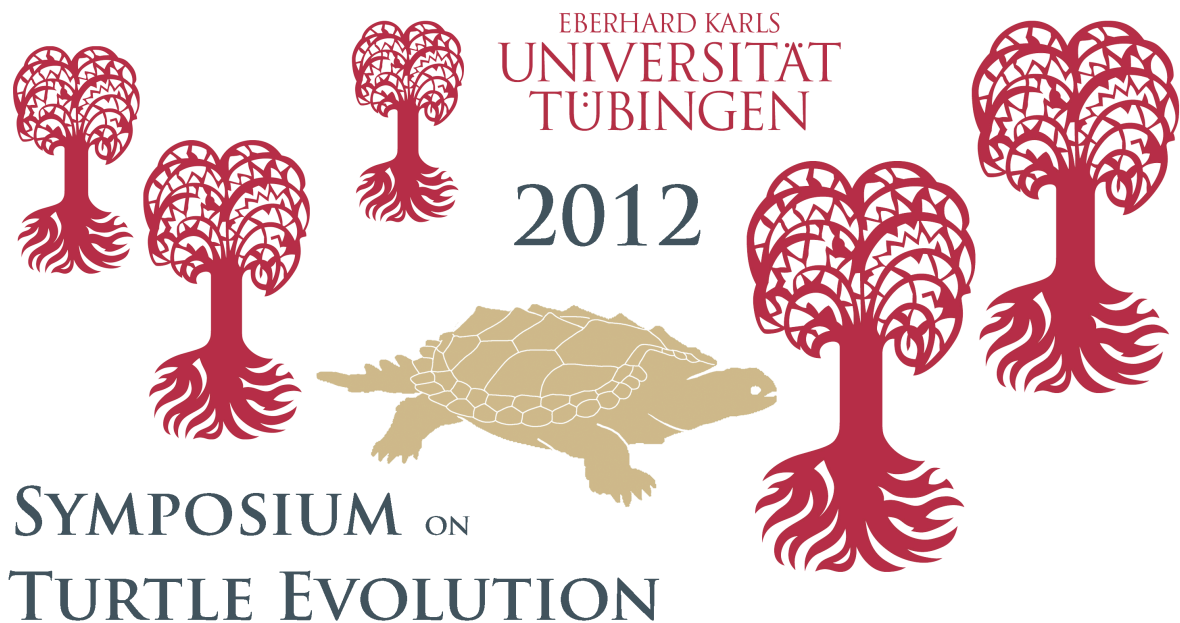


PROGRAM AND ABSTRACTS



UNIVERSITY OF TÜBINGEN

DEPARTMENT OF GEOSCIENCES

JUNE 01-04, 2012

SYMPOSIUM ON TURTLE EVOLUTION 2012

University of Tübingen

Department of Geosciences

Tübingen, Germany

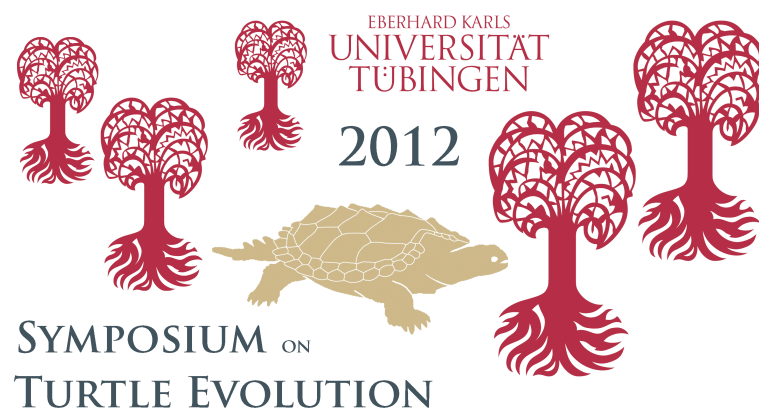
Host Committee:

Walter G. Joyce

Joe A. Corsini

Ingmar Werneburg

Márton Rabi



Tübingen 2012

ABOUT THE SYMPOSIUM LOGO



The University of Tübingen was founded in 1477 by Count Eberhard V (a.k.a. *Eberhard the Bearded*), who later became the first Duke of Württemberg. The University is approximately the 50th institution of higher learning to be founded in Europe and is the third oldest continuously operating university in modern Germany after Heidelberg and Leipzig. Count Eberhard travelled in 1468 on a pilgrimage to the Holy Land and became a knight of the Order of the Holy Sepulcher. To advertise this accomplishment, he chose *attempto!* (Latin: I dare!) as his motto and the exotic palm tree as his personal symbol. These serve to this very day as the official symbols of the university he founded.

The University of Tübingen has a history of innovative thought, particularly in theology. Particularly eminent students and/or professors have been the astronomer Johannes Kepler, Joseph Ratzinger (a.k.a. Pope Benedict XVI), the poet Friedrich Hölderlin, and the philosophers Friedrich Schelling, Georg Wilhelm, Friedrich Hegel, and Albert Schweizer. Friedrich Miescher discovered DNA while working at Tübingen. The University became a major center for paleontology through the founding of the Institute for Paleontology. The most prominent professors include Friedrich August von Quenstedt (stratigraphy), Friedrich von Huene (basal reptiles), Otto Heinrich Schindewolf (Evolutionary Theory), and Adolf Seilacher (trace fossils, constructional morphology). The fossil collections housed at Tübingen are vast and have a worldwide scope, but include only few turtles of importance. The most notable exception is the holotype of *Proganochelys quenstedti*, a steinkern found at the nearby town of Esslingen.

The Symposium Logo uses the official University of Tübingen livery (gold, carmine, and slate grey) and depicts the silhouette of *P. quenstedti* among the modified logo of the University consisting of a forest of palm trees.

Sources: wikipedia.de, wikipedia.org

PROGRAM

Friday, June 1, 2012

Registration and Icebreaker

Location: Hölderlinstr. 12, S309 & Back Parking Lot

17:00 – 20:00	Registration
18:00 – 22:00	Icebreaker, Dinner and Drinks will be Served

Saturday, June 2, 2012

Opening

Location: Hölderlinstr. 12, S320

09:00 – 09:05	M. Böhme	Welcome address by the Curator of the Paleontological Collections of the University of Tübingen
09:05 – 09:10	H. Bocherens	Welcome address by the Head of the Biogeology Workgroup of the University of Tübingen
09:10 – 09:15	W.G. Joyce	Opening by the Conveners of the 2012 Symposium on Turtle Evolution

Session 1: Turtle Origins and Stem Turtles

Chairperson: J. Sterli

Location: Hölderlinstr. 12, S320

09:20 – 09:40	T.R. Lyson	Evolutionary Developmental Model for the Origin of the Turtle Shell
09:40 – 10:00	T. Sulej	New Turtles from the Triassic of Poland
10:00 – 10:20	W.G. Joyce	The Pectoral and Pelvic Girdles of the Late Triassic Turtle <i>Proterochersis robusta</i>
10:20 – 10:40	J. Sterli	New Findings of Meiolaniid and Meiolaniid-like Taxa from Patagonia, Argentina

COFFEE BREAK

Session 2: Panpleurodira		
Chairperson: P.S.R. Romano		
Location: Hölderlinstr. 12, S320		
11:10 – 11:30	M. Vremir	A New Dortokid Panpleurodire from the Maastrichtian of Transylvania, Romania
11:30 – 11:50	I.J. Maniel	New Material of <i>Hydromedusa casamayorensis</i> from the Middle Eocene of Patagonia and Its Phylogenetic Implications
11:50 – 12:10	P.S.R. Romano	On a New Side-necked Turtle from the Lower Cretaceous (Upper Barremian) of Northeastern Brazil
12:10 – 12:30	F.O. Deantoni	Analysis of Internal Structures of the Skull of Pelomedusoides Based on Three-dimensional Helical Tomography

LUNCH BREAK

Session 3: Asian Mesozoic Eucryptodires		
Chairperson: D.B. Brinkman		
Location: Hölderlinstr. 12, S320		
14:00 – 14:20	I.G. Danilov	A New Xinjiangchelyid Turtle from the Middle Jurassic of Siberia, Russia
14:20 – 14:40	D.B. Brinkman	A New Turtle from the Early Cretaceous Changma Basin of North-western Gansu Province, P. R. China
14:40 – 15:00	M. Rabi	New Insights into the Evolution of the Carotid Circulation System in Eucryptodiran Turtles
15:00 – 15:20	R. Hirayama	Morphology and Evolution of Nanhsiungchelyidae (Cryptodira: Trionychia)
15:20 – 15:40	H. Tong	A revision of <i>Sinaspideretes wimani</i> Young et Chow, 1953

COFFEE BREAK

Session 4: European Turtle Faunas		
Chairperson: C.A. Meyer		
Location: Hölderlinstr. 12, S320		
16:10 – 16:30	A. Pérez-García	The Mesozoic Turtles from the Iberian Peninsula: an Update
16:30 – 16:50	T.M. Scheyer	Bone Microstructure of Selected Fossil Turtle Shell Plates from the Cretaceous of Spain
16:50 – 17:10	C.A. Meyer	Oxygen isotope compositions of Late Jurassic turtles in Europe: new data from Switzerland and Germany
17:10 – 17:30	M. Jansen	A Diverse Turtle Fauna from the Upper Jurassic of Lower Saxony and its Implications for Taxonomic Distribution and Ecology

Conference Dinner	
Location: Kronenstraße 8, Weinstube Forelle	
19:00 – 22:00	Group meets directly at <i>Weinstube Forelle</i>

Sunday, June 3, 2012

Session 5: Testudinoids		
Chairperson: J. Claude		
Location: Hölderlinstr. 12, S320		
09:00 – 09:20	J. Claude	A Reinterpretation of Pre-Eocene Testudinoids
09:20 – 09:40	W. Naksri	The Late Oligocene Turtle Assemblage from Nong Ya Plong, Petchaburi Province, Thailand
09:40 – 10:00	J. A. Corsini	<i>Testudo antiqua</i> and the Lost Miocene Quarry at Hohenhöwen
10:00 – 10:20	E.V. Syromyatnikova	Fossil Turtles of the Genus <i>Baicalemys</i> (Emydidae): New Data on Morphology and Phylogenetic Position

