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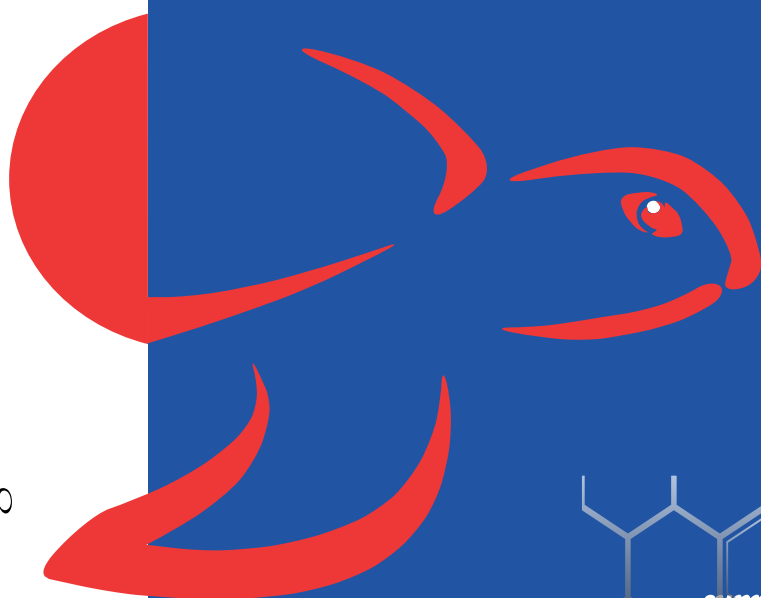
2018

TURTLE EVOLUTION Symposium

Program & Abstracts

第六回・カメ類の進化に関する国際シンポジウム

於 早稲田大学



Waseda University
School of International Liberal Studies

supported by the Palaeontological Society of JAPAN



Scidinge Hall

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Presentation and Brief History of the Symposia

The Symposium on Turtle Evolution is a scientific meeting for discussions on every aspect about turtle evolution and systematics. This is the first time it is held in Asia and the host institution is the School of International Liberal Studies, Waseda University. The meeting will take place at the conference room of the 11th Building on Waseda Campus in Tokyo, Japan.

Turtle Symposiums started as focused on fossil turtles only (for conference photos of all meetings see end of this volume). The first was the “Premiere table ronde internationale sur les tortues fossiles”, held at the Institut de Paléontologie, Paris, France in 1983, and organized by mainly France de Broin. Twenty years later, in 2003, an international team led by Igor Danilov organized the second meeting, the “Symposium on Turtle Origins, Evolution and Systematics”, that was held at the Zoological Institute of the Russian Academy of Sciences in Saint Petersburg, Russia. In 2009, Donald Brinkman and collaborators organized the “Gaffney Turtle Symposium”, in honor of Eugene Gaffney, at the Royal Tyrrell Museum, Drumheller, Canada. In 2012, Walter Joyce, Joe Corsini, Ingmar Werneburg, and Márton Rabi organized the Symposium on Turtle Evolution, which was held at the Department of Geosciences of the University of Tübingen, Germany. Three years ago, in 2015, Pedro Romano and Gustavo Oliveira organized the Fifth Symposium on Turtle Evolution at the Museu Nacional of Rio de Janeiro, Brazil. This was first turtle meeting to be hosted on the South Hemisphere. Also in Rio de Janeiro, the venue of the next event – Tokyo, Japan – was voted by the attendants. Therefore, the sixth meeting regarding the evolution of turtles will finally be hosted in Asia for the first time.

The 6th Turtle Evolution Symposium will include 40 oral and poster presentations from May 26th to May 27th, 2018. In addition to one poster session, five thematic sessions for oral presentations will be organized: “Early Evolution”, “Living Turtles”, “Functional Morphology”, “Mesozoic Turtles”, and “Cenozoic Turtles”. Also, two keynote lectures, “Development and Evolution of the Turtle Shell” on the first day, and “Two New Paracryptodire Turtles from Western Canada” on the second day, will take place. So far, participants have been confirmed from 15 different countries: Brazil, Canada, China, Egypt, England, France, Germany, Hungary, Japan, Nigeria, Poland, Russia, Switzerland, Thailand, and USA, setting a broad group for discussion.

At first glance, the Turtle Evolution Symposium seems to be very restricted – considering that it is focused on a single vertebrate group. On the other hand, the variety of presentations reveals a wide range of research areas. The main focus is to understand how evolution works using turtles as a model. Based on this background, the presentations will address a variety of topics – for example the use of radiology and medical imaging tools, genomics, geometric morphometric, taxonomy, systematic, paleontology, molecular biology, zoology etc.

Looking forward to meeting you in Tokyo,
Ren Hirayama & the Host Committee of the 6th Turtle Evolution Symposium
April 26th, 2018

PROGRAM

Corresponding (Presenter) Chair person

| Day 1 (Saturday, May 26) | | | | |
|---------------------------------|--|------------------------------|-----------------------------------|--|
| 9:00 - 9:10 | | Introduction | Hirayama R. | Opening Adress |
| 9:10 - 10:00 | | Keynote | Kuratani S. | Development and evolution of the turtle shell |
| 10:00 - 10:10 | | break | | |
| 10:10 - 10:30 | | Early Evolution | Szczygielski T. | Osteodermal mosaic in the carapace of the earliest turtles |
| 10:30 - 10:50 | | | Szczygielski T. | Shell variability and sexual dimorphism in the earliest turtles |
| 10:50 - 11:10 | | | Hirasawa T. | Evolutionary origin of the turtle shell accompanied with the loss of the sternum |
| 11:10 - 11:30 | | | Obraztsova E. M. | Comments on the cranial morphology of <i>Heckerochelys romani</i> Sukhanov, 2006, a basal turtle from the Middle Jurassic of European Russia |
| 11:30 - 11:50 | | | Lambertz M. | At the interplay of developmental conservativeness and adaptive plasticity: Form and function in chelonian lungs and their value for phylogenetic considerations |
| 11:50 - 13:40 | | Lunch break | | |
| 13:40 - 14:00 | | Living turtles (1) | Garbin R. C. | Intraspecific variation in the shell of geoemydid turtles: Applications to systematics and paleontology |
| 14:00 - 14:20 | | | Vlachos E. (Rabi M) | A total evidence phylogeny of Pan-Testudinidae |
| 14:20 - 14:40 | | | Suzuki D. | Phylogeographic studies about the freshwater turtles in the Japanese main islands |
| 14:40 - 15:00 | | Coffee break | | |
| 15:00 - 15:20 | | Functional Morphology | Kawabe S. (Sonoda T.) | Morphological variation in inner ear of extant turtles: Possible application in paleontology |
| 15:20 - 15:40 | | | Ando K. | Relationship between the paddling locomotion and the inertia moment of carapace in testudines |
| 15:40 - 16:00 | | | Werneburg I. | Considerations on the development of the akinetic skull in pleurodire and cryptodire turtles |
| 16:00 - 16:20 | | | Ferreira G. S. | Biomechanical analyses suggest relation between neck-retraction and the trochlear mechanism in extant turtles |
| 16:20 - 16:30 | | break | | |
| 16:30 - 16:50 | | Mesozoic turtles (1) | Yoshida M. | Marine turtle remains from the Upper Cretaceous Yezo Group (Hokkaido, Northern Japan) suggest the continuous dispersal of the oldest known sea turtle lineage to Northwest Pacific |
| 16:50 - 17:10 | | | Hirayama R. | Limb morphology of the genus <i>Bothremys</i> (Bothremyidae; Pleurodira) from the Late Cretaceous of Morocco, Northern Africa |
| 17:10 - 17:30 | | | Danilov I. G. | Cretaceous chelonoid turtles of Northern Eurasia: previous records and new findings |
| 18:00 - 20:00 | | Conference Dinner | Hirayama R. | |
| Day 2 (Sunday, May 27) | | | | |
| 9:00 - 9:40 | | Keynote | Brinkman D. | Two new paracryptodire turtles from Western Canada |
| 9:40 - 10:00 | | Mesozoic turtles (2) | Tong H. | Turtle assemblages from the Phu Kradung Formation of the Khorat Group, NE Thailand and their stratigraphical and palaeobiogeographical implications |
| 10:00 - 10:20 | | | Sonoda T. | A new nanhsiungchelyid from the Upper Cretaceous in Jiangxi, China |
| 10:20 - 10:40 | | | André C. (Anquetin J.) | A new turtle cranium from the Early Cretaceous of the Purbeck Group (Dorset, UK) |
| 10:40 - 11:00 | | | Danilov I. G. | <i>Tienfucheloides undatus</i> – a turtle puzzle from the Cenomanian of Uzbekistan |
| 11:00 - 11:10 | | break | | |
| 11:10 - 11:30 | | Mesozoic turtles (3) | Joyce W. G. | " <i>Carteremys</i> " <i>pisidurensis</i> and <i>Piramys auffenbergi</i> , two poorly understood pleurodires from India |
| 11:30 - 11:50 | | | Nakajima Y. | Bone microanatomy of <i>Mesodermodochelys</i> , the Cretaceous shelled dermochelyid turtle |
| 11:50 - 12:10 | | | Uno H. | U-Pb dating of turtle fossils from the upper Cretaceous Tamagawa Formation in Kujū, Iwate, Japan |
| 12:10 - 13:30 | | Lunch break | | |
| 13:30 - 14:40 | | Poster Presentations | Chapman S. D. | The anatomy of <i>Notochelone</i> Lydekker, 1889 an Early Cretaceous protostegid (Testudines) from Australia and its bearing on the origin and early evolution of sea turtles |
| | | | Cherepanov G. | Variability of carapace scutes in newborn olive (<i>Lepidochelys olivacea</i>) and green (<i>Chelonia mydas</i>) turtles from Sri Lanka |
| | | | Cordero G. A. (Werneburg I.) | Reconstructing the evolution of neck retraction in turtles |
| | | | Gnetneva A. N. | Tortoises of the genus <i>Agrionemys</i> : phylogenetic position, systematics and fossil record |
| | | | Hermanson G. | Bioerosion on a pelomedusoid shell from the Late Cretaceous of Brazil |
| | | | Hermanson G. | A 3D geometric morphometric analysis of the palate of pleurodiran turtles |
| | | | Kato T. | A large soft-shelled turtle from gravity flow deposits of the Upper Cretaceous Nakaminato Group in Ibaraki Prefecture, Japan |
| | | | Lambertz M. | High-resolution x-ray tomography of large chelonians: A case study on <i>Rafetus swinhoei</i> (Gray, 1873) |
| | | | Tokugawa H. | Three-dimensional life restoration model of <i>Anomalochelys angulata</i> (Nanhsiungchelyidae; Cryptodira) |
| | | | Zvonok E. A. | Paleogene turtles of Eastern Europe: new findings and reinterpretation of the previous materials |
| 14:40 - 15:00 | | Cenozoic turtles (1) | Chkhikvadze V. M. (Danilov I. G.) | Chelonological collection of the Institute of Paleobiology (Tbilisi, Georgia): brief history, current state and problems |
| 15:00 - 15:20 | | | Claud J. | An extinct lineage of testudinoid turtle from the Early Eocene of Denmark |
| 15:20 - 15:40 | | | Abdel Gawad M. K. | New materials on the Testudines remains from Early Miocene, Wadi Moghra, North Western Desert, Egypt |
| 15:40 - 16:00 | | Coffee break | | |
| 16:00 - 16:20 | | Cenozoic turtles (2) | Takahashi A. | Late Pleistocene terrestrial turtle fauna of the Ryukyu Archipelago, southwestern Japan |
| 16:20 - 16:40 | | | Ko, J. | A foundational framework for the study of turtles in archaeological sites in China |
| 16:40 - 17:00 | | | Scheyer T. M. | The re-emergence of the Aldabra Atoll during the Late Pleistocene – community structure and trophic interactions |
| 17:00 - 17:15 | | Closing Remarks | Hirayama R. | |
| 17:15 - 18:00 | | Business Meeting | Hirayama R. | |
| 18:30 - | | Farewell party | | |



**6th Turtle Evolution Symposium
in Tokyo 2018**

New materials on the Testudines remains from Early Miocene, Wadi Moghra, North Western Desert, Egypt

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Abstract

Moghra Formation, Qattara Depression, Egypt, is considered a perfect window for the Early Miocene sites in Africa especially in North Africa. Testudines paleontological investigation was previously known in nineteenth century from the Moghra Formation including *Podocnemis aegyptiaca*, *Podocnemis bramlyi* and *Trionyx senckenbergianus*. By the early twentieth century Testudines re-identification indicate absence of *Podocnemis aegyptiaca* and *Podocnemis bramlyi* and appearance of *Mogharemys*, *Latentemys* and *Lemurchelys* based on skull fragments. This research focused on the different genera based on their carapace and plastron. With new materials, *Erymnochelys* and *Trionyx* are reported in the Testudines assemblage. The Testudines fauna supports the tide dominated estuarine environment with a tropical, warm, Miocene climate in northern Africa. Comparisons of other African Miocene vertebrate faunas suggest that Moghra may be older than Gebel Zelten, Libya, but similar in age to deposits at Rusinga, Kenya and Napak, Uganda.

Key words: Early Miocene, Egypt, Tide dominated estuary, Turtle, Wadi Moghra

Introduction

The Moghra Formation has been known from its type locality at Wadi Moghra, North Western Desert, Egypt. The Moghra Formation is characterized by diversity and abundance of vertebrate fauna both mammalian and non-mammalian (Miller, 1996; Abdel Gawad, 2011, Abdel Gawad et al., 2012, Abdel Gawad, 2016 and Abdel Gawad, et al., 2016). Testudines fossils are one of the most common vertebrates that are preserved there. The first vertebrate paleontological investigation had been carried out by Fourtau (1918 and re-published 1920) and he identified three genera of testudines such as *Podocnemis aegyptiaca* (Andrews, 1900a), *Podocnemis bramlyi* and *Trionyx senckenbergianus* (von Reinaoh, 1903). El- Khashab (1977) mentioned the same three genera as Fourtau. With new materials, Gaffney, et al. (2011) re-identify three new genera based on skull fragments preserved in Natural History Museum, London and the three genera are *Mogharemys*, *Latentemys* and *Lemurchelys*. Dacquè (1912, cited in Williams 1954) had describe another imperfect skull from the Moghra Formation, lacks the temporal and occipital region, which he named *Sternothacrus blanckenborni*. Williams (1954) had re-described (NHMUKPVR8440) a skull remain testudines from the Moghra Formation. The skull had been described and belonged to genus *Podocnemis*. This skull had been interpreted as an intermediate between *Dacquemys* and *Erymnochelys*, perhaps somewhat closer to *Erymnochelys*. Also, he refers *Podocnemis aegyptiaca* (Andrews, 1900) as *Erymnochelys aegyptiaca* (Andrews, 1900).

Wadi Moghra is located on northeastern portion of the Qattara Depression, north Western Desert, Egypt. The geological study of the Moghra Formation consists of series of shale- sandstone interbedded units with several ichnofossil assemblages composed of *Ophiomorpha*; *Thalassinoides*;

root system of mangrove trees and a large number of silicified tree trunks (Abdel Gawad, 2011 and Abdel Gawad, et. al., 2012). The geological investigation deduce the main environment which is a tide-dominated estuary with a large river system trending SE-NW with an alternation of tidal channel, tidal flat and tidal sand bars (fluvialite - estuarine and marine deposits). Abdel Gawad et al, 2010 and Abdel Gawad, 2011 had recognized four stratigraphic horizons for the fossil bearing units all over the whole section of the Moghra Formation. These four horizons are characterized by the diversity and abundance of vertebrates especially mammals, while the reptiles are only concentrated in the first lower horizon.

Materials

The described specimens are housed in Cairo Geological museum (CGM), Egypt; Duke Lemur center, Division of Fossil Primates, Duke University (DPC), USA.; and Natural History Museum in United Kingdom (NHMUK).

