused on the cephalic vasculature. Although the cephalic vasculature including the rostral part is important in moderating the temperature of neurosensory tissues in amniotes, detailed information on anatomy and osteological correlates of this system is just being explored in recent years. Here the cephalic vasculature in four extant cryptodiran turtles were examined using vascular injection and  $\mu$ CT scanning as well as through gross dissection. Although these turtles share an arterial vascular pattern similar to that of lepidosaurs and are suggested anatomically to possess the thermal control function, they have a specific characteristic in the rostral region that the inframaxillary artery has a significant contribution to the narial vascularization. The degree of contribution of the artery in the narial vascularization is evaluated in fossil forms based on the position of the foramen through which the artery from the palate enters the nasal cavity. As a result, the stem lineage is found to show a gradual increase in its contribution toward the crown clade. In particular, one of the earliest turtles, *Proganochelys quenstedtii*, possessed a relatively rostrally positioned foramen, suggesting that this arterial arrangement in the rostrum represents an ancestral condition for Testudinata.

# First Description of the Cranium and Mandible of the Testudinid *Gopherus hexagonatus* from the Pleistocene (Rancholabrean) Beaumont Formation (Texas, USA): Insights into the Phylogenetic Relationships among North American Fossil Gopher Tortoises

Kelly A. Vega-Pagán<sup>1</sup>, David M. Alba<sup>1</sup>, Àngel H. Luján<sup>1</sup>

<sup>1</sup> Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain; kelly.vega@icp.cat.

*Gopherus* is the only extant testudinid genus in North America. It includes at least six living species according to the most recent molecular analyses. Nonetheless, its fossil record dates to the Oligocene, being represented by giant species that lasted until the Late Pleistocene. Although they are abundantly represented in the fossil record, their taxonomy and phylogeny are still debated. In particular, *Gopherus hexagonatus*, one of the four large-sized tortoises that lived during the Pleistocene in South Texas, has recently been considered a nomen vanum (given the lack of diagnostic features) or a junior subjective synonym of *Gopherus donlaloii* (from the Late Pleistocene of Mexico). The inclusion of *G. hexagonatus* in phylogenetic analyses has consistently resulted in a polytomy among *Gopherus* species. We describe an almost complete and well-preserved individual attributed to *G. hexagonatus* from the Rancholabrean (Pleistocene) locality Los Coyotes (Beaumont Formation) in Willacy County (Texas, USA). It consists of shell, postcranial, and cranial remains, which allow us to provide the first descriptions of the skull for this taxon. We compare its cranial features to those of other members of the genus (particularly *G. donlaloii*) to evaluate the distinctiveness of *G. hexagonatus*. Additionally, we coded the craniomandibular characters and ran updated cladistic matrices for testudinids using implied weight maximum parsimony to investigate their phylogenetic relationships. Morphological comparisons revealed differences that support the distinction of *G. hexagonatus*, while the cladistic results provided a better resolved *Gopherus* phylogeny and supported a sister-taxon relationship between *G. hexagonatus* and *Gopherus edae*.

## Turtle species extinction across the Cretaceous / Palaeogene boundary

Evangelos Vlachos<sup>1</sup>

<sup>1</sup> CONICET and Museo Paleontológico Egidio Feruglio, Trelew, Argentina, evlacho@mef.org.ar.

The last mass extinction event that took place some 66 million years ago at the Late Cretaceous/Palaeogene boundary caused the extinction of many clades, including the non-avian dinosaurs. Turtles, as well as several other vertebrate clades, survived. However, the debate about whether the diversity of turtles has been affected during this event is still ongoing. During the last two decades a huge amount of new data on the turtle fossil record has been published, accompanied by joint efforts to curate it together with previously published information in open databases like the PaleoBiology Database. This dataset now allows the construction of global diversity curves at the species level, which indicate that global turtle diversity not only was affected during the last mass extinction events at the end of the Cretaceous, but it was already in decline during the last 20 million years prior to the extinction event. Compared to the historical peak of turtle diversity in the Campanian, the global turtle diversity was reduced at half during the Danian, approximately, only to gradually recover during the Cenozoic. These results are different compared to previous analyses not only because they are based on a more updated dataset but also because previous estimations are based on generic counts, shown herein to add a significant and artificial taxonomic bias in vertebrate groups like turtles that contain multispecific genera. The sample coverage of turtle occurrences at the stage level is calculated and discussed as well.