10:20 – 10:40	N.S. Vitek	Cf. <i>Terrapene carolina</i> : a complicated evolutionary history
10:40 – 11:00	E. Vlachos	Special Remarks on the Posterior Limb morphology of the Giant Continental Tortoises from the Pliocene of Thessaloniki area (Macedonia, Greece)

Session 6: Poster Presentations and Coffee Break

Location: Hölderlinstr. 12, S309

11:00 – 12:30	S. Chapman	A new specimen of <i>Puppigerus camperi</i> from the London Clay of Walton-on-the Naze, Essex, United Kingdom
	G. Ferriera	New Specimens, Redescription and Phylogenetic Position of <i>Bauruemys elegans</i> from the Late Cretaceous of Brazil
	P. Havlik	A Carettochelyine Turtle from the Early Miocene of Libya
	H.-V. Karl	The First Shell Remains of <i>Rhinochelys cantabrigiensis</i> from the Upper Cretaceous of NW-Germany (Testudines: Protostegidae)
	D. Lawver	Turtle Eggs and Embryos from the Upper Cretaceous Judith River Formation of Montana
	G. Oliviera	A <i>Podocnemis</i> Skull from the Upper Miocene Solimões Formation, Acre Basin, Brazil
	C. Puentner	Taxonomy and Phylogeny of <i>Tropidemys</i> (Eucryptodira) Based on New Specimens from the Kimmeridgian of the Swiss Jura
	A. Takahashi	The Genus <i>Ocadia</i> (Testudines: Geoemydidae) from the Middle Miocene of Tanegashima Island, Southwestern Japan, and Its Paleobiogeographic Implications

LUNCH BREAK

Session 7: Miscellanea		
Chairperson: M. Delfino		
Location: Hölderlinstr. 12, S320		
14:00 – 14:20	R. W. Burroughs	Exploring and Evaluating the Impact of Anatomical Partitions on Morphology-based Phylogenetic Analyses
14:20 – 14:40	M. Delfino	Ossicle Gross Morphology and Microstructure of <i>Psephophorus polygonus</i> Meyer, 1847
14:40 – 15:00	M. Lambertz	Insights into the Evolution of the Respiratory Apparatus in Cryptodiran Turtles
15:00 – 15:20	I. Werneburg	An integrative study on the anatomy and development of the 'hooked fifth metatarsal' in the turtle pes
15:20 – 15:40	N. Natchev	Considerations on the Evolution of Feeding Systems in Turtles

COFFEE BREAK

Session 8: Taphonomy		
Chairperson: J.-P. Billon-Bruyat		
Location: Hölderlinstr. 12, S320		
16:10 – 16:30	M. J. Knell	In the Footsteps of Weigelt: A Century of Extant Observations, Experiments, and Fossil Analyses in Turtle Taphonomy
16:30 – 16:50	Brian Roach	Evidence for Periods of Increased Aridity during the Latest Cretaceous of North America: A Description of Several Mass Death Assemblages of Turtles
16:50 – 17:10	J.-P. Billon-Bruyat	Under the Feet of Sauropods: a Trampled Coastal Marine Turtle

Closing

Location: Hölderlinstr. 12, S320

17:10 – 17:30	W.G. Joyce	Final Remarks, Conference Volume, Identification of Next Conference Venue
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Informal Social Gathering for Those Staying for Field Trip

Location: Gartenstraße 4, Neckarmüller (good weather)

Location: Wilhelmstraße 44, Saints and Scholars (bad weather)

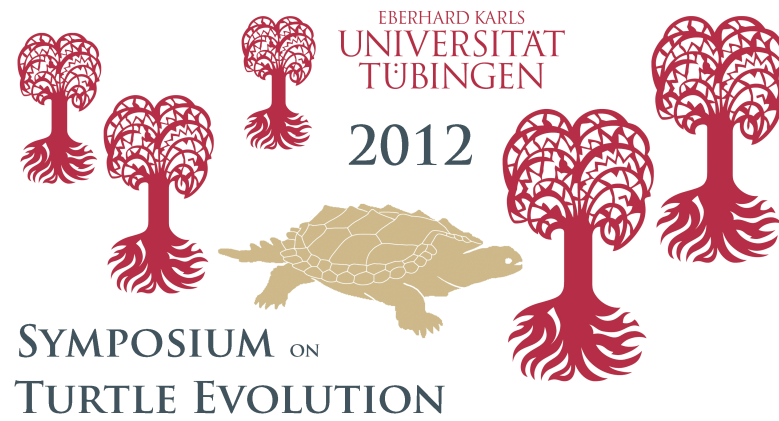
18:00 – 22:00	The final destination will depend on weather
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Monday, June 4, 2012

Solnhofen Field Trip

07:45	Meeting in front of Paleontological Museum at the corner of Sigwartstraße and Nauklerstraße
08:00	Departure
11:00	Visit of the Quarry at Langenaltenheim near Solnhofen
13:00	Lunch at <i>Gasthaus Krone</i> in Eichstätt (included in registration)
15:00	Visit of Jura-Museum in Eichstätt
16:30	Departure from Eichstätt
19:30	Approximate arrival time in Tübingen

ABSTRACTS



Under the Feet of Sauropods: a Trampled Coastal Marine Turtle

Jean-Paul Billon-Bruyat¹, Daniel Marty¹, Loïc Bocat¹, Géraldine Paratte¹

¹ Section d'archéologie et paléontologie, Office de la culture, République et Canton du Jura, Hôtel des Halles, 2900 Porrentruy, Switzerland; jean-paul.billon@palaeojura.ch

The hypothesis that sauropod dinosaurs (the largest terrestrial herbivores of all time) entered into coastal marine environments on occasion or habitually is matter of debate. While the body fossil record generally indicates an inland preference, the ichnological record rather suggests (at least for the Jurassic and Early Cretaceous) that sauropods are frequently associated with low-latitude, coastal marine carbonate platform environments. This may partially be related to different preservation biases for bones and tracks in various environments. In the Late Jurassic, for example, many basal eucryptodiran turtles are known from coastal marine deposits throughout Europe (*e.g.*, in Solnhofen, 'Solothurn Turtle Limestone', Cerin), but never directly associated with sauropod tracks. Here, we report a remarkable shell of a coastal marine turtle (*Craspedochelys*, Plesiochelyidae, Eucryptodira) discovered within dinosaur track-bearing tidal biolaminites (Kimmeridgian) of the Jura carbonate platform, in the vicinity of Porrentruy (Canton Jura, NW Switzerland). The well-preserved shell (nearly complete, articulated carapace and plastron; upside down) was quickly buried (no post-mortem incrustation; no evidence for scavenging) and secondarily mechanically broken. Due to a vertical pressure, the most posterior part of the shell was broken and the shell was pushed down by about 7 cm. The shell was discovered just below 10–15 cm deep medium-sized sauropod tracks, surrounded by large displacement rims. The shell was embedded in a soft and thick layer of carbonate mud when a sauropod may have walked on it. The track-bearing layer lacks desiccation cracks, indicating that it was not subaerially exposed or at least not for a longer time period. The coeval presence of this coastal marine turtle and sauropod tracks is direct evidence that sauropods entered into environments that were located very close to the coast.

A New Turtle from the Early Cretaceous Changma Basin of Northwestern Gansu Province, P. R. China

Donald B. Brinkman¹, Chong-Xi Yuan², Qiang Ji², Da-Q. Li³, Hailu You⁴

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² Institute of Geology, Chinese Academy of Geological Sciences, 26 Baiwanzhuang Road, Beijing 100037, P.R. of China

³ Gansu Geological Museum, 6 Tuanjie Road, Chengguan District, Lanzhou, Gansu Province, 730010, P. R. China.

⁴ Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xizhimenwai Street, Beijing 100044, P. R. China

A new genus of turtle from the Early Cretaceous Xiagou Formation, Changma Basin, northwestern Gansu Province, adds to our understanding of the diversity of Early Cretaceous turtles of Asia. The Changma turtle is similar to Early Cretaceous turtles from Asia included in the Sinemydidae/ Macrobaenidae in having an oval carapace with a reduced, cruciate plastron with buttresses that do not extend onto the costals. With a shell that exceeds 35 cm in length, it is the largest Early Cretaceous "macrobaenid." A dominant feature of the shell is the presence of large costal-peripheral fenestrae. Although the size of costal-peripheral fenestrae is generally an unreliable taxonomic character, their presence is considered to be significant in this case because the large size of the type specimen indicates that it is an adult. The skull is similar to that of *Hangaiemys* and different from *Ordosemys* in being relatively long, having prefrontals that contact one another at the mid-line, and having a foramen palatinum posterior that is very large and includes the maxilla in its border. It is similar to both of these in that the suture between the basioccipital and the basisphenoid is located at the posterior edge of the pterygoid and the pterygoid only contacts the antero-lateral corner of the basioccipital. Despite the addition of the new species and new characters to previous phylogenetic analyses the relationships of the "macrobaenid" turtles are still not well resolved.

As well as representing a new genus, the material is of interest because each specimen documents a distinct stage of ontogenetic development of the shell. In the carapace, the dermal portions of the costals are unossified in the most juvenile specimen but peripherals are present. In contrast with the late ossification of the dermal bone of the carapace, the plastron ossifies relatively early.

Exploring and Evaluating the Impact of Anatomical Partitions on Morphology-based Phylogenetic Analyses

Robert W. Burroughs¹

¹Jackson School of Geosciences, The University of Texas at Austin, 1 University Station, C1100, Austin, Texas 78712-0254; rburroughs@utexas.edu

I tested the hypothesis that two anatomical partitions (cranial and shell) can provide complimentary phylogenetic signal using a dataset of extant Emydid turtles. I conducted a series of tests to evaluate how those partitions affect resulting phylogenetic trees. Traditional parsimony approaches were used to evaluate congruency between partitions when they are independently analyzed, including the partition-homogeneity test. In addition to parsimony, congruency was evaluated using Bayesian partition analyses, Bayes factor calculations, and topological congruency between reconstruction methods. The results of these tests indicate that the phylogenetic hypotheses generated by each partition independently are not fully congruent regardless of reconstruction method, and that a loss of resolution is generally found when using only cranial characters. Compared to other reconstruction methods (e.g., Bayesian or maximum likelihood) parsimony has increased topological resolution, regardless of the partition used. The partition-homogeneity test was inconclusive, with partitions appearing to be no more, or less, congruent than incongruent with one another. Bayes factors indicated that partitioning the data into two anatomical partitions is appropriate and statistically preferred. Bayesian partition analyses showed that tree topology was improved when each partition is allowed to inform tree topology independently. This indicates that each partition is appropriate within the dataset and that each partition is potentially evolving at a different rate. If the partitions exhibit rate heterogeneity then selection of characters for evaluating older (stem) versus younger (crown) taxa is greatly impacted. These data indicate that exploration of a dataset is critical to understanding how character partitions may be informing tree topology and may produce biased results; these data also provide an insight into the selection of characters and character partitions for turtle systematics.