Results

PODOCNEMIDODDA Cope, 1868
ERYMNOCHELYDAND Broin, 1988
Erymnochelys Baur, 1888

The specimen DPC7400 recorded the *Erymnochelys* as it represents an anterior lobe of a plastron where the front half is well preserved with broken edges and without mesoplastrons and the specimen is broken on some parts of the sutures. The plastron contains a highly curved suture line between the different scutes. The middle part of the carapace is characterized by hexagonal structure and it is raised and curved. The anterior lobe of the plastron of this genus is characterized by flat, thin and almost oval in outline. The ventral surface of the anterior lobe seems to be smooth with no roughness and with present sharpness suture lines. The sutures line between the pectoral scute and the hyoplastron is straight in shape from the ventral side while from the dorsal side, it is slightly depressed. The suture line between the hyoplastron and mesoplastron is may be rounded. The entoplastron is diamond in outline. The suture separating the humeral scute and pectoral scute (suture humeral-pectoral) is forming an almost undulate concave-convex line. There is no obvious or smooth surface decoration in this genus.

TESTUDINES, Batsch, 1788
CRYPTODIRA, Cope, 1868
TRIONYCHIDAE, Gray, 1825
Trionyx, (Forskal, 1775) (Geoffroy Saint-Hilaire, 1809)
Trionyx senckenbergianus von Reinaoh, 1903

The specimen DPC7789 recorded the *Trionyx* as it represents almost a complete carapace. *Trionyx* carapace is characterized by elongated to oval in shape. The surface decoration is formed by slightly crests and ridges which are parallel to the lateral border of the shell with a small regular pits and a small polygonal with deep boundaries. The prolonged bone is one of the main diagnostic features of genus *Trionyx* and it is characterized by flat, thin and not sharp. The central scutes are polygonal in shape. There are seven coastal scutes that are rectangular in shape and seven marginal scutes that are curved downward and forming the prolonged parts.

Discussion

With new materials, it was found that Testudines represented by five genera which are *Erymnochelys*, *Mogharemys*, *Latenemys*, *Lemurchelys* and *Trionyx*. Hirayama, 1992 had recognized three different turtle's families from the Sinda Beds of eastern Zaire (Latest Miocene). Among the three families, there is the first known occurrence from Africa of carettochelyid, the pig-nosed turtle, *Erymnochelys*, the bigheaded side necked turtle, which once flourished in African during Tertiary, is restricted to Madagascar, today. *Podocnemididae* family represented by *Mogharemys*, *Latenemys* and *Lemurchelys* are all aquatic, inhabiting streams and other flowing water. Their shells are streamlined to aid in swimming, while *Erymnochelys* appears to be freshwater turtle especially in permanent slow streaming rivers, swamps, backwaters and lakes. *Trionyx* is found to be in almost all the environments. It is known as soft-shell turtles. Also it is known as fish eater and carnivore.

Phylogenetic relation

In North Africa and Arabia basin the Carettochelyidae are appeared by the Early Miocene (Broin, 1977). The first appearance of Trionychidae Cyclanorbininae was at the same time as the Carettochelyidae in Arabia basin and North Africa; these two taxa might arrive together by crossing the eastern Tethys and following the coastline (Broin, 2000). Broin, 2000 recorded that the three Eurasiatic taxa *Trionyx*, *Mauremys* and *Testudo* were immigrated during the Middle-Miocene and found in lower part of the Late Miocene in Algeria and in Tunisia, and he recorded the first known appearance of *Erymnochelys* in Early Cretaceous sediments of Niger, and it continued its development in North Africa (Egypt) during the Late Eocene and Early Miocene. By the Early Miocene, *Erymnochelys* group reached East Africa and Namibia, and continued its development during the Late Miocene-Pliocene only in East Africa. Havlik, et al., 2014, introduced *Allaeochelys libyca*, from the Middle Miocene (Langhian) of Gabal Zelten (Libya). *Trionyx* known to be phylogenetic far related from Podocnemidodda.

Conclusions

Moghra testudines assemblages containing two families including five genera with morphological and anatomical diversity and abundance. The two families are Podocnemidodda which include taxa such as *Erymnochelys*, *Mogharemys*, *Latenemys* and *Lemurchelys*, and the other family is Trionychidae which include *Trionyx*. The five testudines fauna collected from Moghra Formation (*Erymnochelys*, *Mogharemys*, *Latenemys*, *Lemurchelys*, and *Trionyx*) represent a combination between differentiated genera of Eurasia between the Eocene-Miocene ages, some are indeterminate in Asia, some are immigrated and arrived by 3 crossing the eastern Tethys and others are African endemic fauna. There is a pattern observed, with intersection between endemic African taxa (*Erymnochelys*) and immigrated fauna (*Trionychidae Cyclanorbininae*, *Carettochelyidae* and *Trionyx*). The biogeographic implications of these five genera of testudines indicate the presence of fresh to brackish water environment to be the source of these materials. The appearance of turtle remains concordant with that the ecology and environment was adaptive to such reproduction, diversity and abundance of reptile's communities. Wadi Moghra is known to be the earliest Miocene African sites, overlap Gabal Zelten, Libya and almost older than all the east African Miocene sites.

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Relationship between the paddling locomotion and the inertia moment of carapace in Testudines

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Many terrestrial tetrapod lineages have readapted to life in water, and have acquired various swimming methods. To explain how these various swimming methods have been evolved among tetrapods, it is important to reconstruct the swimming locomotion of each extinct taxon as accurate as possible. However, due to our poor knowledge on the relationship between the swimming locomotion and the skeletal morphology, it remains difficult to evaluate the precise reconstruction of the swimming strategies in the extinct taxa. Here we used Testudines to study the above-mentioned relationship. This is because, Testudines has been adapted to various environments (terrestrial, aquatics, semi-aquatics), and has been diversified in terms of the shapes and swimming abilities—the way they use their body and limbs for swimming. The testudines propel in the water by the paddling, however they do not use the undulation, because their trunks are co-ossified to be immobile. For the reasons described above, the testudines are the best taxa to study the relationship between the body shape and their swimming strategy in terms of the paddling.

In the water, the body of the animal is rotated about the center of gravity by multiple forces applied to the body (the driving force generated by the fin, water resistance, and so on). These forces rotate the animal body in the water about the three axes of inertia—the roll, yaw, and pitch axes, which roughly correspond with the cranio-caudal, dorso-ventral, and medio-lateral axes of the body, respectively. The animal in the water needs to control the orientations of their body against the rotation caused by these forces. Here we proposed a new method to differentiate the various swimming methods based on the combination of the two biomechanical indices, such as inertia moment (physical index which reflects the difficulty of rotation), and area moment (product of the effective cross sectional area and the leverage of the fin), which can be measured from the skeletal morphologies.

The paddling of the testudines can be roughly categorized by the rotational axes of the limb locomotion—(T) the transverse paddle; (H) the horizontal paddle; and (S) the sagittal paddle. In addition to the variation in the orientation of the limb locomotion, there are different patterns of the timing of right/left limb movements: (a) asymmetric alternative and (b) symmetric bilateral movements. Therefore, there are numerous ways of the swimming locomotion using the paddling, and the directions of rotational forces applied to the body are different, respectively. The swimming locomotion of the extant testudines can be categorized as follows: (Tb) bilateral transverse paddlers (e.g., *Caretta* and *Carettochelys*), (Ha) alternative horizontal paddlers (e.g., *Amyda*, *Kinosternon*, *Pelomedusa*), (Sa) alternative sagittal paddlers (e.g., *Chelydra*, *Platysternon*), and (N) non-swimmers (e.g., terrestrial turtles). The three-dimensional (3D) shapes of the whole bodies of testudines specimens were scanned using micro X-ray computed tomography scanners. We compared the inertia moment and the area moment among these four groups (Tb, Ha, Sa, N). The inertia moment and the area moment were measured using Voxelcon2013 (software for 3D shape analysis).

The bilateral transverse paddlers (Tb) emphasized the inertia about the yaw and pitch axes, and emphasized the area moments about the pitch and yaw axes; the alternative horizontal paddlers (Ha) emphasized the inertia about the yaw and pitch axes, and deemphasized the area moments about the yaw and pitch axes; the alternative sagittal paddlers (Sa) emphasized the inertia about the yaw and pitch axes blazingly, and deemphasized the area moments about the yaw and pitch axes; the non-swimmers (N) emphasized the inertia about the roll axes, and deemphasized the area moments about the pitch and yaw axes.

New methods to differentiate the various swimming methods in testudines based on the biomechanical indices which can be measured from the morphologies were proposed. These biomechanical indices would be powerful tools to estimate the swimming methods in the extinct taxa.

A new turtle cranium from the Early Cretaceous of the Purbeck Group (Dorset, UK)

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Background

The Purbeck Group of southern England has yielded a rich turtle assemblage dated from the Berriasian (Early Cretaceous). Four taxa have been described from these layers, including three paracryptodires. The most common of these taxa is the pleurosternid *Pleurosternon bullockii*, which is known by numerous sub-complete shells as well as by one cranium (Milner, 2004). The latter was originally assigned to the species *Mesochelys durstonensis* (Evans and Kemp, 1975), but associated postcranial material strongly suggests it belongs to *Pleurosternon bullockii* (Gaffney and Meylan, 1988; Milner 2004). *Dorsetochelys typocardium*, the second paracryptodiran species, is known by about ten shells previously referred to ‘*Glyptops*’ *typocardium* and one skull initially described as *Dorsetochelys delairi* (Evans and Kemp, 1976; Milner, 2004; Pérez-García, 2014). The third Purbeck paracryptodire is *Compsemys anglica*, which is mostly known by incomplete shell material and limb osteoderms (Barrett et al., 2002; Milner, 2004; Joyce et al., 2011). This material needs revision. And finally, the fourth turtle of the Purbeck Group is *Hylaeochelys belli*, a eucryptodire of uncertain phylogenetic relationships known by abundant shell material from the Purbeck and Wealden (Milner, 2004; Pérez-García, 2012).

Cranial material from the Purbeck Group remains relatively rare. Two nice skulls were described in the 1970s (Evans and Kemp, 1975, 1976) and, as mentioned above, are now referred to *Pleurosternon bullockii* and *Dorsetochelys typocardium* (Gaffney and Meylan, 1988; Milner 2004; Pérez-García, 2014). Milner (2004) also mentioned a skull held in the collections of the Royal College of Surgeons Museum that is now lost and two mandibles in the Natural History Museum of London, which are still undescribed. Finally, there is a last skull housed in the Dorset County Museum (DORCM G.10715) that was until now only partly prepared and provisionally referred to *Dorsetochelys delairi* (Milner, 2004), now *Dorsetochelys typocardium*. This last skull is the object of the present study.

Methods

The skull DORCM G.10715 was taken out of the surrounding matrix and completely prepared. This specimen was described in detail and compared with relevant material mostly from the Late Jurassic and Early Cretaceous of Europe.

Results

In contrast to previous observations before preparation (Milner, 2004), DORCM G.10715 clearly differs from *Dorsetochelys typocardium*, as well as from all known basal paracryptodires. The temporal emargination is much more developed, the prefrontals are well developed on the skull roof and apparently meet in the midline, and the foramen palatinum posterius is large and open posterolaterally. Unfortunately, the ventral basicranial area is partly damaged. The internal carotid artery runs in a gutter on the ventral surface of the pterygoid and basisphenoid. It is unclear whether this gutter was partly floored or not, so that the position/presence of the foramen posterius canalis carotici interni is uncertain. In the anterior third of the basisphenoid, the canalis caroticus internus

appears to be naturally open ventrally and the foramen posterius canalis carotici cerebralis and foramen posterius canalis carotici palatinum are apparent in ventral view and lie close to one another. There is no basiptyergoid process. DORCM G.10715 was provisionally included in the global turtle matrix of Zhou and Rabi (2015) and found to be more closely related to crown-group turtles than to Pleurosternidae and Baenidae.

Discussion

The morphology of DORCM G.10715 sets it apart from all known paracryptodires. By many characters, DORCM G.10715 actually recalls basal eucryptodires such as the Late Jurassic thalassochelydians. Unfortunately, the preservation of the material prevents the description of the internal cranial anatomy, which is so important for the systematics of these turtles.

The passage of the internal carotid artery in the posteroventral part of the basicranium in some basal paracryptodires (e.g., *Dorsetochelys typocardium*, *Arundelemys dardeni*) is morphologically very close to the condition often observed in basal eucryptodires (e.g., in some xinjianchelyids, sinemydids, macrobaenids and thalassochelydians), which complicates identification of imperfect specimens. However, DORCM G.10715 is tentatively interpreted here as a basal eucryptodire.

There is a possibility that DORCM G.10715 represents the skull of *Hylaeochelys belli*, the only other eucryptodire currently known from the Purbeck Group. The size at least is coherent, but the new skull is not associated with postcranial material and no other cranial remains of *Hylaeochelys belli* is known to date.

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Two new paracryptodire turtles from Western Canada

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Two new paracryptodire turtles from Western Canada provide information on the diversity distribution of turtles in this area. One of these is from Early Cretaceous beds exposed in the Bowser Basin of northwestern British Columbia, and the second is from Paleocene beds exposed along the Highwood River in the foothills of western Alberta.

The new paracryptodire from Early Cretaceous of the Bowser Basin of northwestern British Columbia (Fig. 1A-B), referred to here as the Bowser Basin turtle, is represented by the carapace of a large individual seen in dorsal and ventral views. It is included in the Paracryptodira because of the presence of mesoplastra contacting one another at the midline. Within the Paracryptodira, the Bowser Basin turtle is similar to specimens that have been identified as juvenile individuals of *Dinohelys whitei* in that the vertebral scutes are wide and ornamented by plications that radiate forward from a point on the midline at the posterior end of the scute. However, the specimen of the Bowser Basin turtle is interpreted as an adult because it is relatively large and the carapace lacks fenestra between the costals and peripherals. The retention of a highly plicated carapace in the Bowser Basin turtle demonstrates that this feature can be retained during growth, and therefore, brings into question the interpretation that the small individuals with highly plicated shells are juveniles of *Dinohelys whitei*, the type specimen of which is an adult with a smooth shell. It is possible that the small shells previously interpreted as juvenile specimens of *Dinohelys whitei*, the morphologically similar taxon *Desmemys*, and the Bowser Basin turtle are members of a distinct, previously unrecognized group.

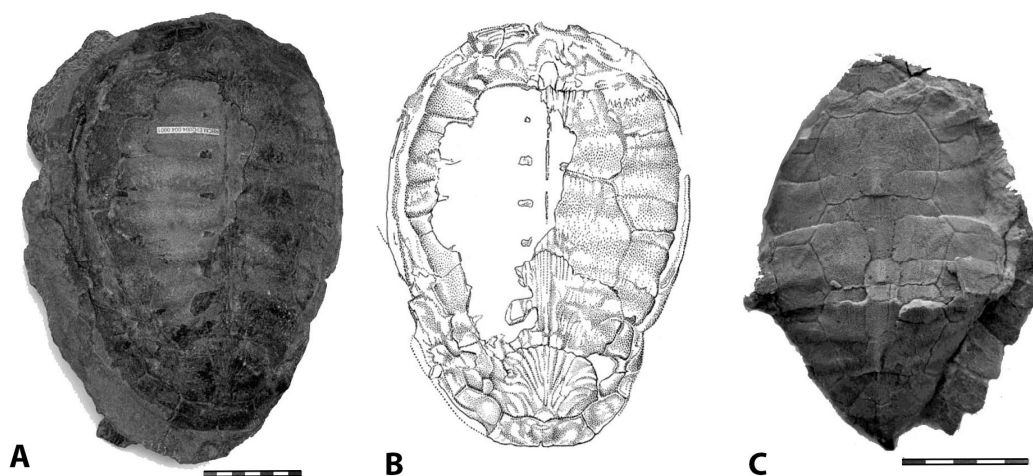


Figure 1. New paracryptodire turtles from Western Canada. A-B) the Bowser Basin turtle, carapace in dorsal view. Royal British Columbia Museum specimen RBCM 2004.4.1, C) The Highwood turtle, carapace in dorsal view. Royal Tyrrell Museum of Palaeontology specimen TMP 2015.22.28. Drawings by Donna Sloan of the Royal Tyrrell Museum of Palaeontology. Scale bars in cm.

The second new paracryptodire from the Paleocene of the western Alberta foothills, referred to here as the Highwood turtle, is represented by a carapace (Fig. 1 C). It is included in the Baenodda because the fifth vertebral scute enters the posterior edge of the carapace. Within the Baenodda, it is similar to *Boremys* and small turtles from the Green River Formation that have been identified as juvenile individuals of *Baenia* in that the posterior end of the carapace is strongly serrated. However, in contrast to *Boremys*, supramarginal scutes are absent. A distinctive feature is the presence of a low mid-dorsal ridge with nodes developed at the posterior end of the vertebral scutes. Isolated neurals with this feature from the Late Campanian Dinosaur Park Formation are present in a single locality that has been interpreted as being deposited in a quiet water environment near the mouth of a river. Previously, Brinkman et al. (2015) had referred these neurals to a marine turtle from the overlying Bearpaw Formation, identified as *Lophochelys niobrarae* by Nicholls et al. (1990) because it was the only other turtle from Alberta with this feature. However, based on comparison with the new baenid, this identification is unlikely. It is more probable that these neurals are from a baenid closely related to the Highwood River turtle. Since they are only found in one locality within the Dinosaur Park Formation, the turtle must have had a very restricted distribution, likely for paleoecological reasons.

The new paracryptodire turtles reported here demonstrate the presence of a previously unrecognized level of diversity of the group. Significantly, both specimens were recovered from geographic areas, environments of deposition, and time periods, which were previously poorly documented, demonstrating the importance of sampling from new and distinct localities.

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The anatomy of *Notochelone* Lydekker, 1889 an Early Cretaceous protostegid (Testudines) from Australia and its bearing on the origin and early evolution of sea turtles.

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Introduction

The skeletal material of *Notochelone* kept at the Natural History Museum of London (NHM) and in the Queensland Museum (QM), Queensland was collected in 1978 from sites in north and west Queensland. The specimens come from the Toolebuc Formation and the Allaru Mudstone and both are of Albian age and where the depositional environment was one of restricted shallow marine to offshore marine. These collections contain six skulls plus a shared number of imperfect shells and isolated bones that have never been described before.

Method

We fully described the morphology of the *Notochelone*, in particular NHMUK PV R11977 a matrix free skull with an associated shell, axial bones, and provided insights into the anatomy, taxonomy and phylogeny of protostegid sea turtles. In addition, braincase morphology was reconstructed from CT scans of the largest isolated skull NHMUK PV R 9590 – amongst the first undertaken for any protostegid. Protostegids possess a unique internal carotid circulation in that following their split from the palatine arteries, the two cerebral arteries join into a single, fully roofed canal and that the palatine artery is fully enclosed in the pterygoid and therefore the lateral head vein and the palatine artery canals are completely separated by bone.

Institutional Abbreviation – NHMUK, Natural History Museum, London.

Discussion

This detailed description of *Notochelone* was crucial to improving morphological data deficiency in sea turtle evolution and since our knowledge of the primitive sea turtle "bauplan" is poor these advancements have contributed to solving some major issues around the origin and early evolution of sea turtles 1) the problematic monophyly of chelonoid sea turtles: some phylogenies say the extinct protostegids are part of the sea turtle crown whereas others recognize them as a completely separate marine turtle radiation and argue for extreme parallels between representatives of Protostegidae and crown sea turtles 2) the origin of sea turtles since we don't know which freshwater taxa they are derived from and how and where the transition took place to the marine environment and we know very little about the morphological adaptations accompanying this transition 3) the age of the sea turtle crown is highly controversial. If protostegids were closely related to crown-sea turtles, the age of the crown has to be pushed back by 35 million years relative to molecular clock divergence estimates but such backdating would also pull back the entire turtle crown into unexpected deep time (i.e. the Paleozoic). Consequently, three solutions are possible: 1) protostegids are either not related to crown-sea turtles; 2) the molecular phylogeny and the divergence dates are flawed; or 3) protostegids are true sea turtles but the rate of molecular and morphological evolution was greatly accelerated during their initial radiation. The morphological data obtained from *Notochelone* provided a critical test of these hypotheses and opened up new

directions in the study of the macroevolution of Mesozoic sea turtles. Past studies have shown that *Cratochelone berryi* Longman, 1915 thought to have co-existed with *Notochelone* belongs to the Protostegidae (Kear, 2006).

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Variability of carapace scutes in newborn olive (*Lepidochelys olivacea*) and green (*Chelonia mydas*) turtles from Sri Lanka

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To identify the natural variability spectrum in scutes of the turtle shell, wild populations of olive (*Lepidochelys olivacea*) and the green (*Chelonia mydas*) sea turtles from the south coast of Sri Lanka have been investigated. The eggs were collected from natural clutches and incubated at the territory of a hatchery in Kosgoda (Kosgoda Sea Turtles Conservation Project). The study was conducted during two seasons (November-February of 2015-2016 and 2016-2017). Newborns were photographed, followed by a detailed description of the characteristics of their folioidosis. In total, 655 specimens of *L. olivacea* and 341 specimens of *C. mydas* were investigated.

According to the structure of the horn cover, the olive turtle is a unique species, characterized by a significant variability of scutation. Thus, it is a good model object, which makes it possible to obtain a mass material on the variability of the scutes without the use of an experimental interfering embryogenesis. The green turtle, on the other hand, is characterized by a stable scutation of the horny shell. The variability of folioidosis in this species is mainly due to the influence of external factors (Ergine, et al., 2011) and, consequently, *C. mydas* can serve as a natural indicator of the state of the external environment.

Investigated newborns of *C. mydas* (N = 341) are characterized by a low level of variability in the mosaic of the scutes. The vast majority of individuals (97%) have a symmetrical plan for the structure of folioidosis with a pattern typical for this type - 1-12-4-5-4-12 (nuchal - left marginal - left costal - vertebral - right costal - right marginal scutes). Only 10 turtles (3%) have additional abnormal scutes. The low level of variability of newborn green turtles on the coast of Sri Lanka (compared to the data for the Mediterranean population of *C. mydas* with 21.9% of neonatal abnormalities, Ergine, et al., 2011) seems to indicate optimal conditions for incubating of their eggs. It can be assumed that these conditions are also suitable for another nesting species, *L. olivacea*.

Among the newborns of *L. olivacea* (N = 655), 120 different patterns of carapace scutes were revealed. Symmetrical patterns were found in 399 turtles (60.9%) and were represented by 34 variants (28.3%). The most common were 4 patterns (1-13-5-5-5-13, 1-13-6-5-6-13, 1-13-6-6-6-13 and 1-13-7-7- 7-13) found in 249 turtles (38%) in approximately equal proportions. The number of asymmetric patterns predominated (86 variants or 71.7%). The frequency of manifestation of each was not great and did not exceed 4.1%. The most variable were the vertebral and costal series, the number of scutes in which varied from 4 to 10. The most frequent and proportionally equivalent variants were variants with the presence of 5, 6 and 7 vertebral scutes (30.2%, 28.4%, 35.8% % of turtles). The increase in the number scutes of the vertebral series is primarily due to the appearance of additional elements in the posterior half of the carapace. In the fore-part of the carapace, additional scutes were relatively rare. Standard for most sea turtles, equal to five costal scutes, was observed in relatively few *L. olivacea* (16.5%) studied. Asymmetries and symmetries among them occurred in a ratio of 1 to 4. Newborn olive turtles with 6 and 7 pairs of costal scutes were met with the same frequency of 21.1%, with 8 pairs - 7%, with 9 pairs - 1.2%. In general, an equal numbers of left and right costals were found in 409 newborn turtles, which is 62.4% of the individuals studied. The number of marginal scutes varies from 10 to 15. The majority of hatched turtles (92.7%) have 13 of their pairs, and this can be considered a normal state. Only 7 turtles (1,1%) demonstrated fewer than 13 marginal scutes on one or both sides of the body. A more frequent variant of abnormality is the presence of one or a pair of additional marginal scutes in the caudal part of the carapace (6.25%).

The presence of a great number of variants of the structure of the horny carapace in the absence of any one prevailing pattern of scutes in *L. olivacea* indicates a unique character of the organization of foliosis in this species of turtles. One can agree with Pritchard's opinion (Pritchard, 1969) that the structure of the carapace scutes of this turtle is so variable that it is not possible to single out its norm. Nevertheless, in the studied population of the olive turtle, several relatively high-frequency conditions of foliosis are found (1-13-5-5-5-13, 1-13-6-6-6-13, 1-13-7-7-7-13), demonstrating the general tendency of polymerization of scutes while maintaining their bilateral symmetry.

The scutation of *L. olivacea* from different nests is characterized by a different range of variability than the others. For comparison, we present data here just on two clutches. Turtles from the first clutch (N = 108) have the minimum number of patterns (17) among the studied clutches, the most common variant is 1-13-6-5-6-13 (27.8%). The number of vertebral and costal scutes varies in the range from 5 to 7. The majority of turtles have 5 vertebral scutes (57.4%), with 5 costals being not characteristic to this group (found only in 5.5% of the individuals of the clutch). The share of turtles with an equal number of costal scutes on both sides of the body (symmetrical state) is 68.5%, which is significantly higher than the average value for all clutches.

Turtles from the second clutch (N = 80) realize 48 patterns of foliosis, with the most common pattern - 1-13-7-7-7-13 (18.7%), while the rest of the variants found mainly in single specimens. Vertebral and costal scutes vary in number in a wide range, but with a clear bias towards its increase (up to 8-10 in the series). The share of turtles with an equal number of left and right costal shields is below the average level of 56.2%, which indicates a relatively high degree of their asymmetry. In addition, turtles from this clutch have several specific high-frequency anomalies (the presence of a pair of nuchal scutes (15%), additional marginal scutes (21.2%), fusion of the first and the second vertebral scutes (12.5%)), which are unusual or rare in turtles from other clutches.

Most researchers associate the appearance of anomalies of the scutes with the influence of unfavorable environmental factors during the incubation period (Lynn, Ullrich, 1950; Bujes, Verrastro, 2007; Zimm et al., 2017; and other sources). However, some anomalies are assumed to be of a genetic nature (Zangerl, 1969; Cordero-Rivero et al., 2008; Velo-Antón et al., 2011). Our data on the olive turtle indicate that differences in the nature of the anomalies of the scutes can also appear at the level of individual breeding pairs. Differentiation of the variability spectra of scutes in *L. olivacea* newborns from different clutches and the presence of specific anomalies for a number of clutches are apparently due to the genetic differences of their parents rather than to the influence of external factors, since all the clutches were incubated under similar conditions.

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Chelonological collection of the Institute of Paleobiology (Tbilisi, Georgia): brief history, current state and problems

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Institute of Paleobiology of the Georgian National Museum houses one of the largest and most important collections of fossil and recent turtles within the territory of the former USSR. This collection began in 1960s mostly due to activity of Prof. V.M. Chkhikvadze, who collected materials himself, or received them from numerous Soviet geologists, paleontologists, and zoologists. The collection includes specimens from the Early Cretaceous – Quaternary interval of different regions of the former USSR (Armenia, Azerbaijan, Georgia, Kazakhstan, Kyrgyzstan, Moldavia, Russia, Tajikistan, Turkmenistan, Ukraine, and Uzbekistan) and Mongolian People's Republic (MPR). The collection contains 69 types of fossil and recent turtles, which belong to 61 valid species/subspecies, 24 genera and 10 families (see Table 1). In addition, there are also non-type materials from more than 150 fossil and unknown number of recent localities. The most abundant fossils come from the Caucasus, Kazakhstan, and MPR. The Caucasus fossils come from about 20 Cenozoic (mostly Neogene and Quaternary) localities (see Chkhikvadze, 1983). The materials from Kazakhstan (especially those from the Zaisan Depression) provide one of the most complete fossil records of Cenozoic turtles within Asia, from more than 60 localities (see Chkhikvadze, 1973, 1989, 1990). Finally, of all the Mongolian materials (from about 30 localities) the most significant are the Cretaceous ones, coming from both well-known and numerous rare localities (Shuvalov and Chkhikvadze, 1975, 1979; Chkhikvadze and Shuvalov, 1988a, b). The quality of fossils varies from isolated shell fragments (which are the most abundant) to partial or complete shells, skulls and skeletons. Recent turtles are represented by skeletonized specimens and shells of *Agrionemys* spp. from Middle Asia and Kazakhstan (more than 200 specimens; see Chkhikvadze et al. 2008), and *Testudo graeca* spp. from the Caucasus (more than 100 specimens; see Chkhikvadze, 2013), as well as other turtle taxa (more than 100 specimens) from Northern Eurasia and other regions of the world. Most of the materials were described or mentioned in numerous publications of V.M. Chkhikvadze (partially cited above) and used in his constructions on systematics, phylogeny and biogeography of fossil and recent turtles (see Chkhikvadze, 1973, 1984, 1987, 1990; for most complete list of references see Danilov et al., 2017).

Since its foundation, the collection is located in the old building of the Institute of Paleobiology (Potochnaya Street 4, Tbilisi). In post-Soviet time, the collection fell into decay. Due to the lasting lack of young specialists and laboratory assistants, the collection has no curation for many years. In 2000s, it was moved from the special storage to a small, unsuitable laboratory room of the same institute. As a result, the collection was piled chaotically throughout the room, being for a long period inaccessible for specialists.

In 2017 and 2018, the authors of this contribution undertook a search for the type and other described materials of the collection in order to document and organize them, and to prepare for transfer to the main building of the Georgian National Museum, which, most probably, will take place in 2018. In course of this search, more than 1000 collection units (more than 600 boxes with fossil specimens and more than 400 shells and skeletons of recent turtles) were sorted out. However, the task of saving and curation of this important collection may require in future efforts of the international scientific community.

Table 1. Fossil and Recent turtle taxa, which type materials are stored in the Institute of Paleobiology. Abbreviations: Ab – Abkhazia; Ar – Armenia; Az – Azerbaijan; ERu – European Russia; Ge – Georgia; K – Cretaceous; Ka – Kazakhstan; MA – Middle Asia; Mo – Mongolia; N – Neogene; P – Paleogene; Q – Quaternary; R – Recent.