A New Specimen of *Puppigerus camperi* from the London Clay of Walton-on-the Naze, Essex, United Kingdom

Sandra Chapman¹, Richard T. J. Moody²

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² Emeritus Professor of Geology, Kingston University London; rtj.moody@virgin.net

The London Clay of the Walton-on-the-Naze area overlays the Harwich Formation, which is dated c.50 million years by analyses of the volcanic ash beds found throughout the sequence. The London Clay in the Walton-on-the Naze area is comprised of fine grained, clay-rich deposits that yield a host of invertebrates, fossil plant debris and seeds together with mostly disarticulated skeletons of fish, birds, mammals and reptiles.

Turtles belonging to the marine Cheloniidae and the Erquelinnidae are recorded from the lower levels of the London Clay in the area of the Essex coast the majority of material being poorly preserved skulls and shells. In 1977 a fossiliferous calcareous nodule was presented to the NHM in London and a preparation request made to the Palaeontology Department preparation laboratory in the same year. This was mainly undertaken using acid preparation and several years elapsed before the specimen was fully prepared. It was then placed in the collections and overlooked until recently with the discoveries of primitive cheloniids in Russia and North Africa refreshing the memories of the authors of this poster.

The work undertaken by Ron Croucher has resulted in access to a beautiful skull, excellent limb and girdle material and numerous vertebrae and the incomplete presentation of a very delicate shell. This material enables the authors to draw comparisons with the wonderful material housed in The Institut Royal des Sciences Naturelles in Bruxelles. The comparison raises as many questions as answers and the skull in particular some unique features. This presentation provides a description of in particular the skull and lower jaw and a comparison with sister group material from Europe, Africa and Russia.

A Reinterpretation of the Pre-Eocene Testudinoids

Julien Claude¹, Haiyan Tong²

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² Palaeontological Research and Education Centre, Mahasarakham University, Kantarawichai, Mahasarakham 44150, Thailand; htong09@yahoo.fr

The fossil record indicates that testudinoid turtles diversified rapidly during the Eocene worldwide, suggesting that this diversification was probably related to Early Eocene global changes. The group has a relatively poor pre-Eocene fossil record, exclusively documented in Asia. For a while, these pre-Eocene forms have often been classified in Dermatemydidae because of the presence of intermarginal scutes. They, however, exhibit some few synapomorphic features of testudinoid turtles, and most of them (if not all) are currently classified in the family Lindholmemydidae. Except the presence of inframarginal scutes (a primitive character), no apomorphic feature characterizes this family.

Recent molecular phylogenies and dating of modern testudinoid diversification suggest that members of the Emydidae, Platysternidae, and Testudinidae + Geoemydidae clades were present well before the Paleocene-Eocene boundary. Because inframarginal scutes are present in Platysternidae, it is likely that this character was lost independently in several lineages within Testudinoidea. The family Lindholmemydidae must be suppressed as it is united by only one primitive character (the presence of inframarginal scutes). Most pre-testudinoid fossils are only known by shells and too few characters have been identified for addressing systematic questions. In the lights of geometric morphometrics and by reanalyzing some fossils for which new material is now available, we try to propose a set of characters and some working directions that could help for reinterpreting the systematics of pre-Eocene Testudinoidea.

Testudo antiqua and the Lost Miocene Quarry at Hohenhöwen

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¹ Department of Biology, Eastern Oregon University, La Grande, Oregon, 97850, USA

² Department of Geosciences, University of Tübingen, Hölderlinstr. 12, D 72074 Tübingen, Germany

³ Senckenberg Center for Human Evolution and Palaeoecology, Tübingen, Germany

By virtue of its close relationship with *Testudo graeca* Linnaeus 1758 and its naming in the early part of the 19th century, *Testudo antiqua* Bronn 1831 is one of the few fossil turtles to have survived the past 200 years of taxonomic reshuffling with its original genus and specific epithet intact. The ten currently known specimens were collected from the middle Miocene Hohenhöwen locality in southern Germany. After initial descriptions by Bronn in 1831 and von Meyer in 1865, specimens came to be distributed in four different museums, three in Germany and one in France. It is impossible to identify the type material among specimens currently available because the early descriptions by Bronn and von Meyer did not refer to catalogued specimens, rendering the lectotype assignment by Schleich 1981 somewhat dubious. Because the available Hohenhöwen material was never fully analyzed, we completely photographed, described, and illustrated each specimen to provide a comprehensive morphological review of this taxon from the type locality. In addition, we conducted cladistic analyses to better understand the evolutionary relationships between *T. antiqua* and 15 closely related fossil and extant *Testudo* species. Our preliminary results place *T. antiqua* in a basal polytomy within the clade *Testudo*, suggesting that this form may represent the basal morphology of the group. In addition, there is not sufficient morphological evidence to resolve relationships between the three extant *Testudo* lineages (i.e. the *hermanni*-group, the *graeca/kleinmanni/marginata*-group, and the *horsfieldii*-group), hinting at a possible star phylogeny. Finally, with hopes of locating more turtles and in order to better understand the geological and ecological context of these tortoises, we visited the Hohenhöwen locale to search for the original collection sites, at least one of which was reportedly covered by landslides in the early 1900's. We discovered a relatively recent gypsum mine on the south flank of the mountain that, while devoid of fossils, allowed us to re-describe the gypsum sediments from a modern perspective. The original fossil quarries (according to Schreiner 1992) on the northeast flank of the mountain resisted detection and remain hidden by overgrowths of forest and cow pasture.

A New Xinjiangchelyid Turtle from the Middle Jurassic of Siberia, Russia

Igor G. Danilov¹, Sergei A. Krasnolutskii²

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² Sharypovo Regional Museum, 2nd Microrayon 10, Sharypovo, 662311 Krasnoyarsk Territory, Russia, krasnolucki.ser@mail.ru

During the last decade, abundant material of turtles was collected from the upper part of the Middle Jurassic (Bathonian) Itat Formation of Berezovsk Quarry, Krasnoyarsk Territory, West Siberia, Russia. This material consists of thousands of isolated bones and several, more complete specimens, including a partial braincase and larger portions of the shell. Study of this material shows that it belongs to a single taxon, which, probably, represent a new species of the family Xinjiangchelyidae. The attribution of this taxon to Xinjiangchelyidae is based on a combination of the following characters: canals for internal carotids open ventrally; 1st thoracic rib relatively short; anterior peripherals with prominently guttered edges; middle marginals extend onto costals; dorsal processes of epiplastron present; entoplastron longer than wide; mesoplastra absent; formed cervical articulations absent. This taxon is also characterized by a midline contact of costals 7, vertebrals 2 and 3 narrower than vertebral 1, a ligamentous plastron-carapace connection, pectorals and abdominals similar in length, and a sinuous midline sulcus of the plastron. The new taxon demonstrates variation in the formula of the anterior neurals, number of suprapyrgals, position and shape of sulcus between vertebrals 2 and 3, and presence/absence of an anal overlap onto the hypoplastron. The inclusion of this taxon in a cladistic analysis of Xinjiangchelyidae (Xinjiangchelyidae and Bashuchelyidae are considered to represent a monophyletic group and *Kayentachelys aprix* used as an outgroup) reveals a sistergroup relationship with *Annemys latiens* and *A. levensis* (both from the Late Jurassic of Mongolia) supported by two synapomorphies (vertebrals 2 and 3 narrower than vertebral 1; sulcus between vertebrals 3 and 4 V-shaped). However, the relationship of the new taxon within the *Annemys* clade remains unresolved.

This study is supported by grants of the President of Russian Federation NSh-6560.2012.4 and Russian Foundation for Basic Research 11-04-91331-NNIO_a.

Analysis of Internal Structures of the Skull of
Pelomedusoides (Testudines, Pleurodira)
Based on Three-dimensional Helical Tomography

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² Departamento de Biologia Animal, Universidade Federal de Viçosa; psrromano@gmail.com

We evaluate intracranial features of the extant taxa *Pelusios sinuatus*, *Podocnemis unifilis*, *Po. expansa*, and *Peltocephalus dumerillianus* and of the fossil taxa *Hamadachelys escuilliei*, *Bauruemys elegans*, *Caninemys tridentate*, *Peiropemys mezzalirai*, and *Pricemys caiera*, using 3D reconstructions produced from helical CT-scans. We are able to identify several cavities, canals, foramina, and structures of distinct cephalic regions. Based on a phylogenetic analysis, we conclude that reduction and expansion of some cephalic regions may have evolved more than once in Pelomedusoides and that these were probably associated with eco-physiological specializations. Since the presence of a well-developed pineal organ is indicative of rhythmic and circadian functions, we speculate that all fossil species analyzed except *Pr. caiera* (with a small pineal region) might have had seasonal migratory behavior, possibly associated with reproductive cycles. The evolution of the cavum pterygoidei in Podocnemidina indicates bite strength enhancement and is compatible with what is known about feeding habits of living species. The morphology of the semicircular canals (short common crus and wide anterior canal circuit) corroborates aquatic to semi-aquatic habits of the living species and indicates similar behaviors in the fossil ones, except *Pe. mezzalirai*, which we suggest had more terrestrial habits. The possibility of more terrestrial habits in *Pe. mezzalirai* and low migratory capacity in *Pr. caiera* suggest that both species may have preferred shallow freshwater habitats. Similarities in general morphology and development of the pineal organ and cavum pterygoidei between *P. dumerillianus* and *C. tridentate* suggest that the latter may have been a carnivore with aggressive behavior. It appears that Cretaceous Pelomedusoides not only had a greater morphological diversity than extant Pelomedusoides, but also displayed a more diverse behavioral and ecological repertoire.