| No. | Original name [current name if different or status; after Danilov et al., 2017] | Family | Age | Region |
|-----|---|--------------------|--|--------|
| 1 | <i>Adocus kazakhstanica</i> Chkhikvadze, 1973 [“A.” <i>kazakhstanica</i>] | Adocidae | P ₂ ² | Ka |
| 2 | <i>Agrionemys caucasica</i> Chkhikvadze, 2001 [<i>A. (Agrionemys) caucasica</i>] | Testudinidae | N ₁ ³ | ERu |
| 3 | <i>Agrionemys bogdanovi</i> Chkhikvadze, 2008 [<i>A. (A.) bogdanovi</i>] | Testudinidae | R | MA |
| 4 | <i>Agrionemys kazakhstanica kuznetsovi</i> Chkhikvadze, 2008 [<i>A.(A.) kazakhstanica kuznetsovi</i>] | Testudinidae | R | MA |
| 5 | <i>Agrionemys borsfieldi kazakhstanica</i> Chkhikvadze, 1988 [<i>A.(A.) kazakhstanica</i>] | Testudinidae | R | Ka |
| 6 | <i>Agrionemys borsfieldi rustamovi</i> Chkhikvadze et al., 1990 [<i>A.(A.) rustamovi</i>] | Testudinidae | R | MA |
| 7 | <i>Agrionemys ranovi</i> Amiranashvili et al in Sharapov et al., 1988 [<i>A. (Agrionemys) ranovi</i>] | Testudinidae | N ₂ ² | MA |
| 8 | <i>Altaytrionyx burtschaki</i> Chkhikvadze, 2008 | Trionychidae | P ₂ ² | Ka |
| 9 | <i>Altaytrionyx devjatkini</i> Chkhikvadze, 2008 | Trionychidae | P ₂ ¹ | Ka |
| 10 | <i>Amyda menneri</i> Chkhikvadze in Chkhikvadze et Shuvalov, 1988 [Trionychidae nomen dubium] | Trionychidae | K ₂ | Mo |
| 11 | <i>Anosteira shuvalovi</i> Chkhikvadze in Shuvalov et Chkhikvadze, 1979 [“A.” <i>shuvalovi</i>] | Carettochelyidae | K ₂ | Mo |
| 12 | “ <i>Baicalemys moschifera</i> ” Chkhikvadze in Khosatzky et Chkhikvadze, 1993 [“B.” <i>moschifera</i>] | Emydidae | N ₁ ²⁻³ | Ka |
| 13 | <i>Centrochelys natadzei</i> Chkhikvadze, 1989 [“C.” <i>natadzei</i>] | Testudinidae | N ₁ ³ | Ge |
| 14 | <i>Charitonyx tajanikolaevae</i> Chkhikvadze in Chkhikvadze et Shuvalov, 1980 [Nanhsiungchelyidae nomen dubium] | Nanhsiungchelyidae | K ₂ | Mo |
| 15 | <i>Chehydropsis kuznetsovi</i> Chkhikvadze in Gaiduchenko et Chkhikvadze, 1985 | Chelydridae | N ₂ ¹ | Ka |
| 16 | <i>Chehydropsis minax</i> Chkhikvadze, 1971 | Chelydridae | P ₂ ³ | Ka |
| 17 | <i>Chehydropsis poena</i> Chkhikvadze, 1971 | Chelydridae | N ₁ ² | Ka |
| 18 | <i>Chrysemys index</i> Chkhikvadze, 1971 [<i>Zaisanemys index</i>] | Emydidae | P ₂ ³ –P ₃ ¹ | Ka |
| 19 | <i>Chrysemys polydectes</i> Chkhikvadze, 1973 [“ <i>Zaisanemys</i> ” <i>jegalloi</i> Chkhikvadze, 1973] | Emydidae | N ₁ ¹⁻² | Ka |
| 20 | <i>Echmatemys borisovi</i> Chkhikvadze, 1990 | Geoemydidae | P ₂ ³ | Ka |
| 21 | <i>Echmatemys orlovi</i> Chkhikvadze, 1970 | Geoemydidae | P ₂ ³ | Ka |
| 22 | <i>Echmatemys zaisanensis</i> Chkhikvadze, 1970 | Geoemydidae | P ₂ ³ | Ka |
| 23 | <i>Emydoidea tasbaka</i> Chkhikvadze, 1989 [<i>Emys taraschuki</i> (Chkhikvadze, 1980)] | Emydidae | N ₁ ³ | Ka |
| 24 | <i>Ergilemys saikanensis</i> Chkhikvadze, 1972 | Testudinidae | P ₂ ³ –P ₃ ¹ | Ka |
| 25 | <i>Hadrianus davitashvili</i> Chkhikvadze et Amiranashvili, 1999 | Testudinidae | P ₂ ² | Ka |
| 26 | <i>Hadrianus obailiensis</i> Chkhikvadze, 1980 | Testudinidae | P ₂ ² | Ka |
| 27 | <i>Ergilemys vialovi</i> Chkhikvadze, 1984 [<i>Hadrianus vialovi</i>] | Testudinidae | P ₂ ¹ | MA |
| 28 | <i>Grayemys amoena</i> Chkhikvadze, 1970 | Geoemydidae | P ₂ ² | Ka |
| 29 | <i>Grayemys gigantea</i> Chkhikvadze, 1990 | Geoemydidae | P ₂ ² | Ka |
| 30 | <i>Grayemys minutissima</i> Chkhikvadze, 1990 | Geoemydidae | P ₂ ² | Ka |
| 31 | <i>Grayemys zersi</i> Chkhikvadze, 1990 | Geoemydidae | P ₂ ² | Ka |
| 32 | <i>Lindholmemys martinsoni</i> Chkhikvadze in Shuvalov et Chkhikvadze, 1975 | Lindholmemydidae | K ₂ | Mo |
| 33 | <i>Mauremys alekperovi</i> Chkhikvadze, 1989 | Geoemydidae | Q ₁ | Az |
| 34 | <i>Mauremys caspica gambariani</i> Chkhikvadze in Melik-Adamyanyan et al., 1988 | Geoemydidae | N ₂ ¹ | Ar |
| 35 | <i>Melanochelys fontinalis</i> Chkhikvadze, 1973 [<i>Ocadia iliensis</i> (Khosatzky et Kuznetsov, 1971)] | Geoemydidae | N ₁ ¹⁻² | Ka |

| | | | | |
|----|---|------------------|--|--------|
| 36 | <i>Melanochelys longilabiata</i> Chkhikvadze, 1973 [<i>Kaisakya longilabiata</i>] | Geoemydidae | P ₂ ³ | Ka |
| 37 | <i>Mlynarskiella mariani</i> Shuvalov et Chkhikvadze, 1986 [Shachemydinae nomen dubium] | Adocidae | K ₂ | Mo |
| 38 | <i>Palaeochelys gabunii</i> Chkhikvadze, 1973 [“P.” <i>gabunii</i>] | Geoemydidae | N ₁ ¹ | Ge |
| 39 | <i>Planiplastron tatarinovi</i> Chkhikvadze, 1971 | Platysternidae | P ₃ | Ka |
| 40 | <i>Planiplastron zaisanense</i> Chkhikvadze, 1981 [<i>Kazachemys zaisanensis</i>] | Platysternidae | N ₁ ² | Ka |
| 41 | <i>Plastomenus gabunii</i> Chkhikvadze, 1984 [<i>Altaytrionyx gabunii</i>] | Trionychidae | P ₂ ² | Ka |
| 42 | <i>Plastomenus minusculus</i> Chkhikvadze, 1973 [<i>Francedebroinella minuscula</i>] | Trionychidae | P ₂ ² –P ₃ ¹ | Ka |
| 43 | <i>Plastomenus mlynarskii</i> Chkhikvadze, 1970 [<i>Paraplastomenus mlynarskii</i>] | Trionychidae | P ₂ ² | Ka |
| 44 | <i>Protestudo alba</i> Chkhikvadze, 1971 | Testudinidae | N ₁ ¹ | Ka |
| 45 | <i>Protestudo darenskii</i> Chkhikvadze, 1971 | Testudinidae | N ₁ ² | Ka |
| 46 | <i>Protestudo illiberalis</i> Chkhikvadze, 1971 | Testudinidae | N ₁ ³ | Ka |
| 47 | <i>Protestudo lavrovi</i> Chkhikvadze, 1989 | Testudinidae | N ₁ ¹ | Ka |
| 48 | “ <i>Rafetus</i> ” <i>yexiangkuii</i> Chkhikvadze, 1999 | | P ₃ ¹ | Ka |
| 49 | <i>Sakya kolakonskii</i> Chkhikvadze, 1968 | | N ₁ ³ –N ₂ ¹ | Ab |
| 50 | <i>Testudo burtschaki</i> Chkhikvadze, 1975 | Testudinidae | N ₁ ³ | Az, Ge |
| 51 | <i>Testudo chernovi transcucasica</i> Chkhikvadze, 1979 | Testudinidae | N ₂ ² | Ge |
| 52 | <i>Testudo dagestanica</i> Chkhikvadze et al., 2011 | Testudinidae | R | ERu |
| 53 | <i>Testudo graeca armeniaca</i> Chkhikvadze et Bakradze, 1991 | Testudinidae | R | Ar |
| 54 | <i>Testudo graeca pallasi</i> Chkhikvadze et Bakradze, 2002 | Testudinidae | R | ERu |
| 55 | <i>Testudo graeca nikolskii</i> Chkhikvadze et Tuniyev, 1986 | Testudinidae | R | ERu |
| 56 | <i>Testudo meschethica</i> Gabunia et Chkhikvadze, 1960 [<i>Ergilemys meschethica</i>] | Testudinidae | N ₁ ¹ | Ge |
| 57 | <i>Tienfucheloides jastmelchyi</i> Chkhikvadze, 1981 [Lindholmemydidae nomen dubium] | Lindholmemydidae | K ₁ | Mo |
| 58 | <i>Trionyx danovi</i> Chkhikvadze, 1988 [“T.” <i>danovi</i>] | Trionychidae | N ₁ ² | ERu |
| 59 | <i>Trionyx jakhimovitchae</i> Chkhikvadze, 1989 [“T.” <i>jakhimovitchae</i>] | Trionychidae | N ₁ ^{1–2} | Ka |
| 60 | <i>Trionyx kbosatzkyi</i> Chkhikvadze, 1983 [“T.” <i>kbosatzkyi</i>] | Trionychidae | N ₁ ³ | ERu |
| 61 | <i>Trionyx ninae</i> Chkhikvadze, 1971 [Ultrionyx <i>ninae</i>] | Trionychidae | P ₃ | Ka |
| 62 | <i>Trionyx turgaicus</i> Kuznetsov et Chkhikvadze, 1977 [Ultrionyx <i>ninae</i>] | Trionychidae | P ₃ | Ka |
| 63 | <i>Trionyx zaisanensis</i> Chkhikvadze, 1989 [Ultrionyx <i>ninae</i>] | Trionychidae | P ₂ ³ –P ₃ ¹ | Ka |
| 64 | <i>Zaisanemys borisovi</i> Chkhikvadze, 1973 [<i>Z. index</i> (Chkhikvadze, 1971)] | Emydidae | P ₂ ³ | Ka |
| 65 | <i>Zaisanemys gilmorei</i> Chkhikvadze, 1990 | Emydidae | P ₂ ³ | Ka |
| 66 | <i>Zaisanemys jegaloi</i> Chkhikvadze, 1973 [“Z.” <i>jegaloi</i>] | Emydidae | N ₁ ^{1–2} | Ka |
| 67 | <i>Zaisanemys longicervicalis</i> Chkhikvadze, 1990 | Emydidae | P ₂ ³ | Ka |
| 68 | <i>Zaisanemys tolstikovae</i> Chkhikvadze, 1990 | Emydidae | P ₂ ³ | Ka |
| 69 | <i>Zaisanonyx jimenezjuentesi</i> Chkhikvadze, 2008 | Trionychidae | P ₂ ² | Ka |

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An extinct lineage of testudinoid turtle from the Early Eocene of Denmark

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The Early Eocene Fur formation from Denmark has yielded an interesting assemblage consisting of terrestrial and marine fauna and flora, including, plants, insects, fishes, birds, snakes and turtles (Hoch, 1975; Pedersen & Surlyk, 1983; Bonde, 1987). The preservation is often exceptional due to very good taphonomic condition. Among turtles, a complete skeleton of freshwater turtle has been discovered including a complete shell, limb bones, cervical vertebrae, hyoid apparatus, lower jaw and a skull exposed in dorsal view. The carapace and skull were flattened during fossilisation but the material is exceptionally well preserved. The specimen is partially disarticulated, showing a partial decay before burial.

The fossil turtle belongs to the superfamily Testudinoidea based on the buttresses development. It displays advanced features such as the presence of an epiplastral lip and the absence of inframarginal scutes. The general morphology is partly reminiscent of the genus *Palaeoemys*, a common geoemydid turtle found in the Early to Middle Eocene of France, Germany, and England (Claude & Tong, 2004). However, by contrast to this taxon, nearly no character can clearly help for assigning it to the family Geoemydidae. In contrast to most Early Eocene taxa, the vertebral scutes are relatively wide. The fossil displays several character states that are found in emydid but we consider as primitive: the pygal is long and intersected by the posterior sulcus of the 5th vertebral, there is one central keel but the lateral keels are absent, the anal scutes are long, the prearticular does not extend onto the Meckelian groove. Inguinal or axillary musk ducts cannot be evidenced. The presence of a deep anal notch is, however, reminiscent of geoemydids and is also found in *Echmatemys*.

The phylogenetic relationships are hypothesised in using both morphometrics (based on the dataset of Claude et al. (2003)) and cladistic analysis by parsimony and constraint by molecular phylogeny as backbone (based on the character states described in Claude & Tong (2004)). Belonging to a new freshwater testudinoid species, this extinct lineage sheds new light on the evolutionary history of the most speciose turtle group and on the sequence of apomorphies making up modern families, and adds one more taxon for understanding the colonisation of Europe and North America during the Palaeogene by testudinoids which has originated from Asia.

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Reconstructing the evolution of neck retraction in turtles

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Introduction

Turtles are a valuable taxon to study major transitions in the anatomical evolution of vertebrates (Joyce 2007). Of great interest are the anatomical transformations, beginning over 210 million years ago, that led to novel structural and functional modifications of the tetrapod skeleton: An extraordinarily shelled trunk (Pritchard 2008, Cordero 2017), an extremely mobile neck (Herrel et al. 2008), and a highly compact skull (Werneburg 2012). By holistic integration of data from paleontology, comparative phylogenetics, and functional morphology (Scheyer et al. 2013, Maier and Werneburg 2014), we discuss our current research on the biomechanics of neck retraction in living turtles.

Currently, there is no agreement on the selective pressures underpinning the initial evolution of neck retraction (Werneburg et al. 2015a). Illuminating the origins of this mechanism is important, because it maximized the protective capacity of the turtle and altered the subsequent course of turtle evolution. Specifically, early steps in the evolution of neck retraction probably influenced the 190-million-year-old divergence of side-necked (Pleurodira) and hidden-necked (Cryptodira) turtles (Werneburg 2015, Werneburg et al. 2015a, b).

Hidden-necked turtles retract the entire neck in a vertical S-shape motion (vertical plane) inside the shell. By contrast, side-necked turtles retract their neck sideward in a horizontal (lateral) plane below the anterior edge of the carapace (Kiliias 1957, Gaffney 1975). How these drastically different modes of neck retraction evolved remains obscure, though the iconic fossil from the late Triassic of Germany, *Proganochelys*, has provided important clues (Werneburg et al. 2015a, Lautenschlager et al. 2018). Even so, the conditions of many muscle and skeletal characters are uncertain in this 210-million-year old stem turtle. In particular, the form and function of the neck retraction apparatus, including several specialized muscle and vertebra modifications, are not entirely known (Werneburg et al. 2015b).

Methods

We highlight efforts to explain the phylogenetic bifurcation of side-necked and hidden-necked turtles by employing X-ray Reconstruction of Moving Morphology (XROMM) (Orsbon et al. 2018) on five extant turtle species. We discuss how to apply XROMM data to *in silico* experiments to reconstruct the ancestral state for neck retraction in the stem fossil turtle *Proganochelys*. We discuss details on a minimally invasive XROMM variant (scientific roscoping [Gatesy et al. 2010]) that does not require placement of markers on animals, but that is still capable of recording high-resolution biplane x-ray videos of neck vertebrae that can be used for a three-dimensional visualization of movement. Overall, our aim is to test two hypotheses: i) neck retraction originated from lateral displacement of the neck in *Proganochelys*; (ii) neck retraction originated from neck-uplifting movements in *Proganochelys*.

Results

Results from our previous studies suggest that lateral displacement was limited in *Proganochelys* (Werneburg et al. 2015a), but more data are needed to test this assumption. Here, we present a preliminary ancestral state reconstruction analysis that provides some support for a side-necked ancestral ground state for neck retraction (*Fig. 1*). Data generated by our *in silico* experiments will be used, first, to generate a consensus model for the ancestral mode of neck retraction to proof whether our hypothesis of side-necked motion in *Proganochelys* is biomechanically plausible. Anticipated results will then be used to evaluate either a lateral displacement origin or a neck-uptilting origin for neck retraction in ancestral stem turtles.

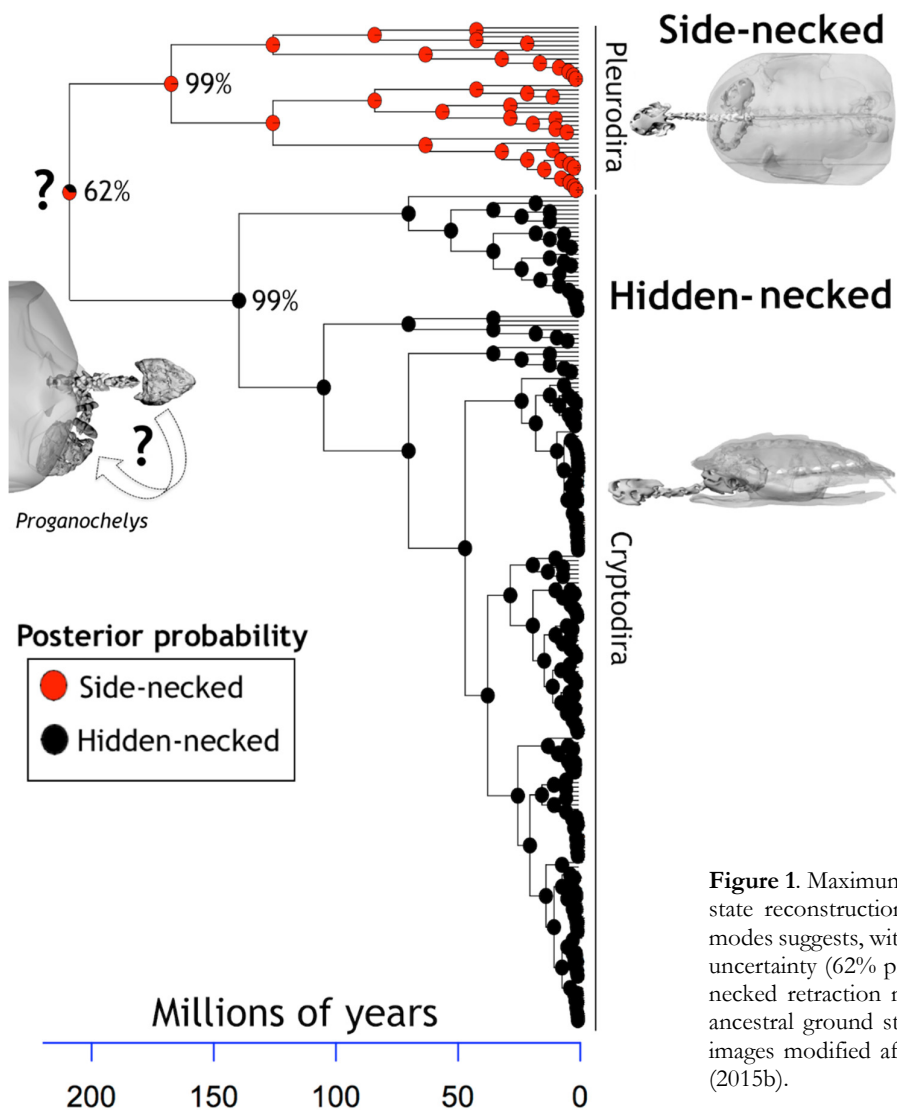


Figure 1. Maximum likelihood ancestral state reconstruction of neck retraction modes suggests, with a moderate level of uncertainty (62% probability), that side-necked retraction might have been the ancestral ground state in turtles. Turtle images modified after Werneburg et al. (2015b).

Conclusions

Knowledge on how the specialized turtle ‘body plan’ originated (Joyce and Gauthier 2004, Scheyer 2007, Kuratani et al. 2011, Lee 2013, Nagashima et al. 2013, Lyson et al. 2014) and subsequently diversified (Joyce 2007, Foth et al. 2017) continues to grow. Still, despite nearly two centuries of scientific interest (Bojanus 1823), origins of the shell and correlated skeletal traits have

only recently come to light (Lie et al. 2008, Schoch and Sues 2015). Our current project will build on this momentum to further clarify how key evolutionary transitions, such as the origins of neck retraction, influenced the remarkable diversity of form and function in modern turtles. Using turtle evolution as a model, we aim to stimulate further discussion on how the study of biomechanics, within a comparative phylogenetic framework, may serve to clarify key macroevolutionary trends in the past and present.

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Cretaceous chelonioid turtles of Northern Eurasia: previous records and new findings

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Chelonioid turtles (superfamily Chelonoidea, the crown and panstem clades Chelonoidea and Pan-Chelonoidea respectively) traditionally unite three families of sea turtles: Cheloniidae, Dermochelyidae, and Protostegidae (Hirayama, 1997, 1998; Joyce et al., 2004). Some authors exclude Protostegidae from Chelonoidea and Pan-Chelonoidea (Joyce, 2007; Parham and Pyenson, 2010), whereas others extend the latter clade to include basal eucryptodiran taxa, such as Xinjiangchelyidae, Sinemydidae and Macrobaenidae (Cadena and Parham, 2015). The oldest chelonioids (in the traditional sense) are known since the Early (protostegids, cheloniids) and Late (dermochelyids) Cretaceous (Hirayama, 1997). The Cretaceous chelonioid records from Northern Eurasia (territory of the former USSR; NE) was recently summarized by Danilov et al. (2017) based on published data. Here we briefly comment on some of these records (1–10; names of taxa are given after Danilov et al., 2017) and report new material (11–20) from this territory.

Abbreviations: AMNH, American Museum of Natural History, New York, USA; IP, Institute of Paleobiology, Tbilisi, Georgia; CYG, Club of Young Geologist, Orsk, Russia; PIN, A.A. Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; ZIN PH, Zoological Institute of the Russian Academy of Sciences, Paleoherpological Collection, St. Petersburg, Russia.

1) *Teguliscapha rossica* Nesson in Nesson et al., 1988 (Protostegidae; Nesson et al., 1988): dentary symphysis with a wide and flat triturating surface (holotype), frontal, opisthotic, nuchal, bridge peripheral, costal, hypoplastron, xiphoplastron, and humerus from Lebedinskii and Stoylenskii quarries (= Gubkin and Staryi Oskol; Averianov, 2002), Belgorod Province, Russia; Sekmenov Formation, upper Albian – lower Cenomanian. The humerus specimen mentioned by Nesson (1987; Nesson et al., 1988) was not found by us. Examination of the type specimens and new materials from the same locality, including maxillae with pronounced labial and lingual ridges, dentaries with narrow triturating surface and sagittal crest, serrated peripheral, T-shaped entoplastron, and humeri, allows us to suggest that the holotype of *T. rossica* belongs to a stem-chelonioid (sensu Parham and Pyenson, 2010), whereas shell elements from the type series and new material belong to a true protostegid, showing similarities with *Rhinochelys* and *Calcarichelys* (see Hooks, 1998).

2) Other materials from NE previously attributed to protostegids (*Teguliscapha* sp. indet. 1 and 2, Protostegidae gen. indet. 1–3; see Danilov et al., 2017) are diagnostic only to the level of Chelonoidea.

3) Dermochelyidae gen. indet. 1 (Dermochelyidae indet.; Averianov, 2002:139): collection ZIN PH 195, shell, scapular and ilial fragments from Lebedinskii and Stoylenskii quarries (Averianov, 2002; see 1 for locality data). This material shows similarity with *Mesodermochelys undulatus* (Hirayama and Chitoku, 1996) in shape of the iliac blade, broad and robust peripherals with undulated medial border, much expanded between costal ribs, and with recent *Dermocheleya coriacea* and the Chico Formation dermochelyid (lower Campanian of USA; Parham and Stidham, 1999) in the presence of the acromion tubercle on the scapula.

4) *Turgaiscapha kushmurunica* Averianov, 2002 (Dermochelyidae; Averianov, 2002): pygal (holotype) and other shell fragments without surface sculpturing from Kushmurun, Kazakhstan; lower part of the Eginsai Formation, upper Campanian – ?lower Maastrichtian. Hirayama (2006)

suggested considering this taxon as a nomen dubium (Chelonioidea indet.). The anterior neural with surface sculpturing of interconnected ridges, tentatively attributed to *Turgaiscapha kushmurnica* by Averianov (2002), is considered here as Cheloniidae indet. based on similarity with other sculptured cheloniids from the Cretaceous of NE (see 10, 15).

5) Chelonioidea fam. indet. 1 (Chelonioidea fam. gen. et sp. indet.; Nessov and Khosatzky, 1981:77, fig. IV, 11, 12): two bridge peripherals and plastron (?hypoplastron) fragment from Motnya I, Buryatiya, Russia; lower part of the Khilok Formation, Aptian. Given that there are two macrobaenid taxa reported from the same formation (Nessov and Khosatzky, 1981; Skutschas, 2003), this material may belong to macrobaenids as well.

6) Chelonioidea fam. indet. 2 (Knochenbruchstücks von einem Individuum des indeterminierten fossilen Reptils; Kiprijanow, 1883:15–17, 27, Taf. III): storage unknown, proximal part of the humerus from unknown locality, Kursk Province, Russia; “Severischen Osteolith”, Cenomanian. The humerus is poorly preserved, but clearly different in morphology from those of *Teguliscapha rossica*.

7) Chelonioidea fam. indet. 5 (Desmatochelyidae?; Nessov and Udovichenko, 1986:pl. 1, fig. 13; Chelonioidea indet.; Averianov, 2002:141): posterior peripheral from Alymtau, Kazakhstan; Darbaza Formation, lower Campanian? – middle Campanian. This peripheral belongs to a large individual and, as well as additional shell fragments from the same locality (collection ZIN PH 113), bears surface sculpturing made of a net of grooves. Cheloniidae indet. from Alymtau (= Kyrkkuduk II; see Averianov, 2002) was reported without designation of any material. The available turtle material from Alymtau in ZIN PH cannot be attributed to Cheloniidae.

8) Chelonioidea fam. indet. 6 (Chelonioidea indet.; Averianov and Yarkov, 2000:162, fig. 2; Chelonioidea incertae sedis sp. 1; Averianov and Yarkov, 2004:46, figs. 5, 6): frontal, dentaries, shell, and limb bones from Polunino 2, Volgograd Province, Russia; Campanian. Primarily, this material was considered as belonging to “a currently unrecognized group of relatively generalized and large sized protostegids” (Averianov and Yarkov, 2000:163), but later, based on additional material, was reassigned as similar to a cheloniid *Allopleuron* (Averianov and Yarkov, 2004; Karl et al., 2012).

9) Chelonioidea indet. (Averianov, 2002:142): material was not designated; Zhuravlevskii, Kazakhstan; lower part of the Zhuravlevskii Formation, upper Campanian. Material from Zhuravlevskii in IP examined by one of us (ID) consists of peripherals 5 – 7 in articulation, which are similar to those of the macrobaenid *Anatolemys* spp.

10) Testudines subord. indet. 8 (Cryptodira incertae sedis sp. 1; Averianov and Yarkov, 2004:42, figs. 2, 3): fragment of the dentary symphysis, two fragments of the scapula, and a neural with sculpturing made of tubercles and interconnected ridges (all specimens from gigantic individuals) from Rasstrigin 1, Volgograd Province, Russia; Maastrichtian. Additional material of this taxon from the same locality (collection ZIN PH 133) includes several sculptured shell fragments (peripherals and ?costals) from large individuals. Averianov and Yarkov (2004) mentioned similarity of this taxon with *Peritresius ornatus*, a cheloniid turtle from the Maastrichtian of USA, in shell sculpturing, but also noted difference from it in a flat (non-keeled) neural. Here we consider this taxon as a *Peritresius*-like cheloniid.

11) *Teguliscapha* sp. from Saratov (= Lysaya Gora), Saratov Province, Russia; upper Cenomanian: collection ZIN PH 39, dentary symphysis very similar in morphology to the holotype of *Teguliscapha rossica* (see 1). Previous chelonioid material reported from this locality (see Danilov et al., 2017: Chelonioidea fam. indet. 3) included dentaries with narrow triturating surface.

12) Protostegina indet.: collection ZIN PH 244, left maxilla, right jugal, humerus, scapula, several peripherals, and plastral fragments of giant individuals, as well as shell bones from individuals of smaller size, which come from Beloe Ozero, Saratov Province, Russia; Rybushka Formation, Lower Campanian. This material is assigned to protostegids based on large jugal with nearly straight ventral border, and lateral process of the humerus restricted to anterior portion of the shaft (Hirayama, 1997). Absence of the pronounced lingual ridge on the maxilla and shallow

groove on ventral surface of the posterior peripheral suggest attribution to *Protostegina* (Hooks, 1998). The maxilla, jugal and humerus are very similar to those of *Protostega gigas* (AMNH 1503).

13) Chelonioidea indet. from Beloe Ozero (see 12 for locality data): collection ZIN PH 244, large peripheral fragment without clear scute sulci and different in morphology from peripherals of *Protostegina* indet.

14) *Desmatochelys* sp.: complete skull and some postcranial bones in matrix (PIN) from Sengiley locality, Ulyanovsk Province, Russia; lower Aptian. This material is referred to *Desmatochelys* based on large size (skull is about 21 cm in length), similar outline of the skull, large nasal opening facing anteriorly, presence of large nasal bones, and absence of medial contact of prefrontals (see Cadena and Parham, 2015).

15) Cheloniidae indet.: collection ZIN PH 245, fragments of two costals in articulation from Penza, Penza Province, Russia; Campanian – Maastrichtian. This material was mentioned and figured by Nessov (1997:129, pl. 57, fig. 9) as “a girdle bone of a giant sturgeon with a smoothed relief of ridges.” The attribution of this material to turtles is supported by presence of the intercostal suture and remains of two rib thickenings on the internal surface of the specimen.

16) Chelonioidea indet.: collection ZIN PH 246, entoplastron (about 5 cm in length as preserved) from Dmitrievskii, Aktobe Province, Kazakhstan; lower Campanian. The entoplastron is longer than wide, with its posterolateral parts, at life, covered by hyoplastra from the external side that resulted in subtriangular shape of the entoplastron externally.

17) Chelonioidea indet.: collection ZIN PH 247, fragment of costal 1 with estimated medial length of about 6 cm from Karyakino, Saratov Province, Russia; Campanian.

18) Protostegidae indet.: collection ZIN PH 248, right maxilla from Polpino, Bryansk Province; Cenomanian. The maxilla has the same morphology as in the protostegid from Lebedinskii and Stoylenskii quarries (see 1).

19) Chelonioidea indet.: collection ZIN PH 249, peripheral (about 45 mm in length) from Pervomayskoe, Saratov Province, Russia; Cenomanian.

20) Chelonioidea indet.: CYG, complete odd costal (about 22 cm in width) from Izhberda, Orenburg Province, Russia; Campanian.

To summarize, our review demonstrates presence of representatives of stem-chelonioids as well as protostegids, cheloniids, and dermochelyids in the Cretaceous of NE. Stem-chelonioids are represented by *Teguliscapha rossica*, which record is extended to the upper Albian – Cenomanian. Reliable protostegids are known only from the European Russia: *Desmatochelys* sp. from the Aptian (first record for this territory), Protostegidae indet. from the upper Albian – Cenomanian, and *Protostegina* indet. from the Campanian (first record for this territory). Dermochelyids are represented by *Dermochelyidae* gen. indet. 1 from the upper Albian – lower Cenomanian of the European Russia. Probable cheloniids are represented by *Allopleuron*-like forms in the Campanian of the European Russia and *Peritresius*-like forms with sculptured shell in the Campanian – Maastrichtian of the European Russia and Kazakhstan (new record and reinterpretation of the previous records). Available material confirms presence of only one chelonioid taxon in Alymtau (7), two taxa in Beloe Ozero (12, 13), Kushmurun (4), and Saratov (11), and three taxa Lebedinskii and Stoylenskii quarries (1, 3). Some materials primarily assigned to chelonioids (5, 9) more likely belong to macrobaenids. Finally, new materials support cosmopolitanism of *Desmatochelys*, hitherto known from the upper Barremian – lower Aptian of Columbia, upper Cenomanian – Turonian of North America and Japan, and *Protostegina*, hitherto known from the ?Santonian – Campanian of North America and Japan (Hirayama, 1997; Cadena and Parham, 2015)

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Tienfucheloides undatus – a turtle puzzle from the Cenomanian of Uzbekistan

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Tienfucheloides undatus and *Tienfucheloides* sp. (hereinafter *T. undatus*) were described by Nessov (1978) based on 16 figured shell fragments of about 90 available specimens from the lower Cenomanian Khodzhaikul Formation of Uzbekistan (see Vitek and Danilov [2014] for more information about turtle assemblage of the Khodzhaikul Formation). Additional specimens were figured later (Nessov, 1981, 1987, 1997; Nessov and Krasovskaya, 1984; see Table 1). Primarily, *T. undatus* was placed among Testudinata incertae sedis, but later considered as similar to the basal eucryptodiran family Sinemydidae in articulation of the free ribs of the posterior costals between adjacent peripherals, and in narrow xiphiplastron (Nessov, 1981, 1987; Brinkman and Peng, 1993). On the other hand, Nessov and Krasovskaya (1984) reported a mesoplastron for this taxon, a character absent in Sinemydidae. Based on published data, Danilov et al. (2017) considered *T. undatus* among Eucryptodira superfam. et fam. indet. In this study, we revised all previously figured specimens of *T. undatus*, and examined other available material of this species, including fragments of the nuchal, neurals, costals 1, 3 – 8, peripherals 7, 8, 10, 11, and hyoplastron (total more than 100 specimens). All together, these materials allow us to present the first shell reconstruction of *T. undatus* (Fig. 1), which appeared to be a true turtle puzzle. In addition, we briefly describe morphology of this species and discuss its phylogenetic position.

Abbreviations: CCMGE, Chernyshev's Central Museum of Geological Exploration, St. Petersburg, Russia; ZIN PH, Zoological Institute of the Russian Academy of Sciences, Paleoherpological Collection, St. Petersburg, Russia; n/n, no number, storage is unknown.