Ossicle Gross Morphology and Microstructure of *Psephophorus polygonus* Meyer, 1847 (Testudines, Dermochelyidae)

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The reanalysis of all the known topotypes of *Psephophorus polygonus* Meyer, 1847 (middle Miocene, Devínska Nová Ves, Slovakia), the first fossil leatherback turtle to be named, allowed us to revise the variation of the diagnostic characters and to propose its first comparative diagnosis. In particular, contrary to what was previously stated, the ridged ossicles of *P. polygonus* may have a distinctly concave ventral surface as well as a tectiform shape in cross section. Thanks to the new diagnosis of *P. polygonus*, the validity of some *Psephophorus*-like species can be preliminarily re-evaluated. Significant differences in terms of thickness, development of keels and sutures, as well as number and size of ossicles, easily discriminate *P. polygonus* from *Dermochelys coriacea*, the only living leatherback turtle. The comparative analysis of the microstructure of the ossicles of these two dermochelyids revealed that *D. coriacea* has proportionately thinner ossicles that tend to lose the internal cortex, and thus their diploe structure, during ontogeny. The ossicles of both *P. polygonus* and *D. coriacea* have growth centers that are situated at the plate centers just deep to the external bone surface. As such they differ from carapacial polygonal ossicles or platelets of other amniote lineages (e.g., armadillos, placodonts), in which the centers lie well within the cancellous core or closer to the internal compact layer. *P. polygonus* and *D. coriacea* share significant morphological similarities that suggest a comparable ecology. The large size of *P. polygonus* is consistent with an adaptation to gigantothermy and therefore to a pelagic lifestyle and a cosmopolitan distribution. *D. coriacea* routinely dives to significant depths and its shell is able to deform under pressure, returning to its original shape upon ascent. The micro- and macromorphological features of *P. polygonus* could reflect a different flexibility of the shell and therefore different diving skills.

New Specimens, Redescription and Phylogenetic Position of *Bauruemys elegans* Suárez, (1969) from the Late Cretaceous of Brazil

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Upper Cretaceous rocks of the Bauru Basin have yielded seven chelonian taxa: "*Podocnemis*" *harrisi*, "*P.*" *brasiliensis*, *Roxochelys wanderleyi*, *Cambaremys langertoni*, *Peiopemys mezzalirai*, *Pricemys caiera*, and *Bauruemys elegans*, all belonging to the Podocnemoidae. The latter three taxa preserve cranial remains, the better known of which is *B. elegans* (recorded only in the site known as "Tartaruguito", in Pirapozinho-SP). The species was first described as "*P.*" *elegans*, later referred to the genus *Roxochelys*, and now typifies the new genus *Bauruemys*. Although several taphonomic, morphometric, and phylogenetic studies are available of the numerous specimens held in various Brazilian collections, published descriptive accounts of *B. elegans* are poor in anatomical detail. The material of this study includes three well-preserved skulls, one of which preserves the mandible in occlusion, and three partial post-cranial skeletons. Diagnostic characters of *B. elegans* were identified in the skulls (dorsally facing orbits, relatively flat and wide skull, interorbital groove absent, vomer present). However, some variation in these diagnostic characters was also observed (e.g., the foramen palatinum posterius is either restricted to the palatine or positioned near the palatine-pterygoid contact). Two skulls are as large as the holotype whereas the other is one third smaller. The gathered morphological data were employed to recode characters of *B. elegans* in the most recent phylogenetic study of Podocnemoidae. Only a few characters were modified, including the absence of a vomer-maxilla contact and the presence of mesoplastra, and they did not change the position of the taxon as a basal Podocnemoidae.

A Carettochelyine Turtle (Testudines: Carettochelyidae) from the Early Miocene of Libya

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An unusually well preserved skull of a carettochelyid turtle was found at locality Jebel Zelten (Libya) during excavations in 1983. Up to now, scientific research at this important locality has focused on the diverse fauna of small and large mammals and crocodiles, whereas turtles have been accorded only little interest. The "MS 2" locality can be dated using small mammals to be early Middle Miocene (18-19 Ma) and therefore represents the oldest level in the Jebel Zelten Area.

The skull was associated with disarticulated elements of at least two individuals, including plastral and carapacial elements. An incomplete mandible is preserved as well. The skull is missing portions of the snout region and the posterior tip of the sagittal crest, but is otherwise complete and uncrushed. The general size and shape, arrangement of the sutures, and the sculpture of the dermal roofing bones are very similar to the extant *Carettochelys insculpta*. Minor differences can be observed relative to extant *C. insculpta*: the foramen posterius canalis caroticus internus is situated on top of the posterior end of the pterygoideus ridge close to the fenestra postotica, not next to the ridge and far away from the fenestra postotica; the pterygoid fossa is triangular and not connected to the lower temporal fossa; the cavum quadrati is well-developed and defined by thin walls; articular surfaces arranged in a plane instead of being inclined towards the midline. A phylogenetic analysis of fossil carettochelyids places the new turtle as sister to *C. insculpta* and re-interprets "Anosteirinae" as a paraphyletic grade.

Fragmentary remains of carettochelyine turtles have been reported from the Miocene of Germany, Papua, Zaire, Egypt, Oman, Saudi Arabia, and DR Congo, but none have provided much insight into the morphology of Miocene carettochelyids. The new material from Jebel Zelten must therefore be considered the most important record of Carettochelyidae from the Miocene. The new material extends the range of Miocene carettochelyids to Libya thereby further highlighting the geographic restriction of the group today.

Morphology and Evolution of Nanhsiungchelyidae (Cryptodira: Trionychia)

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Nanhsiungchelyidae is an extinct clade of terrestrial chelonians from the Cretaceous of Asia and North America. They were also among the largest known non-marine turtles of the Mesozoic. The cranial and limb morphology of nanhsiungchelyids suggests ecological niches like extant testudinid tortoises. There are two distinct types of cranial morphology among nanhsiungchelyids. One consists of a testudinid-like skull with deep posterior and lower temporal emargination, as seen in *Zangerlia* spp. and *Basilemys* spp. The other type, by contrast, has only minor temporal emargination and is seen in *Nanhsiungchelys wuchingensis* and *Anomalocheilus* sp. (SSTM 1358 of the Shanghai Science & Technology Museum). The latter group also shares a deeply emarginated nuchal region.

WUSILS G359 of Waseda University is a nearly complete skeleton of a medium-sized nanhsiungchelyid with a 45 cm long carapace and 7 cm long skull from the Late Cretaceous (presumed Barungoyot Formation) of Mongolia. This specimen is identified as *Hanbogdemys jaganchobili* based on a shallow nuchal emargination and ventral folding of the anterior portion of epiplastron. Thus, this is the first known material of this genus with skull associated. The skull of WUSILS G359 shares deep posterior temporal emargination with *Zangerlia* and *Basilemys*, but its lower temporal (or cheek) emargination is less developed, as in *Nanhsiungchelys* and *Anomalocheilus*. *Hanbogdemys* has been presumed to be the sister taxon with *Nanhsiungchelys* and *Anomalocheilus* based on the presence of a deep nuchal emargination, and the cranial morphology corroborates this hypothesis. Finally, we note that the unique combinations of cranial and nuchal morphology suggest that the ability to retract the head inside the shell was secondarily lost in *Nanhsiungchelys* and *Anomalocheilus*, as in extant *Platysternon megacephalum*. This mechanism might have evolved to facilitate sexual displays like those observed in some extant testudinids rather than as a feeding or protective innovation.

A Diverse Turtle Fauna from the Upper Jurassic of Lower Saxony, Northern Germany and Its Implications for Taxonomic Distribution and Ecology

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Late Jurassic turtles from Western Europe are found in fluvial, lagoonal, and shallow marine sediments. These turtles usually show a mixture of basal and derived characters, hampering the interpretation of habitat preferences, especially of earlier ontogenetic stages. A gross morphological description of the Upper Jurassic fossil turtles of the Langenberg Quarry, Oker, Lower Saxony, Germany, gives further insight into the paleoecology and distribution of known taxa and indicates a possible endemic Late Jurassic turtle fauna at Oker.

Two skulls, a nearly complete, articulated shell, isolated shell plates, and postcranial bones were assigned to Plesiochelyidae, Thalassemydidae and one previously undescribed eucryptodiran taxon. The small articulated specimen (FV 853) still remains *in situ* in sediment matrix and was therefore scanned using computed tomography and then morphologically described and compared with extinct and extant turtles. Several characters diagnose the specimen as a juvenile: small size (7.28 cm carapace length), the grade of ossification of the skull elements and preserved limbs, and the presence of large and sculptured carapacial scutes and of lateral carapacial fontanelles surrounding the costals. Furthermore, FV 853 shows clear aquatic adaptations. Forelimb ratios of this specimen and other Mesozoic eucryptodire taxa were compared to forelimb ratios of extant cryptodires using data from an existing study that showed that these ratios reflect habitat preferences independently of ontogenetic stages. The specimens plot together with turtles preferring more open aquatic conditions and were therefore interpreted as being slightly more derived morphologically and ecologically than *Plesiochelys* spp. Since the locality is interpreted as a shallow marine environment in a coastal region with periodic regressions and transgressions, it is reasonable to expect a higher degree of aquatic adaptation during transgressive periods. We conclude that FV 853 inhabited near shore to offshore areas of the coastal region.

The Pectoral and Pelvic Girdles of the Late Triassic Turtle

Proterochersis robusta

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The Late Triassic *Proterochersis robusta* from Murrhardt, Germany is the world's oldest amniote with a fully formed turtle shell, but it is only poorly known and therefore rarely featured in discussions regarding the origin of turtles. Historically *P. robusta* was regarded as the world's oldest pleurodire because of the putative presence of a sutural pelvis, but more recent, global studies place it along the turtle stem while questioning the sutural nature of the pelvis. About ten specimens are available of *Proterochersis robusta*, but most are poorly preserved or not prepared.

Preparation of a poorly preserved specimen housed at the Staatliches Museum für Naturkunde Stuttgart yielded surprising insights into the pectoral and pelvic anatomy of *P. robusta*. Both scapulacoracoids are present in situ, of which one is uncrushed and only lacks the tip of the acromion process. The scapulacoracoids are fused and resemble those of other Late Triassic turtles by being dominated by a horizontal blade that exhibits a large coracoid foramen. The base of the elongate scapular process is connected to the short acromion process by an anterodorsal ridge. In contrast to *Proganochelys quenstedti*, the dorsal scapular process is oriented vertically. The epiplastral process does not contact the carapace. The pelvis is attached to the carapace and plastron via three pairs of sutural contacts. Only two pairs of regular, sacral ribs contact the pelvis. The epipubis is greatly elongated and does not contact the shell.

The pelvis of *P. robusta* shows differences in the identity of the sacral ribs to those of extant pleurodires, but there is no reason to doubt the primary homology of the sutured pelvis. A comprehensive phylogenetic analysis nevertheless reveals that *P. robusta* is not only the oldest, but also the most primitive known amniote with a full turtle shell. The sutural pelvis must therefore be viewed as an early homoplastic acquisition.

The First Shell Remains of *Rhinochelys cantabrigiensis* from the Upper Cretaceous of NW-Germany (Testudines: Protostegidae)

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The first fossil remains of a protostegid turtle from the Upper Cretaceous of northwestern Germany are described and discussed. The material includes a carapace and a plastron and represents the best-preserved material of the species *Rhinochelys cantabrigiensis*. The specimen was donated in 1988 to the Museum of Natural History in Münster, Germany. It had been found by a private collector at the Hollekamp quarry in Ahaus-Wüllen, which is well known for its rich echinoid fauna. Exposed layers include the upper part of the Brochterbeck Formation, the Hesseltal Formation, and the Wüllen Formation and sediments therefore range from the lower Cenomanian to the lower Coniacian. Unfortunately, the exact age of the specimen cannot be given with high confidence, because it lacks detailed locality information. The fossil is embedded in a light grey carbonate, however, and these carbonates only occur in the Brochterbeck Formation and in the Wüllen Formation. The Hesseltal Formation can therefore be excluded.

Three species of the genus *Rhinochelys* from England are currently recognized as valid. Additional, fragmentary material was described over the years from the Cretaceous of the Czech Republic under the name *Chelone benstedti* and *Pygmaeochelys michelobana*, but all of this material is referable to *Rhinochelys*. The new material is the first such record from northwestern Germany and expands the range of this taxon to the northeast.

In the Footsteps of Weigelt: A Century of Extant Observations, Experiments, and Fossil Analyses in Turtle Taphonomy

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In the 1920's, the German taphonomist Johannes Weigelt was one of the first scientists to observe and document the decomposition of extant turtles in their natural habitats in order to link modern taphonomic processes to preservation trends seen with fossil turtle specimens. Some of the patterns that Weigelt identified included (1) a common death pose in which the head and limbs were often extended in a relaxed position at the time of burial and (2) a preference for the turtle to be deposited in a carapace-up position. Over the next several decades, subsequent research by multiple researchers has added to our understanding of turtle taphonomy through the use of field observations and laboratory experiments to identify and explain additional patterns in turtle decomposition and disarticulation. This subsequent research has concluded that (1) turtles typically begin to disarticulate distally with the skull and limbs followed much later by the carapace and plastron, (2) that turtle carcasses will bloat and float in water prior to final deposition, and (3) the transport and deposition of turtle elements is different from other vertebrate groups due to their unique morphology. My own dissertation research examining the transport and deposition of freshwater turtles in fluvial settings integrating flume observations has aided in our understanding of turtle taphonomy by revealing (1) a link between turtle morphology, depositional environment, and preservation quality for freshwater turtle taxa and (2) that there is a preferred orientation and alignment for some turtle taxa in fluvial depositional environments, which can possibly be used as a paleoflow indicator in paleoenvironmental reconstructions. As noted by Weigelt, we are fortunate to have a variety of extant turtle taxa, which can all be observed in their natural habitats during life and also during post-mortem processes to better understand the paleoecology and depositional history of fossil turtles.

Insights into the Evolution of the Respiratory Apparatus in Cryptodiran Turtles

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In turtles, as in all amniotes, the lungs are the primary organ for satisfying oxygen demand and all amniotes are true aspiration breathers. The unique, shelled bauplan of turtles consequently required the evolution of a highly specialized muscular mechanism to achieve a proper ventilation of the respiratory surfaces. The principal structure of the gas exchanger, however, is a relatively simple, multichambered lung, which is probably very similar to that suggested to be the plesiomorphic condition for amniotes. Nevertheless, among the various turtle clades there is a conspicuous diversity of pulmonary structure evident. Detailed study of this diversity serves two purposes: it sheds some light on the evolution of this organ system within the taxon and may help our understanding of lung evolution in amniotes as a whole.

After a brief introduction into the unique chelonian breathing mechanics and its muscular basis, we focus on other structural aspects of the respiratory apparatus. These include the morphological diversity of the extrapulmonary airways and the lungs themselves, as well as the coelomic integration of these elements. We have examined specimens from all major cryptodiran taxa (Carettochelyidae, Chelydridae, Emydidae, Geoemydidae, Kinosternidae, Platysternidae, Testudinidae, Trionychidae) except marine turtles, which are considered relatively well substantiated in the literature. Based on this comparison we provide some insights into a possible evolution of the cryptodiran respiratory apparatus and also discuss its value in systematics.

Turtle Eggs and Embryos from the Upper Cretaceous Judith River Formation of Montana

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Hard-shelled turtle eggs are unique among amniotes because they produce eggshells comprised of aragonite. This mineral composition and distinctive microstructure allow for confident identification of turtle eggs within the fossil record. However, assignment of fossil turtle eggs and eggshell to specific turtle clades remains impossible without the presence of embryos or gravid females.

The Judith River Formation of central Montana contains numerous dinosaur eggs and eggshell localities; however, fossil turtle eggs and eggshells are rare from this formation. A clutch of unhatched turtle eggs (MOR 710) consists of at least 13 eggs, some containing embryonic remains. The weathered but mostly intact specimens occurred at the base of the outcrop and therefore provide little taphonomic information about nest construction. The relatively smooth, cream-colored eggs measure 3 x 4 cm and exhibit minor lithostatic compaction. The rigid eggshell consists of a single structural layer comprised of radiating, acicular aragonite crystals that form interlocking shell units that flare slightly toward the outer shell surface. The shell unit width-to-height ratio is approximately 1:2. At least one egg displays abnormal, double eggshell layers, a condition reported in at least nine species of extant turtles.

Synchrotron data reveals extensive preservation of bone throughout the eggs. The embryonic remains are partially articulated and show a late stage of ossification, suggesting that they were close to hatching at time of death. Histological thin sections of the embryonic bone show enlarged vascular spaces, within the cortex, surrounding the marrow cavity. Vascular spaces are mostly circular in transverse section and orientated longitudinally. Numerous osteocytes are preserved but show little organization. The distinctive shape of the premaxilla suggests that the eggs were laid by a trionychid turtle. This taxonomic assignment would not be possible from eggshell characters only.

Evolutionary Developmental Model for the Origin of the Turtle Shell

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The origin of the turtle shell and the constraints it places on how turtles breathe are interdependent problems that have fascinated scientists for the past three centuries. The discovery of the stem turtle *Odontochelys semitestacea* supports the developmental de novo hypothesis, because it confirms that the costals and neurals are produced through the outgrowth of (sub)dermal bone from the perichondral collar of the dorsal ribs and vertebrae. This discovery allows for the integration of developmental and fossil data into an evolutionary developmental (evo-devo) model for the shell's origin that makes explicit predictions for the contentious early history of the turtle stem. We expand this model by integrating novel anatomical and bone histological data for *Eunotosaurus africanus*, a species recovered as a stem turtle in both global phylogenetic analyses of amniotes and parareptiles. We consider the phylogenetic signal within a dataset based on shell-related characters and shelled taxa currently considered as potential relatives of turtles. This analysis tests the hypotheses that the de novo shell appeared once in amniote history and that *E. africanus* is a stem turtle.

Results support these hypotheses, with character support including: ten or less elongate dorsal vertebrae, nine pairs of anterior-posterior expanded ribs, loss of intercostal muscles, insertion of muscles on the ventral side of the dorsal ribs, and (sub)dermal outgrowth of bone from the developing perichondral collar of the dorsal ribs. The successive divergences of *E. africanus* (broadened ribs; dermal outgrowth of bone from the ribs; re-organization of locomotion/respiratory muscles), *O. semitestacea* (broadened ribs/neurals), and finally *Proganochelys quenstedti* (fully ossified carapace) results in a sequence of character acquisitions that is fully congruent with predictions drawn from the evo-devo model.

New Material of *Hydromedusa casamayorensis* from the Middle Eocene of Patagonia and Its Phylogenetic Implications

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In the present study new specimens of *Hydromedusa casamayorensis* from the lower levels of the Sarmiento Formation (Casamayoran SALMA, Middle Eocene) of the "Cañadón Hondo" area (eastern central Patagonia) are presented. The new specimens, recognized only by postcranial remains, belong to at least 6 individuals (MEFP-PV 10562-10567). The preserved specimens are represented by three almost complete shells (one with cervical vertebrae, fore and hindlimbs) and by three partially preserved shells. As the original description of *H. casamayorensis* was based on isolated plates, the new findings revealed unknown features of the postcranial anatomy of the species. The new specimens belong to *Hydromedusa* Wagler, 1830 because of the presence of a cervical shield behind the anterior margin of the carapace and to *H. casamayorensis* because of the presence of a wide vertebral scale 1 reaching the peripheral 1 and femoral scale larger than the anal. *Hydromedusa casamayorensis* shares with the extant *H. maximilliani* (Mikan, 1825) the presence of more than 6 neural plates and with *H. tectifera* (Cope, 1870) the participation of the first peripheral plate in the first vertebral shield. In order to evaluate the phylogenetic position of *H. casamayorensis*, this species was incorporated into previous cladistics analysis. The result of the phylogenetic analysis suggests that *H. casamayorensis* is the closest taxon to the living species of the genus *Hydromedusa*, forming a monophyletic group. The extinct genus *Yaminuechelys* from the Upper Cretaceous-Paleocene of Patagonia is recovered as the sister group of *Hydromedusa*, suggesting that the diversification of the group occurred near the K/P boundary.