The revision of the materials attributed previously to *T. undatus* (Table 1) has showed that part of it (“*Tienfucheloides*-like” materials) has different morphology (see below) and belongs either to a basal testudinoid *Lindholmemyx* (orig. *Mongolemys*) *occidentalis* (Nessov in Nessov et Krasovskaya, 1984) or to unknown turtle taxon. The previous attribution of “*Tienfucheloides*-like” materials to *T. undatus* was based on a similar plicated external surface of the shell elements.

The carapace of *T. undatus* is pear-shaped, narrowed anteriorly and widely rounded posteriorly, with a shallow nuchal emargination formed by the nuchal and peripherals 1. The nuchal has no costiform processes. Among neurals, only hexagonal elements are available, both with short anterior and posterior sides, but as reconstructed, the neural series consists of seven neurals, and includes also tetragonal and octagonal elements. Some neurals have medial keels (absent in “*Tienfucheloides*-like” materials). No suprapygal and pygal elements are available. There were eight pairs of costals, all of which, probably, except costal 8, were separated by the corresponding neurals. The rib thickenings of the costals are in form of high and narrow ridges, which are getting wider laterally (in “*Tienfucheloides*-like” materials, rib thickenings are normally developed). As a result the costals are T-shaped in cross-section. The first thoracic rib is fused with costal 1 and represented by high and narrow ridge, reaching contact with peripheral 3 laterally (in “*Tienfucheloides*-like” materials, the first thoracic rib is connected with costal 1 by a suture). The free ribs of costals (C) are not exposed externally and fit the following peripherals (P): C1 – P4; C2 – P5(?); C3 – P5 and 6; C4 – P6 and 7; c5 – P7; C6 – P8; C7 – P9(?); C8 – P10. Costal 8 bears attachment site for the ilium on its internal surface. The tenth thoracic rib is reduced. There are eleven pairs of peripherals, of which peripherals 5 and 9 are reconstructed (not available in the material). Peripherals 3 – 8 bear pits for the buttresses and pegs of the hyo- and hypoplastron (the buttresses do not reach costals, unlike *L. occidentalis*). The scute sulci are narrow and sometimes barely discernable. The cervical

seems to be long and narrow. The vertebrals are relatively narrow. Vertebral 1 contacts marginals 2. Vertebral 3-4 sulcus is presumably positioned on neural 5. The marginals are restricted to the peripherals, except marginals 2 and 12 (sometimes also 11). The supramarginals are absent. The external surface of carapace is strongly plicated and covered with high ridges arranged in a radial pattern within the vertebrals and pleurals and parallel to the free border within the marginals (usually, the plications are less developed in “*Tienfucheloides*-like” materials).

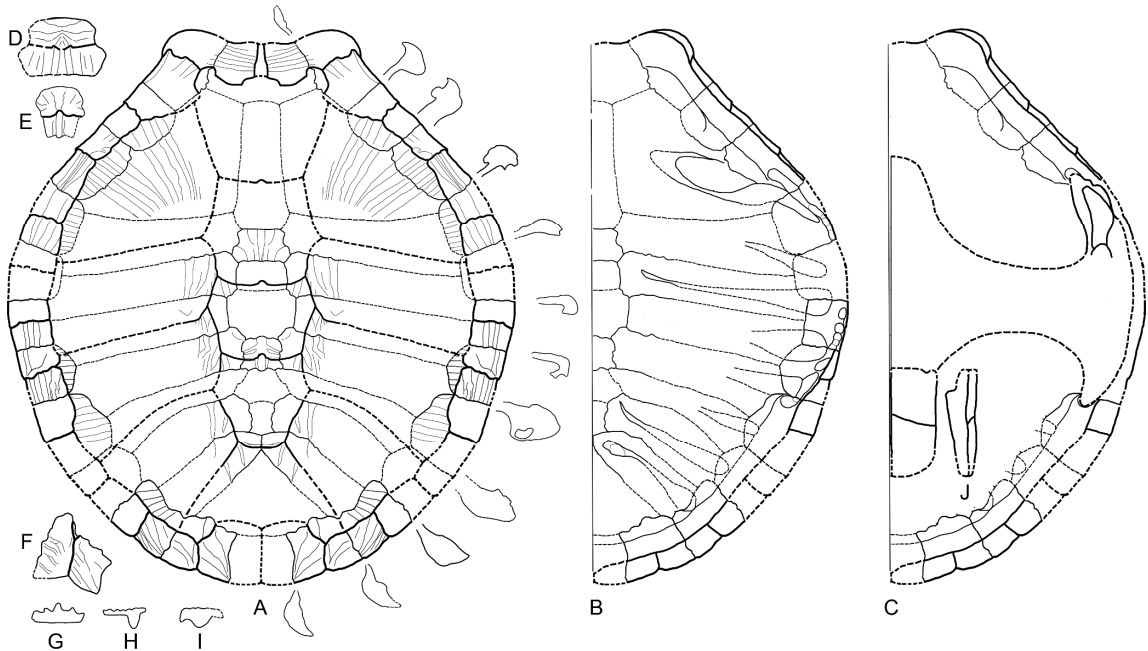


Figure 1. Shell reconstructions of *T. undatus*: **A**, carapace in dorsal view with cross-sections of peripherals at their anterior and posterior borders; **B**, carapace in ventral view; **C**, carapace and plastron in ventral view; **D**, **E**, additional neurals in dorsal view; **F**, additional peripheral 11 in dorsal view; **G**, cross-section of neural 2; **H**, **I**, cross-sections of costals in medial (**H**) and lateral (**I**) parts; **J**, xiphiplastron in lateral view. Without scale.

Only two elements are referable to the plastron of *T. undatus*. These are a lateral hyoplastron fragment with narrow inframarginals 1 and 2, and a narrow and thick xiphiplastron with femoral-anal sulcus distant from the anterior border of the plate. The ?mesoplastron specimen of this species, reported by Nessov and Krasovskaya (1984, fig. 3.9), is considered here as undetermined shell fragment of unknown taxon. The shortened bridge and the narrow xiphiplastron suggest that the plastron was cross-shaped. The available plastral elements have no plications.

Tienfucheloides undatus can be attributed: to the clade Mesochelydia based on the presence of eleven pairs of peripherals and absence of supramarginals (Joyce, 2017); to the clade Testudines based on the reduced tenth thoracic rib (Joyce, 2007); and to the clade Pancryptodira based on a presumed position of vertebral 3-4 sulcus on neural 5 (Joyce, 2007). Within Pancryptodira, *T. undatus* can be attributed to the grade Macrobaenoidea (sinemydid/macrobaenid turtles) based on combination of the cross-shaped plastron, absence of the costiform processes of the nuchal and unreduced distal parts of the costals (Danilov et al., 2017). Within Macrobaenoidea, *T. undatus* shares with *Sinemys* spp. articulation of the free ribs of the posterior costals between adjacent peripherals, narrow xiphiplastron and narrow inframarginals (Brinkman and Peng, 1993; Tong and Brinkman, 2013). In addition, *T. undatus* is characterized by many autapomorphic characters, unique for Macrobaenoidea, including pear-shaped carapace, differentiated and keeled neurals, rib thickenings in form of high ridges, the first thoracic rib fused with costal 1, long and narrow cervical, shortened bridge, and anal distant from the anterior border of the xiphiplastron. It is worth

noting that the pear-shaped carapace, shortened bridge and cross-shaped plastron are also characteristic of the carettochelyid *Kizylkumemys schultzi* known from the same Khodzhakul Formation (Nessov, 1977). Such a resemblance may be explained by similar ecological adaptations of these turtles (Danilov, 1999).

The attribution to the genus *Tienfucheloides* of the materials from other regions of Asia, like *T. jastmelchyi* Chkhikvadze, 1981 from the Aptian-Albian of Mongolia (Chkhivadze, 1981), and *T. cf. undatus* from the Upper Cretaceous Mifune Group of Japan (Hirayama, 1998) is either incorrect or based on poor material (see Danilov et al., 2017).

Table 1. Previously reported specimens of *T. undatus*. Designations: *, Nessov, 1978; **, Nessov, 1981; ***, Nessov and Krasovskaya, 1984; ****, Nessov, 1987; *****, Nessov, 1997; C, costal; M, mesoplastron; N, neural; P, peripheral; X, xiphiplastron.

| Specimen No. | Original illustration | Previous determination | New determination | Taxonomic attribution |
|----------------------------------|-----------------------|--------------------------|-------------------|----------------------------------|
| CCMGE 5/11479 (formerly 1/11479) | *pl. IX, fig. 3 | Penultimate bridge P | P 7 | <i>T. undatus</i> |
| CCMGE 2/11479 | *pl. IX, fig. 1 | P 1 | The same | <i>Lindholmemys occidentalis</i> |
| CCMGE 3/11479 | *pl. IX, fig. 2 | Anterior bridge P | P 3 | <i>T. undatus</i> |
| CCMGE 4/11479 | *pl. IX, fig. 10 | Penultimate bridge P | P 7 | <i>T. undatus</i> |
| CCMGE 8/11479 | *pl. IX, fig. 8 | Last bridge P | P 7 | <i>Lindholmemys occidentalis</i> |
| CCMGE 9/11479 | *pl. IX, fig. 4 | Posterior P | P 10 | <i>T. undatus</i> |
| CCMGE 10/11479, 11/11479 | *pl. IX, figs. 9, 13 | Cs 1 | The same | Unknown taxon |
| CCMGE 12/11479 | *pl. IX, fig. 14 | Part of even C | The same | Unknown taxon |
| CCMGE 13/11479 | *pl. IX, fig. 5 | Distal part of C | P 4 or 5 | <i>T. undatus</i> |
| CCMGE 15/11479 | *pl. IX, fig. 11 | N 1 | The same | Unknown taxon |
| CCMGE 17/11479 | *pl. IX, fig. 6 | Proximal parts of two Cs | The same | <i>Lindholmemys occidentalis</i> |
| CCMGE 18/11479 | *pl. IX, fig. 7 | Proximal part of C 6 | The same | <i>T. undatus</i> |
| CCMGE 19/11479 | *pl. IX, fig. 12 | Odd N | The same | <i>T. undatus</i> |
| CCMGE 20/11479 | *pl. IX, fig. 15 | Proximal part of C | The same | Unknown taxon |
| CCMGE 22/11479 | *pl. IX, fig. 16 | N | The same | Unknown taxon |
| CCMGE 2/12086 | ***fig. 3.2 | P | P 10 | Unknown taxon |
| CCMGE 3/12086 | ***fig. 3.3 | P | P 9 | Unknown taxon |
| CCMGE 6/12086 | ***fig. 3.6 | P | P 6 | <i>T. undatus</i> |
| CCMGE 7/12086 | ***fig. 3.7 | N | The same | <i>T. undatus</i> |
| CCMGE 8/12086 | ***fig. 3.8 | N | The same | <i>T. undatus</i> |
| CCMGE 29/12086 | *****pl. 26, fig. 11 | N | The same | Unknown taxon |
| CCMGE 31/12086 | ***fig. 3.9 | ?M | Shell fragment | Unknown taxon |
| CCMGE 37/12086 | ***fig. 3.1 | Anterior P | P 1 | <i>T. undatus</i> |
| CCMGE 27/12086 | ***fig. 3.5 | Posterior bridge P | P 3 | <i>T. undatus</i> |
| ZIN PH T/S 75-28 | **fig. III, 16 | Proximal part of X | The same | <i>T. undatus</i> |
| ZIN PH 2/6 | ***fig.3.4 | P | P 4 | <i>T. undatus</i> |
| ZIN PH 3/6 | *****pl.I, fig. 6 | Anterior P | P 2 | <i>T. undatus</i> |
| ZIN PH 4/6 | *****pl.6, figs. 6–8 | Anterior Ps | Ps 3 | <i>T. undatus</i> |
| n/n | *****pl.26, fig17 | Part of P | ? | <i>T. undatus</i> |
| n/n | *****pl.26, fig. 25 | N | The same | <i>T. undatus</i> |
| n/n | *****pl.26, fig. 34 | Part of C | ? | Unknown taxon |

To conclude, our study shows that the material previously attributed to *T. undatus* belongs to at least three turtle taxa: *T. undatus*, *L. occidentalis* and unknown taxon. Examination of the previous and new material of *T. undatus* allows us to reveal new details of its morphology and confirm relations of this species with sinemydid/macrobaenid turtles. In addition, *T. undatus* has many autapomorphic characters. Ecologically, *T. undatus* likely was similar to a carettochelyid *Kizylkumemys schultzei*. However, more material is needed to clarify morphology and phylogenetic position of this turtle.

Acknowledgements

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Biomechanical analyses suggest relation between neck-retraction and the trochlear mechanism in extant turtles

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Introduction

Aside from the shell, which is related to several morphological modifications in the skeleton, musculature, and other organs, the anapsid skull of turtles is another unique condition among extant amniotes. Although previously considered a plesiomorphic condition, taxa recently added to the stem-lineage leading to turtles (Schoch and Sues 2017) indicate that the anapsid skull may be instead another derived feature of the group. Although the origin of temporal fenestrae has been traditionally linked to an increase in surface for the origin sites of jaw musculature, decreasing their size has been linked to a series of factors and poses distinct problems, including the need for stabilizing the quadrate due to the development of more powerful bite performance (Werneburg 2012).

More recently, Werneburg (2015) proposed a scenario in which the obliteration of temporal fenestrae was related to the acquisition of the shell and the related neck retraction mechanism in turtles. According to this hypothesis, the development of the shell resulted in an extensive remodelling of the origin of neck muscles from the shoulder girdle to the visceral surfaces of the carapace and plastron (Hoffmann 1890, Lyson et al. 2013, Nagashima et al. 2013). The dermatocranial coverage of the skull would have then increased in size to withstand the distinct tensile forces and may have led to the complete obliteration of the temporal fenestrae in stem-turtles. In addition, morphometric data suggests that the cranial emarginations (marginal dermatocranial bone reductions) in crown- and some stem-turtles are due to the secondarily arising tensile forces acting on the skull caused by the development of advanced neck-retraction (Werneburg 2015).

Another feature found in all crown-turtles is the trochlear mechanism, which is based on a structure formed by bone and cartilage that redirects the external jaw muscles around the enlarged otic chamber (Schumacher 1973). The bony structure can develop either on the outer surface of the otic chamber or in a lateral process of the pterygoid bone. Each of these modes were previously thought to support the respective monophyly of Cryptodira and Pleurodira (Gaffney 1979) (hereafter referred to as ‘cryptodiran’ and ‘pleurodiran’ types, respectively). More recently, however, several taxa with a ‘cryptodiran-type’ trochlear mechanism have been positioned along the stem-lineage, suggesting that it represents the plesiomorphic condition for Testudines and that the ‘pleurodiran-type’ likely developed from a group with a cryptodiran-like trochlear mechanism (Joyce 2007).

It has been hypothesized that the trochlear mechanism evolved in order to circumvent the otic chamber following a surface increase of the origin sites of the external jaw muscles by a posterior expansion of the squamosal and supraoccipital crests (Joyce 2007, Sterli and de la Fuente 2010,

Rabi et al. 2013). Joyce (2007) proposed a ‘transfer of function scenario’ for the origin of the ‘pleurodiran-type’ trochlear mechanism. In this scenario, the external pterygoid process, found in most stem-turtles, became increasingly hypertrophied and gradually gained the function of the trochlea. This shift has been explained by a biomechanical advantage of the ‘pleurodiran-type’ trochlear system as the external jaw muscles supposedly pulled the lower jaw more vertically which in turn may have allowed for more powerful biting. Bite performance studies, however, do not support a consistently stronger bite in pleurodires compared to cryptodires (Herrel et al. 2002) hinting at the possibility that the origin of the pleurodiran trochlear mechanism may be related to other factors.

A roughening on the outer surface of the otic chamber, that potentially implies the presence of a ‘cryptodiran-type’ trochlea, can be observed among the earliest taxa which possess modifications related to a more rigid skull (e.g., fusion of the basiptyergoid process) and higher neck mobility (Joyce 2007, Rabi et al. 2013, Werneburg et al. 2015). Additionally, all crown-pleurodires possess a ‘pleurodiran-type’ trochlear mechanism and a ‘pleurodiran-mode’ of neck retraction, with a higher capacity for lateral flexion of cervical vertebrae (Werneburg et al. 2015). Nevertheless, a relation between the origin of the unique trochlear mechanism of pleurodires and their distinct neck retraction mode has never been suggested.