Oxygen Isotope Compositions of Late Jurassic Turtles in Europe: New Data from Switzerland and Germany

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During the Late Jurassic, basal eucryptodiran turtles were adapted to marine life. Most of the known turtle remains come from coastal marine environments of Europe, however, the composition of their ambient water and their palaeoecology remained questioned so far. Here, we report oxygen isotope compositions of turtle phosphate from three Kimmeridgian localities: Porrentruy and Solothurn (Northern Switzerland) and Oker (Northern Germany). The results show that: (1) the $\delta^{18}\text{O}$ values (‰SMOW) of ambient waters (and indirectly salinity) calculated from the turtle bone isotope composition are variable. Isotopic compositions of waters were typically marine for an ice-free world in Oker (-1.1 ± 0.1 ‰) but most likely brackish in Solothurn (-1.9 ± 0.6 ‰) and Porrentruy (-2.4 ± 0.8 ‰). One turtle taxon (e.g., *Plesiochelys*) could have lived in various marine environments; (2) the associated marine crocodylians (thalattosuchians) reveal a $\delta^{18}\text{O}$ of ambient water similar to turtles in Oker (-1.2 ± 0.5 ‰) and Porrentruy (-2.6 ± 0.6 ‰), but not in Solothurn (-3.3 ± 0.2 ‰) where they could have led a more 'continental' lifestyle than turtles; (3) based on the $\delta^{18}\text{O}$ phosphate from associated fish, the mean calculated surface seawater temperatures (assuming a $\delta^{18}\text{O}$ seawater = -1 ‰) should have been 12 ± 2.2 °C (Oker), 21 ± 6 °C (Porrentruy) and 24 ± 6 °C (Solothurn). By using the mean calculated $\delta^{18}\text{O}$ values of ambient water derived from turtles, similar temperatures are calculated for Oker waters (12 ± 2 °C), but significantly lower for Porrentruy (15 ± 6 °C) and Solothurn (20 ± 6 °C). The genus *Plesiochelys* reveals a temperature tolerance even to cold waters. The cold boreal signal recorded by Oker turtles contrasts with Tethyan data; coastal marine waters throughout Europe were not as warm and thermally homogenous as generally proposed so far for the Late Jurassic.

The Late Oligocene Turtle Assemblage from Nong Ya Plong, Petchaburi Province, Thailand

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The turtle fossil record of the Paleogene in Southeast Asia is not well documented. In this region, turtles are only known from the late Eocene-early Oligocene of the Krabi Basin in Thailand, from the late middle Eocene Pondaung Formation in Myanmar, and from a supposed Oligocene locality in Vietnam. We describe here a new turtle assemblage from Nong Ya Plong in Petchaburi Province (Thailand). Nong Ya Plong locality is an Oligocene lignite basin, which has yielded a variety of well-preserved fossil mammals. Fishes and turtles were also discovered but never described in details. The materials are well preserved and consist of scattered bony plates as well as some nearly complete shells. All turtles found in that locality belong to the family Geoemydidae. Two new taxa can be recognized, one of them clearly displaying three keels on the carapace.

Considerations on the Evolution of Feeding Systems in Turtles

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Among extant turtles, a great variety of feeding strategies are reported. Most taxa are completely carnivorous, some emydids and geoemydids have a mixed diet and most testudinids are herbivorous. Also concerning the surrounding media of the food uptake and food transport, water or air, turtles show a great variability. All pleurodires feed exclusively under water. Within cryptodires, there are pure aquatic feeder species that can fulfill the whole feeding process in both media (air and water) and species that can feed only on land. We investigated the morphology of the feeding apparatus in 14 turtle species using classical dissections, μ CT techniques, and various histological and SEM techniques. In addition, we have made high-speed X-ray video recordings of feeding events in both media. On the base of our research, we provide a hypothetical evolutionary scenario on the development of the design of the feeding apparatus and feeding behavior in turtles. We hypothesize that, on the one hand, some Triassic turtles were terrestrial feeders using jaw food prehension and lingual based transport. On the other hand, there were also aquatic feeders using compensatory suction mechanisms. Compensatory suction under feed-back neuromotor control is probably the ancestral feeding strategy of the crown group turtles. Species which use a pure suction feeding mode under feed-forward neuromotor control represent an aberrant condition. Relatively late in the turtle crown group evolution – with development of the testudinoids – the feeding on land has reappeared. Concerning the feeding on land, our results lead to the hypothesis that the ancestral mode of food uptake in testudinoids was “jaw prehension” and the food transport was lingual based. In extant turtles, “lingual prehension” is an aberrant feeding mode, typical only for the highly derived tortoises.

A *Podocnemis* Skull from the Upper Miocene Solimões Formation, Acre Basin, Northern Brazil

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The Upper Miocene Solimões Formation in the state of Acre, northern Brazil has yielded several turtle fossil remains. These fossils are dominated by chelid and podocnemidid turtles, but some cryptodires are present as well. So far, the only skull recorded from these rocks is the holotype of *Caninemys tridentata*. The genus *Podocnemis* is widely reported in the Solimões Formation, but most of these records are based on postcranial remains (e.g. *Podocnemis negri*). Here we described a *Podocnemis* skull from this Formation. The material was collected by L.I. Price in 1962 in Price's Acre locality 34, in the state of Acre. This specimen was mentioned in others publications, but it remained undescribed. This skull is well preserved ventrally, but is damaged on the dorsal side. It is therefore not possible to see the main diagnostic characteristic of the genus *Podocnemis*, which is the interorbital groove. The following bones are preserved in the specimen: premaxilla, maxilla, a small portion of prefrontal, jugal, quadratojugal, quadrate, palatine, pterygoid, basisphenoid, basioccipital, opisthotic and squamosal. The following features allow identifying this specimen as belonging to *Podocnemis*: the prefrontal does not cover the apertura narium externa; accessory ridges in the triturating surface present; maxillae meet broadly on midline; premaxilla does not reaches the internal nares in palate. This specimen is most similar to *Podocnemis expansa*, an extant species, and *Podocnemis bassleri*, a fossil species from the Miocene of Peru, both from the northern portions of South America, but the taxonomic status of *Podocnemis bassleri* is doubtful. A comparative analyses with others representatives of *Podocnemis* are necessary to determine the validity of *Podocnemis bassleri* and to provide a more specific identification of the new specimen.

The Mesozoic Turtles from the Iberian Peninsula: An Update

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Turtles are relatively abundant in the fossil record of the Iberian Peninsula, particularly from Upper Jurassic to uppermost Cretaceous outcrops. However, the level of knowledge about the diversity represented and the paleobiology of the different groups was until now very limited. The analysis of the abundant and generally unpublished record of Mesozoic turtles from the Iberian Peninsula allows us to identify a high level of diversity, consisting of members of groups present on other continents and representatives endemic to Europe. Although the study of Iberian Mesozoic turtles is currently still underway, some results allow establishing synonymies, refuting the validity of some taxa and of certain previous attributions, and identifying new taxa. Taxa present in other European regions are found on the Iberian Peninsula as well. Two representatives of Pleurosternidae, an indeterminate member of Platycheilyidae, several members of Plesiocheilyidae, and other forms probably related to this group are identified in the Upper Jurassic of the Iberian Peninsula. The turtle fauna recorded in the Lower Cretaceous is markedly different. It is very diverse and consists of an indeterminate member of Dortokidae, two solemydids, and abundant and diverse pan-cryptodirans, including several new taxa. The diversity of continental turtles identified from the Iberian Upper Cretaceous is composed of solemydids, dortokids, and abundant bothremydids, a group not known from the European Lower Cretaceous. Pan-cryptodiran lineages identified in the Lower Cretaceous are not present in the Upper Cretaceous. The identification and classification of Iberian Mesozoic turtles allows proposing hypotheses about their relationships, interpreting the stratigraphic succession at which they appear, and better understanding the paleobiogeographic configuration and paleoenvironmental factors that conditioned their distribution.

Taxonomy and Phylogeny of *Tropidemys* Rüttimeyer, 1873 (Eucryptodira) Based on New Specimens from the Kimmeridgian of the Swiss Jura

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The taxon *Tropidemys* is a representative of Plesiochelyidae, a traditionally recognized group of Late Jurassic eucryptodiran turtles diagnosed by the presence of three cervical scutes and adapted to life in the sea. *Tropidemys* was only known from fossilized carapaces and, possibly, plastra from Europe, most notably the famous 'Solothurn Turtle Limestone' of Switzerland. Due to the sparse fossil record of *Tropidemys*, several questions concerning its taxonomy and phylogeny have remained unanswered. Here, new material of *Tropidemys* is reported from the Kimmeridgian of the region of Porrentruy, Canton Jura, Switzerland. In addition to three well-preserved carapaces, associated plastra and limb bones (humerus and femur) are described for the first time. The *Tropidemys* material from Porrentruy is identified as *Tropidemys* aff. *langii*, because it presents several anatomical differences, primarily shell width and the development of the keel on the carapace, relative to the type material of *T. langii* from Solothurn. A cladistic analysis shows that the combined Swiss *Tropidemys* material from Porrentruy and Solothurn is sister to *Plesiochelys solodurensis*, thereby tentatively confirming for the first time the monophyly of Plesiochelyidae.

New Insights into the Evolution of the Carotid Circulation System in Eucryptodiran Turtles

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The carotid circulation system of turtles has long been considered to be an important anatomical region for assessing the relationships of the major groups of turtles. The evolution of this system in stem-cryptodires is still poorly understood, because the carotid pattern of most Jurassic taxa was unknown and because the phylogenetic position of many basal eucryptodiran taxa, including plesiochelyids, protostegids, eurytternids and angolachelonians, is unstable. A review of Asian stem-cryptodires reveals that the evolution of the carotid circulation system is characterized by the closure of the interpterygoid slit, a reduction of the carotid fenestra or sinus (i.e., a fenestra/sinus located between the basisphenoid and pterygoid within which the split of the carotid artery into the cerebral and palatine branches is exposed), and the resulting reduction of the distance between the foramen posterius canalis caroticus cerebralis and the foramen posterius canalis caroticus lateralis. All of these taxa, including *Annemys* spp., *Ordosemys* spp., *Dracochelys bicuspis*, *Hangaiemys hoburensis* and *Sinemys* spp. still retain a reduced basiptyergoid process of the basisphenoid, a structure that can now be shown to be homologous to that of basal turtles using topology and intermediates. The presence of a reduced carotid fenestra in the stem-trionychian *Adocus* sp., the stem-testudinoid *Mongolemys elegans*, and the tentative stem chelonioid/kinosternoid *Judithemys sukhanovi* and *Macrobaena mongolica* indicate that the closure of the carotid fenestra occurred at least three times independently within crown Cryptodira. The presence of a reduced carotid fenestra in the latter two taxa furthermore confirms the phylogenetic distinction between “true macrobaenids” and the eclectic group of basal eucryptodires traditionally referred to as Macrobaenidae. A reduced carotid fenestra is furthermore present in plesiochelyids, eurytternids, and protostegids thereby hinting at a phylogenetic position derived relative to classic sinemydids or additional levels of homoplasy.

Evidence for Periods of Increased Aridity during the Latest Cretaceous of North America: A Description of Several Mass Death Assemblages of Turtles

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Several localities (N=6) within the latest Cretaceous Hell Creek Formation of southwestern North Dakota and eastern Montana contain remarkable assemblages of numerous fossilized skeletal remains of riverine and ponded water turtles. Baenid turtles dominate the faunal assemblages. While trionychid soft-shelled turtles occur at each of these localities and a macrobaenid is found at one locality, all other North American Late Cretaceous turtles (adocids, chelydrids, kinosternids, and nanhsiungchelyids) are absent. These localities not only provide important insights into the vertebrate fauna and palaeoecology of this region at the period just prior to the momentous K/T extinction, but are also interpreted to be the result of climate-induced mass mortality events. At each locality, differing degrees of articulation indicative of various stages of post-mortem decay among individuals suggest the turtles died over an extended period of time prior to burial. Furthermore, mud cracks are found in the layer immediately below the fossil-bearing bed in at least one of the localities. We review the occurrence of mass mortality events in modern riverine and ponded water turtle populations and interpret the fossil localities to be after-death assemblages. While mass death assemblages of terrestrial dinosaurs are common in the Campanian of Alberta (attributed to monsoonal rains and flooding), evidence for mass mortality events of aquatic animals is absent. We suggest the Western Interior of North America experienced more significant periods of drought during the Maastrichtian compared to the Campanian, and were responsible for the aquatic turtle death assemblages described.

On a New Side-necked Turtle from the Lower Cretaceous (Upper Barremian) of Northeastern Brazil

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A single specimen (UERJ.MC 2) of a new species of Pleurodira was discovered in São Miguel dos Campos Municipality, State of Alagoas, Northeastern Brazil. The specimen is preserved in a carbonate concretion collected from the São Miguel dos Campos Unit, Morro do Chaves Formation, Sergipe-Alagoas Basin and is dated Upper Barremian. UERJ.MC 2 is well preserved and shows in ventral view the skull, mandible, hyoids, plastron, and some elements of the carapace and the appendicular skeleton. The fossil is diagnosed as a side-necked turtle based on pelvic scars preserved on the xiphiplastra. The plastron shows the usual 11 bones present in most Pelomedusoides, laterally reduced mesoplastra, and no fontanelles. Some cranial features, such as the presence of wide maxillary triturating surfaces and a single, reduced vomer, putatively indicate that this new species belongs to Podocnemidera. A pterygoid contribution to the anterior foramen posterius canalis carotici interni, the short basioccipital, and the nearly fully covered prootic suggest a more inclusive position within Podocnemidoidea. To test this assertion, we included this specimen in a published character matrix with 48 taxa and 174 parsimony informative characters (multi-states treated as unordered). A heuristic parsimony search with random addition sequence of taxa, holding 1000 trees per cycle, and TBR branch swap in PAUP yielded 13 most parsimonious trees of 424 steps, 0.57 CI, and 0.80 RI. The strict consensus tree positions UERJ.MC 2 at the base of Podocnemidera within Podocnemidoidea. This specimen therefore represents one of the oldest Pelomedusoides yet discovered. Preparation of UERJ.MC 2 is still in progress and, upon completion, we expect to see additional characters that may provide more complete insights into the anatomy of this taxon and thereby further contribute to our understanding of the evolution of Pelomedusoides.

Bone Microstructure of Selected Fossil Turtle Shell Plates from the Cretaceous of Spain (Solemydidae and Dortokidae)

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The Cretaceous of the Iberian Peninsula is rich not only in regards to dinosaur bones, eggs, and footprints, but also shows a diversity of other reptiles, especially turtles. Stem Testudines, pan-pleurodiran and pan-cryptodiran turtle remains have been found in numerous Lower and Upper Cretaceous localities. Two groups of turtles very common in the European uppermost Cretaceous fossil sites, and specifically in the Spanish record, are also identified in Spanish Lower Cretaceous sites: Solemydidae (stem Testudines), a taxon of North American and European distribution, and the European endemic group Dortokidae (Pan-Pleurodira). Here we present the bone histology of selected carapace and plastron plates (represented by several elements each) of the dortokid *Dortoka vasconica* and solemydids referable to *Solemys vermiculata*, *Solemys* sp. and aff. *Helochelydra* sp. These analyses are based on historical and recently discovered abundant material from several Lower and Upper Cretaceous localities, including material of *Dortoka vasconica* and *Solemys vermiculata* from their type locality (Laño, Burgos). For comparison, shell material from other turtles (e.g. Pleurosternidae) from the Iberian Peninsula, and additional solemydid taxa from Europe and North America were studied. *Dortoka vasconica* shell bones were highly vascularized often showing tendencies to overall osteoporosis, which together with large persistent carapacial fontanelles, indicate that it was an aquatic freshwater turtle. The solemydid turtles instead were characterized by well-developed diploe structures and strong external ornamentation patterns. Bone compactness values in this group indicate terrestrial habitation, a hypothesis that is consistent with the presence of osteoderms known in the limbs of several representatives of Solemydidae.

New Findings of Meiolaniid and Meiolaniid-like Taxa from Patagonia, Argentina

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The objective of the present work is to make a state of the art of the meiolaniid and meiolaniid-like taxa from Patagonia, Argentina. Until 2010 there were only two known species of meiolaniid and meiolaniid-like taxa described for Patagonia, *Niolamia argentina* and *Chubutemys copelloi*. The description of previously collected specimens and the discovery of new specimens in different field works conducted in Patagonia (Argentina) have notably increased the knowledge of the group. Nowadays there are up to six species of meiolaniid-like taxa recognized for South America, all belonging to Argentina. New field work conducted to the Lower Cretaceous sediments of the Cerro Barcino Formation ended in the discovery of more remains of *Ch. copelloi*; bringing valuable information on its postcranial anatomy. There are two species in the Upper Cretaceous of Patagonia, one named (*Patagoniaemys gasparinae* from the La Colonia Formation) and the other unnamed (from the Allen Formation). New findings of cranial and postcranial materials of *Pa. gasparinae* make this taxon the more complete species of meiolaniid-like turtle from South America. Another new species of meiolaniid-like turtle is present in the Paleocene sediments of the Salamanca Formation. In the Middle Eocene (Casamayoran SALMA) of the Sarmiento Formation a new species of meiolaniid has been found in recent field works. This new species is closely related to *Ni. argentina*. All the work conducted allowed increasing the knowledge in the anatomy, evolution, and biogeography of this group of bizarre turtles. The inclusion of other Cretaceous species (*Mongolochelys efremovi*, *Otwayemys cunicularius*, and *Kallokibotion bajazidi*) to the cladistic analysis of the Patagonian species shows that the meiolaniid clade and related taxa could have originated in the South American part of Gondwana sometime between the Middle Jurassic and the Early Cretaceous and it had, almost, a cosmopolitan distribution.

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New Turtles from the Triassic of Poland

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We herein report newly discovered fossil turtles from Norian-Rhaetian fluvial sediments of Poreba (Silesian Voivodeship, southern Poland) possibly belonging to the taxon *Proterochersis robusta*. Poreba is located in the Kraków-Częstochowa uplands and is the first European locality outside of Germany to yield unambiguous Triassic turtle remains. In addition to turtles, the locality has yielded a wide diversity of other Triassic animals, including bony fishes, sharks, aetosaurs, dinosaurs, and temnospondyls. The fossils are found mainly in conglomerates and clays. Although most of the turtle fossils represent isolated or fragmentary carapacial or plastral bones, two well-preserved, nearly complete shells were found, as well as a pelvic girdle, a scapulocoracoid, a few limb bones, and some smaller bones or fragments. The exceptionally preserved scapulocoracoid is interesting as it consists of a long, rod-like scapula, a prominent acromion, and a bee-wing-shaped coracoid. While some characters, like the relatively small pygal notch, may suggest that the new material represents a new species, further study is required to establish this status. Large quantities of shell elements (more than 200 specimens) apparently originate from individuals representing various ontogenetic stages. The new material may therefore provide new insights about ontogenetic patterns in basal turtles, which in turn may shed new light on the early evolution of the turtle shell.

Fossil Turtles of the Genus *Baicalemys* (Emydidae): New Data on Morphology and Phylogenetic Position

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The study of previously unexamined material of *Baicalemys gracilis* Khosatzky et Chkhikvadze, 1993 (type species of the genus *Baicalemys* Khosatzky et Chkhikvadze, 1993), an emydid turtle from the Middle-Late Miocene Khalagai Formation of Olkhon Island in Baikal Lake (Russia), allow us to accomplish characteristics of this species and include it in the modern cladistic analysis of emydids for the first time. Our analysis places *B. gracilis* within the Emydinae clade and as a sister to the clade including *Actinemys marmorata*, *Emys orbicularis*, *Emydoidea blandingii* and *Terrapene* spp. The position of *B. gracilis* within the Emydinae is supported by the presence of an anterior pair of musk ducts, and its placement in one clade with *A. marmorata* and more advanced taxa, by the absence of the sutural plastron-carapace connection. Within the Emydinae, *B. gracilis* is peculiar in the presence of three pairs of inframarginals, with inframarginals 2 and 3 separated by contact of abdominal and marginal scutes. In our analysis, this character is considered to be a reversal of the primitive condition, present in a basal emydid *Pseudochrysemys gobiensis*. This result contradicts to some previous (non-cladistic) hypotheses, which placed *B. gracilis* within the Deirochelyinae. The assignment of other turtle species to *Baicalemys*, suggested by some authors, is either weakly supported or incorrect. Finally, our data suggest that ancestors of *B. gracilis* might come from North America via Beringia, probably, at the same time as ancestors of *Emys*.