Methods

Here, we employed an integrative approach, using anatomical, paleontological, and biomechanical data to investigate the origin of the pleurodiran trochlear mechanism. Using manual dissections and micro computed tomography (μ CT) images, we evaluated the topological relations of skull elements and muscles and identified further osteological correlates that could infer the presence of elements of the trochlear mechanism in fossil taxa. We also conducted Finite Element (FE) analyses in the pleurodire *Podocnemis unifilis* and the cryptodire *Pelodiscus sinensis* during bite performance, in order to compare stress distributions in relation to skeletal and muscle anatomy.

Results & Conclusions

The evolution of the trochlear mechanism only after the reduction in skull kinesis (i.e., fused basiptyergoid articulation (Sterli and de la Fuente 2010, Rabi et al. 2013) hints at the possibility that these two features are related. Redirecting the external jaw muscles might exert a high degree of stress, higher than possible to withstand by a kinetic skull, and evaluating these biomechanical factors may therefore be important to understand the evolution of the trochlear system.

The FE analyses show that the different bone and jaw muscle arrangements are related to distinct stress patterns in *Podocnemis unifilis* and *Pelodiscus sinensis* (Fig. 1). Pleurodires and cryptodires do possess distinct jaw muscle arrangements and volumes and pleurodires are known to have more developed internal jaw musculature (Werneburg 2011). However, the distinct muscle arrangements do not seem to provide a biomechanical advantage in relation to bite forces because the estimated bite forces differ only by 6-8% when models are scaled to the same size. The FE data demonstrates that the basioccipital-basisphenoid region is less exposed to stress in *P. unifilis* in comparison to *P. sinensis*. Thus, shifting the trochlea from the otic chamber to the pterygoid released the basicranium from stress and may have allowed the neck muscles to insert on this more relaxed region of the skull. The muscle rearrangement, in turn, enabled more extensive lateral flexion of the cervical vertebrae in pleurodires (Werneburg 2011, 2015). This preliminary hypothesis will be further tested with ongoing FE analyses on a larger sample of pleurodires and cryptodires and by explicitly modelling their trochlear mechanisms.

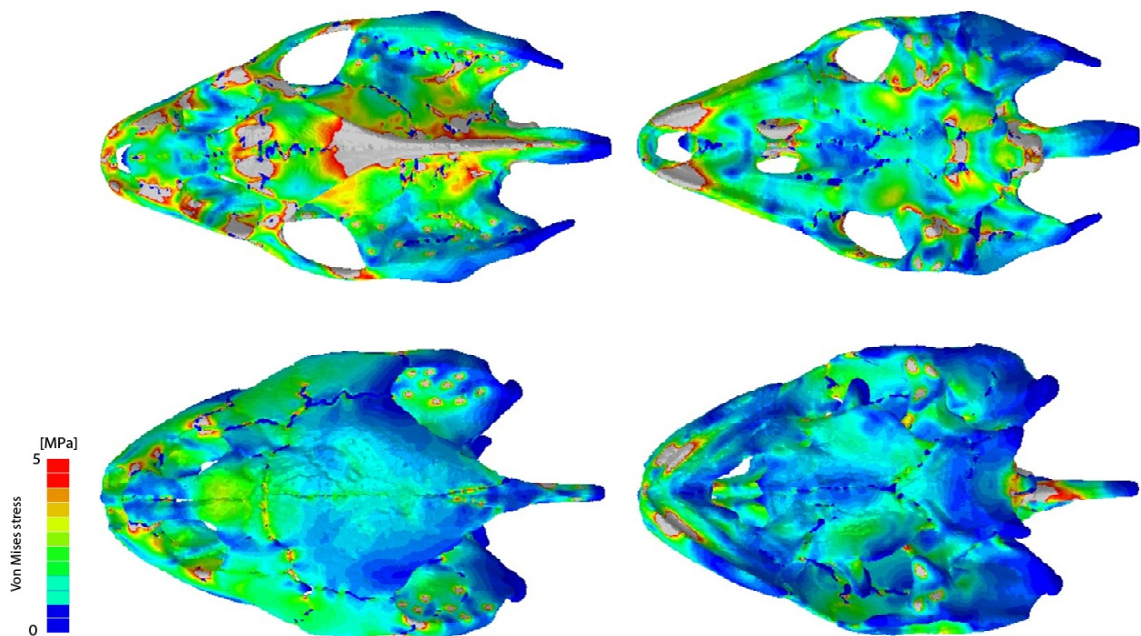


Figure 1. Comparison of Von Mises stress distribution for scaled models of the cryptodire *Pelodiscus sinensis* (top row) and the pleurodire *Podocnemis unifilis* (bottom row) in dorsal (left) and ventral (right) views.

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Intraspecific variation in the shell of geoemydid turtles: Applications to systematics and paleontology

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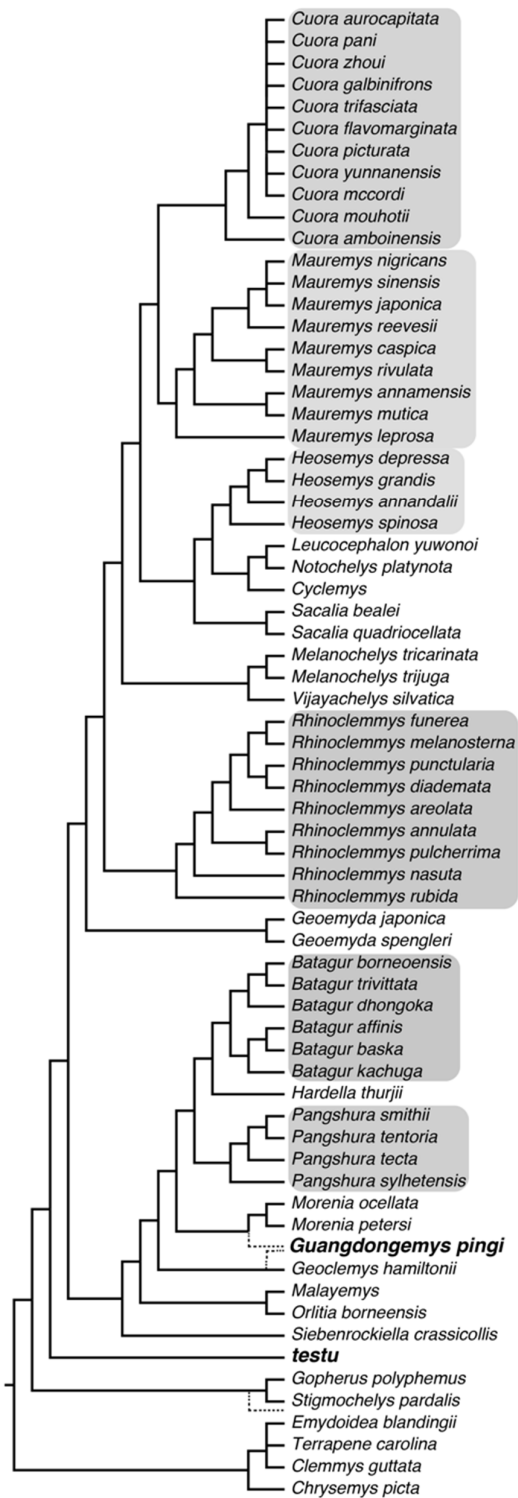
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Geoemydidae is a major clade of extant turtles with approximately 71 species distributed in the tropical to temperate regions of Asia, Europe, North Africa, and the Americas (ITWG, 2017). This group has a particularly rich fossil record in the Tertiary of the Northern Hemisphere (Lapparent de Broin, 2001; Claude *et al.*, 2012). Despite the great diversity of extant and extinct geoemydids, little is still known about the evolutionary history of this clade, as the phylogenetic relationships of most fossils have not been established with confidence (Claude *et al.*, 2012). This has been thought to be related to high levels of homoplasy and polymorphism combined with a scarcity of synapomorphies, which preclude the performance of traditional phylogenetic analyses (Joyce & Bell, 2004).

We constructed a morphological matrix of 96 shell characters, based primarily on that of Joyce & Bell (2004), to tackle the phylogeny of this understudied group, and to estimate the phylogenetic position of a new species from the Late Eocene of Vietnam and other Paleogene geoemydids. More than 350 specimens were examined and scored, comprising 51 extant geoemydid species, 12 extinct geoemydid species from the Paleogene, 2 extant testudinid species and 3 extant emydids, used as outgroup. The “polymorphic” method was preferred (*i.e.*, 0&1; Campbell & Frost, 1993) when coding polymorphic characters. We conducted a total-evidence analysis (TEA) of the morphological data combined with a molecular matrix from 3 mitochondrial and 4 nuclear loci (from Honda *et al.*, 2002, Spinks *et al.*, 2004, and Le & McCord, 2008) in TNT, and pruned rogue species to improve resolution.

The strict consensus of the 24 most parsimonious trees obtained from the TEA is shown in figure 1. In all MPTs the new species (*i.e.*, *testu*) was placed as sister to all other geoemydids. Most extant generic groups of geoemydids (*i.e.*, *Cuora*, *Batagur*, *Rhinoclemmys*) were retrieved as monophyletic, probably from the strong molecular signal in our matrix. *Guangdongemys pingi* Claude *et al.* 2012, an Early Oligocene geoemydid from China, was placed either as sister to *Morenia*, *Geoclemmys*, or Testudinidae, outside Geoemydidae. Pruning all the fossil geoemydid species, with exception of *Guangdongemys pingi* and the new species from Vietnam, was necessary to improve the resolution of the tree.

Our TEA is in broad agreement with recent molecular phylogenies (*i.e.*, Spinks *et al.*, 2004; Le & McCord, 2008). Even though the addition of fossils decreased the resolution of the tree, keeping a good resolution was possible when the fossils added had few missing characters. The matrix will be used in the near future to investigate the placement of other fossil geoemydids, like those from the Paleogene of Europe. As our matrix has a good sample of polymorphism for extant geoemydids (average of 5.5 specimens sampled per species), another future application is to use this data in alpha-taxonomy studies of Neogene and Quaternary fossil geoemydids.



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Figure 1. Strict consensus of the total-evidence analysis. The new taxon from the late Eocene of Vietnam (testu) is placed as sister to all geomydid species in all MPTs. Dashed lines show the possible positions of *Guandongemys pingi* in all MPTs.

Tortoises of the genus *Agrionemys*: phylogenetic position, systematics and fossil record

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Agrionemys Khosatzky et Mlynarski, 1966 is a genus of small Palaearctic burrowing testudinids, uniting from one to five modern species or subspecies with a wide range in Central Asia and adjacent territories and a number of fossil taxa known in the Miocene – Pleistocene interval within the same range, with one possible record in the European Russia (see Bonin et al., 2006; Danilov et al., 2017; Turtle Taxonomy Working Group, 2017). Some modern authors consider *Agrionemys* to be a subclade (subgenus) of the clade (genus) *Testudo* s. l. (Van der Kyul et al., 2002; Fritz et al., 2009; Corsini et al., 2014; Turtle Taxonomy Working Group, 2017), whereas others argue in favour of its generic independence and include in it species, which are usually considered within the genera (subgenera) *Chersine* (= *Eurotestudo*) or *Protestudo* (Gmira, 1993a, b; Lapparent de Broin et al., 2000, 2006a, b; Perälä, 2002). Finally, Chkhikvadze (2001, 2007) divided the genus *Agrionemys* into two subgenera *A. (Agrionemys)* and *A. (Protagrionemys)*, the latter of which unites a number of species from the Neogene of Asia, former members of *Testudo* s.l. or *Protestudo*.

In order to resolve relationships of *Agrionemys* we performed a phylogenetic analysis based on taxon-character matrix of Corsini et al. (2014) with the following modifications: 1) three new characters were added (see Appendix 1); 2) *Testudo promarginata* and *T. antiqua* are excluded from the analysis, because they do not allow to resolve relationships within the ingroup; 3) six taxa added to the analysis: *Agrionemys caucasica* Chkhikvadze, 2001 from the upper Miocene of the European Russia; *A. ranovi* Amiranashvili et al. in Sharapov et al., 1988 from the upper Pliocene of Tajikistan; *Testudo eldarica* Khosatzky et Alekperov in Alekperov, 1978 from the upper Miocene of Azerbaijan; *A. (Protagrionemys) kegenica* (Khosatzky in Bazhanov et Pigulevskiy, 1955) from the middle-Upper Miocene of Kazakhstan, *A. (Protagrionemys) djetyogus* (Kuznetsov, 1964) from the Pliocene of Kyrgyzstan, and *Protestudo karabastusica* Kusnetsov, 1982 from the upper Miocene of Kazakhstan (for references on all newly added taxa see Danilov et al., 2017). The final taxon-character matrix includes 26 taxa and 23 characters (Table 1). The phylogenetic analysis was performed using TNT with traditional search resulted in 8 maximum parsimonious trees with 73 steps (CI = 0.58; RI = 0.74). The strict consensus tree resulted from our phylogenetic analysis (Fig. 1) shows presence of four clades: 1) *Ergilemys bruneti* – *Indotestudo* spp.; 2) *Testudo* sensu stricto spp.; 3) *Agrionemys* spp. + *Protestudo* spp. + *A. (Protagrionemys) kegenica*; and 4) *Paleotestudo* - *Chersine* (= *Eurotestudo*) spp. The *Testudo* clade unites *T. eldarica* and recent species of *Testudo* s.s. The *Agrionemys* clade unites *A. caucasica*, *A. ranovi*, *A. horsfieldii* and *A. kazachstanica*. The *Protestudo* clade unites *P. bessarabica*, *P. karabastusica*, and *P. djetyogus* (formerly considered as *Agrionemys (Protagrionemys) djetyogus*; see Danilov et al., 2017). The *Protagrionemys* clade is not recognized. The *Agrionemys* clade is characterized by two synapomorphies: 22(2), extension of supracaudal on to posterior suprapygal present, due to anterior extension of the supracaudal; 23(1), extension of anterior plastral lobe beyond anterior border of carapace present, anterior lobe rounded. For synapomorphies of the other clades see Fig. 1.

In addition to *Agrionemys* species mentioned above, this genus includes the following species and subspecies (see Chkhikvadze, 2009; Turtle Taxonomy Working Group, 2017 for synonymy and distribution): *A. horsfieldii* Gray, 1844 (= *A. baluchiorum* Annandale 1906; Turtle Taxonomy Working Group, 2017); *A. bogdanovi* Chkhikvadze in Chkhikvadze et al., 2008; *A. rustamovi* Chkhikvadze et al., 1990; *A. kazachstanica kazachstanica* Chkhikvadze, 1988; *A. kazachstanica kuznetzovi* Chkhikvadze et al., 2009; *Agrionemys kazachstanica terbishii* Chkhikvadze, 2009 (possible

synonym of *A. kazachstanica kazachstanica*; Turtle Taxonomy Working Group, 2017). The fossil findings of *Agrionemys*, other than *A. caucasica* and *A. ranovi*, are summarized by Danilov et al. (2017).

Differences in shell morphology of recent species/subspecies of *Agrionemys* spp. published in the literature are summarized in Table 2. Most of them are based on single specimens and do not consider variation.

Our study demonstrates presence of four main clades (genera) of Neogene-Quaternary Palearctic testudinids: *Testudo* sensu stricto spp., *Agrionemys* spp., *Protestudo* spp., and *Paleotestudo-Chersine* (= *Eurotestudo*) spp., which separated since late Miocene. The *Protagrionemys* clade is not supported by our phylogenetic analysis. Further study of the morphological systematics of *Agrionemys* spp. must include classical or geometric morphometrics approaches based on big shell samples.