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The Genus *Ocadia* (Testudines: Geoemydidae) from the Middle Miocene of Tanegashima Island, Southwestern Japan, and Its Paleobiogeographic Implications

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The genus *Ocadia* (Testudines: Geoemydidae) consists of the extant *O. sinensis* from northern Vietnam, southern China and Taiwan and *O. nipponica*, an extinct species found from the Middle Pleistocene of Chiba Prefecture, Honshu, Japan. In addition to these, several fossils referred to *Ocadia* have been found from the Early Miocene to Late Pleistocene of Japan. These fossils suggest that this genus diversified in Japan during the Neogene and Pleistocene, but further investigations had been desired to elucidate their appropriate taxonomic position and their evolutionary history. Recently, we discovered a well-preserved shell fossil of the genus *Ocadia* from an Early Middle Miocene shallow marine deposit (ca. 16 Ma) on Tanegashima Island, located south of Kyushu, Japan. Results of comparisons with two congeneric species revealed that the Tanegashima turtle is an oldest known distinct species. This indicates that the genus had flourished along with *Ocadia* sp. from Honshu in the Early to Middle Miocene and their initial divergence would have started no later than the Early Miocene. In generally prevailed Miocene paleogeographic hypotheses, Japan had mostly been a part of eastern margin of the Eurasian continent in the late Early Miocene and subsequently divided into several islands (including a large island located northwest off Tanegashima Island) by tectonic submergence in the early Middle Miocene. Occurrences of *Ocadia* from the Early to Middle Miocene of several localities of Japan including Tanegashima Island are in concordance with such paleogeographic hypotheses, suggesting that their split was caused by geographic isolation of an island northwest to Tanegashima Island from the remainder. Recently, a molecular phylogenetic study estimated the separation of a clade consisting of *Ocadia* and its close relatives (i.e., *Chinemys* and ancestral lineage of *M. japonica*) occurred after 18-23 Mya, which is also concordant with present finding.

A Revision of *Sinaspideretes wimani* Young et Chow, 1953

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Sinaspideretes wimani Young et Chow, 1953 is based on a single shell from the Jurassic red beds of Sichuan Basin, China, but the exact horizon and locality is unknown. It was originally referred to Trionychidae and was long thought to be the oldest representative of that family. A more recent reinterpretation of the type material, however, led to the tentative assignment of the taxon to the family of Carettochelyidae.

The new interpretation of the carapace presented here shows the presence of regular and elongate neurals, with a neural formula of 6<4>6>6>6>6>6>6; relatively narrow vertebral scutes; and presence of two large suprapyrgals. Further preparation of the plastron revealed a number of additional important characters such as plastron sutured to the carapace, a wide entoplastron, presence of inframarginals and a sinuous midline sulcus. These characters clearly exclude *Sinaspideretes wimani* from both Trionychidae and Carettochelyidae, but unite it with the primitive trionychoid *Yehguia tatsuensis* (Ye, 1963). *Sinaspideretes wimani* is therefore considered to be a basal member of Trionychoidae, together with the representatives of Adocidae and Nanhsiungchelyidae.

Cf. *Terrapene carolina*: A Complicated Evolutionary History

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Multiple complex scenarios have been proposed in which the extant morphological diversity within *Terrapene carolina* is explained by patterns of splitting and reticulation between various subspecies. However, given the notably high level of variation within the species and the lack of phylogenetic context for Pleistocene specimens of *T. carolina*, it is difficult to evaluate competing explanations of evolution within *Terrapene*. The situation presents a circular problem because lineages remain difficult to identify, especially in the fossil record, due to a lack of understanding of variation within *T. carolina*, but patterns of variation across the temporal and geographic range of the taxon remain enigmatic until lineages can be identified, separated and studied individually. To approach this problem, we analyzed several fossils attributed to *T. carolina*, both in specimen-level analyses and in analyses with specimens collapsed into locality-level terminals in an effort to account for population-level variation. Specimen-level analyses were poorly resolved due to signal from intraspecific variation overwhelming characters that traditionally separate species. Fossils tended to sort by locality, but in analyses at all levels they did not definitively resolve in a polytomy with *T. carolina* as they should have according to previous taxonomic assignment. Additionally, not all fossil localities resolved in a polytomy with each other, as they should have if they represented the same species. These results indicate that the patterns of evolution within *T. carolina* in the Pleistocene are complex and that previously proposed explanations cannot adequately explain the patterns observed.

Special Remarks on the Posterior Limb morphology of the Giant Continental Tortoises from the Pliocene of Thessaloniki area (Macedonia, Greece)

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Recent investigations along the coastal area of Western Chalkidiki, near Thessaloniki, lead to the discovery of several giant tortoises, which preserve most of the shell and many skeletal elements. Systematic study reveals that they can be attributed to the genus *Cheirogaster*. These individuals were found in the Gonia Formation deposits, which represents the entire Pliocene. The complex stratigraphy shows alternations of sands, clays, marls, sandstones, gravels, and of massive, marly limestones. The fossils are scattered throughout the formation, specifically at the sites Aggelochori (AGG), Nea Michaniona (MIC), Epanomi (EPN) and Nea Kallikratia (KLK). The KLK individual is the smallest in size, with a calculated carapace length of about 90 cm. Several parts of the shell, most of the pelvis, and various limb bones are preserved, including a well-articulated right posterior limb. Careful preparation reveals that most of the femur, tibia, fibula, and most tarsals and metatarsals are perfectly preserved in situ. The recovered position of the bones suggests that the limb was retracted during or just after death. The fused astragalo-calcaneum shows the primitive condition, preserving the suture. Metatarsals overlap one another, while the four recovered distal digits show large claws. Among the preserved osteoderms, a large pointed bony tubercle and a smaller, rounded one, occur posterior to the femur, surrounded by a set of elliptical osteoderms called thigh tubercles. This arrangement is well known from the African Spurred Tortoise, *Centrochelys sulcata*, which is furthermore characterized by the presence of 2-3 thigh tubercles. This is the first description of these structures in the fossil record of European giant tortoises. While osteoderms and bony tubercles are considered homoplastic in extant chelonians, their presence in the KLK tortoise suggest a close relationship with the African Spurred Tortoise.

A New Dortokid Panpleurodire from the Maastrichtian of Transylvania, Romania

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Dortokids are an enigmatic group of strictly European panpleurodires with a stratigraphic range spanning from the early Cretaceous (Barremian) to the early Eocene (Ypresian) based on several occurrences from Spain, France, Austria, Hungary, and Romania. In addition to *Dortoka vasconica* from the Campanian/Maastrichtian of France and Spain and *Ronella botanica* from the late Paleocene of Romania, a third taxon is present in the Maastrichtian of Romania. Material of this form is known from nine sites spread over the Transylvanian and Hațeg basins and consists mostly of isolated shell and other postcranial elements, with notable exception of a single relatively complete shell. It is as of yet unclear whether the considerable amount of variation seen in this material documents more than one taxon, because previous studies demonstrate great morphological plasticity in the Western European *Dortoka vasconica*. Our preliminary phylogenetic analysis weakly advocates the monophyly of dortokids and places the Maastrichtian taxon from Transylvania in a poorly supported sister-taxon relationship with *Dortoka vasconica* to the exclusion of *Ronella botanica*. However, in some derived characters (e.g., presence of "regular" neural series and laterally shorter second pleurals), the Maastrichtian taxon is reminiscent of the Paleocene *Ronella* lineage, indicating that the separation of dortokids into Western and Eastern European lineages might have happened no later than the Maastrichtian.

Our results confirm the position of dortokids as stem-pleurodires, but we nevertheless note that this is solely based on cervical and caudal vertebral characters scored for *D. vasconica*. However, no vertebrae were found associated with the shells of this species, and another pleurodiran taxon has been also reported from the same site. More complete material would be therefore vital for confirming the proposed placement of dortokids.

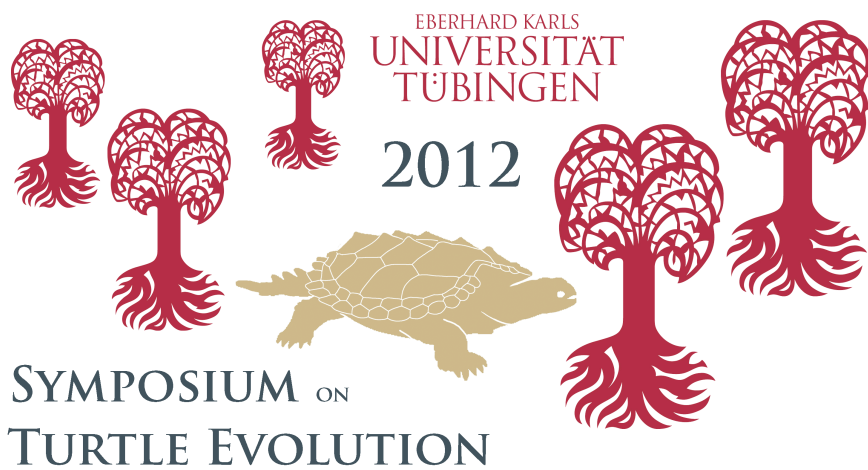
An integrative Study on the Anatomy and Development of the 'Hooked Fifth Metatarsal' in the Turtle Pes

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The hooked fifth element in the hind foot of turtles has repeatedly been homologized with a similar metatarsal structure in lepidosaurs and was used to support a close phylogenetic relationship of both taxa. Other authors have argued for a distal tarsal identity of the hooked element in turtles, which is less consistent with a potential sistergroup relationship of turtles with lepidosaurs. We present new data regarding muscle connectivity, ossification mode, and the fossil record of the turtle pes and critically review other lines of evidence published in previous studies, including digital count, timing of ossification, and parsimony. All lines of evidence, particular the combined endochondral/perichondral ossification of the hooked element, support the hypothesis that the hooked element represents an evolutionary fusion of distal tarsal V and metatarsal V. The hooked element of cryptodires is developmentally dominated by the perichondral metatarsal, whereas the endochondral distal tarsal dominates that of pleurodires. This is the primary reason why recent studies of pleurodires argued for a distal tarsal V identity of the hooked element. The hooked element of cryptodires furthermore differs from pleurodires by being rotated outwards by approximately 90 degrees. Although differences are apparent with the hooked element of lepidosaurs in details of muscle insertions and spatial orientation, the vast majority of data supports a primary homology of the hooked element of both taxa but an independent acquisition of the hook.



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