Table 1. Taxon-character matrix after Corsini et al. (2014) with modifications (see text and Appendix 1).

| Taxa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
|-----------------------------------|---|---|-----|---|---|---|---|---|-----|----|----|----|----|-----|----|-----|-----|----|----|----|-----|----|-----|
| <i>Manouria impressa</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Indotestudo elongata</i> | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| <i>Indotestudo forstenii</i> | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | ? | 1 | 1 | 1 | ? | 0 |
| <i>Ergilemys bruneti</i> | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | ? | 0 | 0 | 2 | 1 | ? |
| <i>Testudo canetotiana</i> | 2 | 0 | 2 | 0 | 1 | 0 | 2 | 1 | 0 | 3 | 2 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| <i>Testudo pyrenaica</i> | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 3 | 2 | 2 | 1 | 2 | 1 | ? | 2 | ? | 0 | 0 | 1 | 0 | ? |
| <i>Testudo globosa</i> | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 3 | 0 | ? | ? | 2 | 0 | 0 | 1 | ? | 2 | ? | ? | 0 | 1 | 0 | 0 |
| <i>Gracia</i> | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 2 | 0 | ? | ? | 2 | 0 | 0 | 1 | ? | 2 | ? | ? | ? | 0/1 | 0 | ? |
| <i>Escale</i> | 2 | 0 | 0 | 0 | 1 | ? | 2 | 3 | 0 | 3 | 2 | 2 | 1 | 0 | 1 | 1 | 2 | 1 | ? | ? | 1 | ? | ? |
| <i>Soave</i> | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 2 | 1 | 3 | 2 | 2 | 1 | 0 | 1 | ? | 2 | ? | ? | ? | 0/1 | 0 | ? |
| <i>Lunel</i> | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 3 | 2 | 2 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | ? | 1/2 | 0 | ? |
| <i>Testudo hermanni boettgeri</i> | 2 | 0 | 0 | 0 | 1 | 1 | 2 | 3 | 1 | 3 | 2 | 2 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Testudo hermanni hermanni</i> | 2 | 0 | 0 | 0 | 1 | 1 | 2 | 3 | 1 | 3 | 2 | 2 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 0 | 1 | 0 | 0 |
| <i>Testudo graeca</i> | 2 | 0 | 0 | 1 | 1 | 2 | 2 | 1 | 0 | 3 | 3 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0/1 | 0 | 0 |
| <i>Testudo eldarica</i> | 2 | ? | 1 | 1 | 1 | 0 | ? | ? | 1 | ? | ? | 3 | 0 | 0/1 | 0 | 1/2 | 1/2 | ? | 0 | 0 | 1 | ? | ? |
| <i>Testudo kleinmanni</i> | 2 | 0 | 0 | 1 | 1 | 2 | 2 | 3 | 1 | 3 | 3 | 3 | 0 | 1 | 0 | 1/2 | 1/2 | ? | 0 | 0 | 1 | 0 | 0 |
| <i>Testudo marmorum</i> | 3 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 3 | ? | 3 | 0 | 0 | 0 | 1 | 1 | ? | ? | ? | 1 | ? | ? |
| <i>Testudo marginata</i> | 3 | 0 | 1 | 1 | 1 | 2 | 2 | 2 | 0 | 3 | 3 | 3 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Agrionemys horsfieldii</i> | 4 | 1 | 0 | 0 | 1 | 2 | 2 | 1 | 0 | 3 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 2 | 1 | 0/1 |
| <i>Agrionemys kazachstanica</i> | 4 | 1 | 0 | 0 | 1 | 2 | 2 | 2 | 0 | 3 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 2 | 1 | 1 |
| <i>Agrionemys caucasica</i> | ? | ? | ? | ? | ? | ? | 1 | ? | 1 | 3 | 2 | 2 | 0 | 0 | ? | ? | 1 | ? | ? | ? | 0 | 1 | 1 |
| <i>Agrionemys ranovi</i> | 4 | 1 | ? | 0 | 1 | ? | ? | ? | ? | 3 | ? | 2 | 1 | 0 | 0 | ? | ? | ? | ? | 0 | 0 | ? | 1 |
| <i>Protagrionemys kegenica</i> | 4 | 0 | 0 | 0 | 1 | 0 | 2 | 2 | 1 | ? | ? | 2 | 0 | ? | 0 | ? | 1 | ? | 1 | 0 | 0 | 0 | 0 |
| <i>Protagrionemys djetyogus</i> | 4 | 0 | 2 | 0 | 1 | 0 | ? | 2 | ? | 3 | ? | 2 | 1 | 0 | 0 | ? | ? | ? | ? | 0 | 0 | ? | 2 |
| <i>Protestudo bessarabica</i> | 4 | 0 | 2 | 0 | 1 | 1 | 2 | 1 | 1 | 3 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | ? | 0 | 0 | 0 | 0 | 2 |
| <i>Protestudo karabastusica</i> | 4 | 0 | 0/2 | 0 | 1 | 0 | 2 | 1 | 0/1 | 3 | ? | 2 | 1 | 0 | 0 | 1 | 1 | ? | 0 | 0 | 0/2 | 0 | ? |

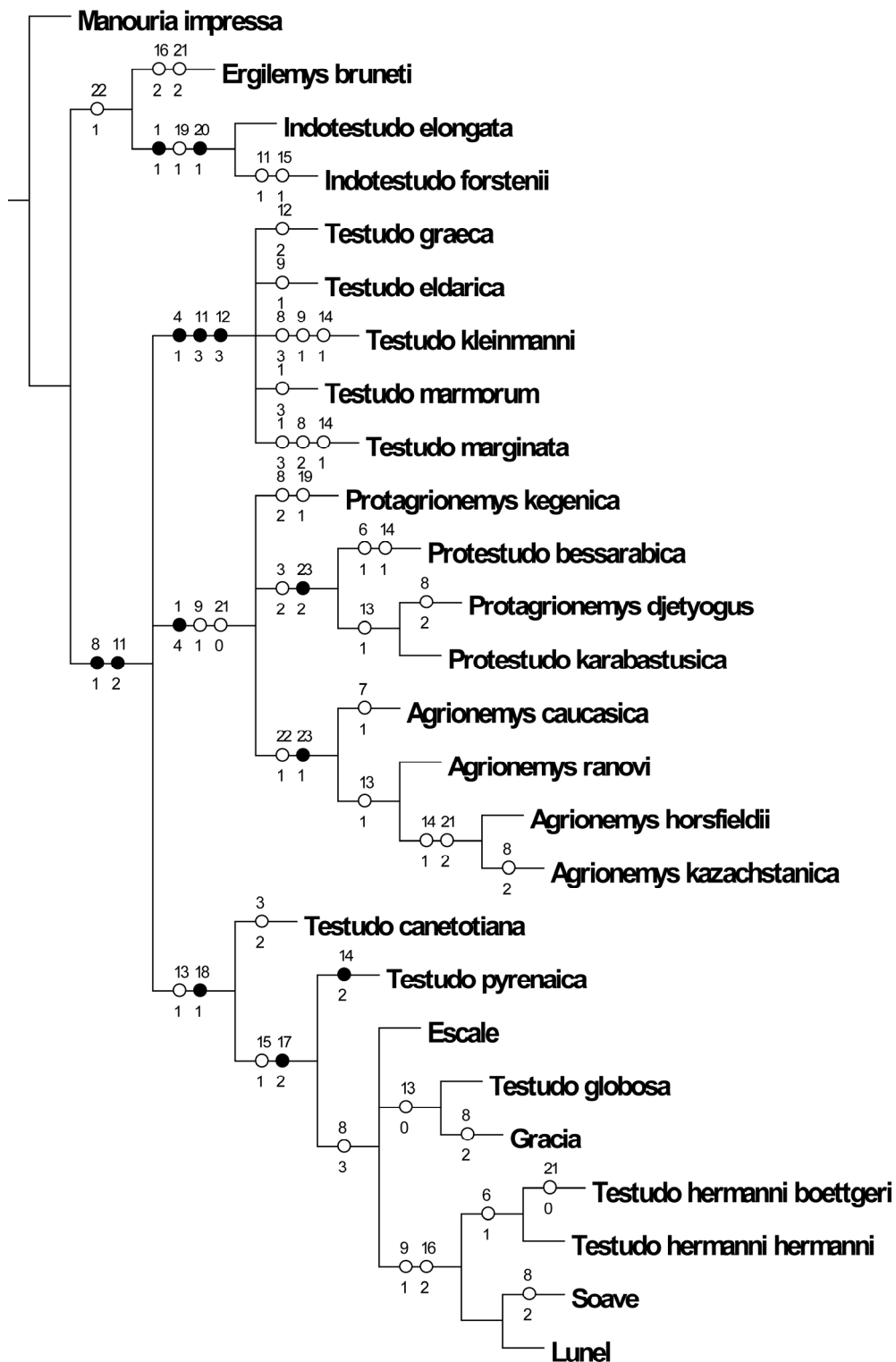


Figure 1. The strict consensus tree resulted from our phylogenetic analysis (see text for explanation).

Table 2. Comparison of recent species/subspecies of *Agrionemys* spp. in shell characters (after Chkhikvadze, 1988, 2009; Chkhikvadze et al., 1990, 2008, 2009; and our data [*]). Abbreviations: *A. b.* – *A. bogdanovi*; *A. b.* – *A. borsfieldi*; *A. r.* – *A. rustamovi*; *A. k. ka.* – *A. kazachstanica kazachstanica*; *A. k. ku.* – *A. kazachstanica kuznetzovi*; *A. k. t.* – *A. kazachstanica terbishii*.

| Characters | <i>A. h.</i> | <i>A. b.</i> | <i>A. r.</i> | <i>A. k. ka.</i> | <i>A. k. ku.</i> | <i>A. k. t.</i> |
|---|--------------------|-----------------------------------|------------------------------|----------------------|-----------------------------|---------------------|
| Carapace length (L)/width (W) | L~W | L>W* | L~W | L>W | L~W (♂), L>W (♀) | L~W |
| Carapace in lateral view | Convex | Flattened | Strongly convex | Convex | Flattened | Convex |
| Nuchal emargination | Deep | Shallow ¹ | Shallow | Shallow | Shallow | Shallow |
| Bosses on vertebrals and pleurals | Present | Absent | Present | Present | Present ² | Absent ³ |
| Cervical | Wide and long* | Narrow and short ⁴ | Narrow and long ⁵ | Narrow and short | Wide and short ⁶ | Narrow and short |
| Serrated peripherals | Present | Present | Present | Absent | Present | Present |
| Direction of free edge of posterior peripherals | Lateral | Lateral | Lateral | Lateral | Ventral | Ventral |
| Posterior carapace curve in lateral view | Sharp* | Gradual | Gradual | Sharp | Gradual | Sharp |
| Lateral keel of bridge peripherals | Oblique | Parallel to plastron ⁷ | Oblique* | Parallel to plastron | Parallel to plastron | Strongly oblique |
| Anterior plastral lobe | Not curved upwards | Not curved upwards | Not curved upwards | Curved upwards | Curved upwards | Curved upwards |
| Medial keel on carapace | Absent | Absent ⁸ | Absent | Absent ⁸ | Absent | Present |

¹nuchal emargination in shape of narrow notch.

²dorsal carapace surface with only two large medial bosses: anterior boss is located in posterior part of vertebral 1 scute, whereas posterior boss, in posterior part of vertebral 4 scute.

³a poorly developed boss is present in posterior part of vertebral 4 scute.

⁴cervical is strongly moved forward.

⁵cervical with parallel lateral borders or slightly widened posteriorly (arrow-shaped).

⁶sometimes x-shaped.

⁷sometimes keel is poorly developed or absent.

⁸medial keel is present in juvenile specimens.

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Appendix 1

Characters added to the phylogenetic analysis (see Appendix 2 for codings): character 21: degree of extension of humeral-pectoral sulcus (hmp) on to entoplastron: 0, hmp lies posterior to entoplastron; 1, hmp touches entoplastron or slightly extends on it; 2, hmp strongly extends on to entoplastron; character 22: extension of supracaudal on to posterior suprapygal: 0, absent; 1, present, due to anterior emargination of the pygal; 2, present, due to anterior extension of the supracaudal; character 23: extension of anterior plastral lobe beyond anterior border of carapace: 0, absent; 1, present, anterior lobe rounded; 2, present, anterior lobe narrowed at gulars.

Bioerosion on a pelomedusoid shell from the Late Cretaceous of Brazil

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Anomalies on turtle shells are either considered to be developmentally driven (e.g. Lynn & Ullrich 1950) or caused by environmental factors, such as trauma, metabolic deficiency, or infections (e.g. Hutchison & Frye 2001; Wallach 1975; Rothschild et al. 2013). In the latter type, shell diseases are somewhat common within extant turtles (Granados et al. 2013) and have also been reported for Eocene cryptodires from North America (Hutchison & Frye 1989; 2001; Rothschild et al. 2013). A wide range of microorganisms are known to produce such diseases, e.g., algae, fungi, bacteria (Barnett 2003), and may leave shallow to deep borings on the surface of turtle shell (e.g. Zonneveld et al. 2015). Here we describe a carapace pitting trace in a new specimen of *Araripemys barretoii*, a pelomedusoid side-necked turtle from the Early Cretaceous of north-eastern Brazil.

The specimen is housed at the Instituto de Geociências, Universidade de São Paulo, and consists of an almost complete and articulated skeleton, with well-preserved skull, axial and appendicular elements, and a complete carapace exposed only in dorsal view. Its bearing rock belongs to the Crato Formation (Araripe Basin), which is believed to have been formed on a freshwater depositional setting, although some authors suggest it could represent a hypersaline lagoon (Oliveira 2007). The pit is visible on the external surface of the ninth left peripheral plate (Fig. 1). It is rounded (9.3 mm diameter), and shallow. It only destroyed the external cortex layer (and likely the epidermal scute as well) and exposing the trabecular bone.

The round morphology resembles the pits found in the fossil geoemydid *Echmatemys*, especially those attributed to the ichnotaxon *Karethraichnus lakikos*, which Zonneveld et al. (2015) interpret as the resulting activity of an infecting parasite, which could have colonized the carapace surface throughout the turtle's lifespan. In *K. lakikos*, the trabecular bone was also not affected and the diameter of the pit (ranging from 0.6 to 9.0 mm) is similar to that reported here. Round holes like those could be related to the action of epibionts (e.g. barnacles) or ectoparasitic (e.g. leeches), and are also commonly found in the shell surface of living turtles, but these tend to be shallower (Sidall & Gaffney 2004; Meyer 2011). They differ from the pits caused by perforations caused by predation, which are deeper (e.g. Hutchison & Frye 2001).

It appears that freshwater turtles are more prone to a wide variety of shell-degrading infections (Zonneveld et al. 2015) and, according to Wallach (1975), turtles that survive these infections permanently bear a pitted shell, like that found in this *Araripemys barretoii*. Gaffney et al. (2006) suggested that *A. barretoii* dwelled in near-shore environments, but its presence in both the Crato and Romualdo formations of the Araripe Basin (more commonly considered freshwater and lagoonal deposits, respectively) suggests it could transit between these environments (Oliveira 2007). Modern freshwater turtles that are tolerant to brackish conditions may end up infested by barnacles (Arndt 1975; Zonneveld et al. 2015). However, when these are found on the surface of the shell, they are usually in much larger numbers (Seigel 1983; Frick & Ross 2001), in contrast to the single pit described here.



Figure 1. Specimen of *Araripemys barretoii* exhibiting a pitted carapace. Pit indicated by white arrow.

Shell pits possibly related to pathologies have been previously recorded only for North America Cenozoic cryptodires (Hutchison & Frye 1989; 2001; Zonneveld et al. 2015). As for fossil pleurodires, shell abnormalities, such as doubling bones and deep pits of parasitic origin, have been reported for bothremydids (Gaffney & Zangerl 1968; Lehman & Wick 2010). The overall morphology of the pit described here allows its attribution to the ichnotaxon *Karethraichnus lakkeos*. Diagnostic features include the circular shape and the shallow penetration through the external cortical layer of the bone plate, exposing the trabecular bone. Although the pit diameter is within the range observed for turtles infected by ulcerative shell disease (Wallach 1975), such pathologies are more common among freshwater and terrestrial turtles (Zonneveld et al. 2015). Hence, this would seem unlikely if *A. barretoii* indeed frequently transited between fresh- and salt-water environments (Oliveira 2007). In the end, this may represent the first record of *K. lakkeos* in an extinct side-necked turtle. Further development of this study will contribute to a more comprehensive understanding of the habitats and life history of *A. barretoii* and of fossil pleurodires in general.

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A 3D geometric morphometric analysis of the palate of pleurodiran turtles

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Extant pleurodires (side-necked turtles) are restricted to freshwater environments of some southern hemisphere continents (Africa, Australasia, Madagascar and South America). They comprise two groups (chelids and pelomedusoids), with nearly one third of the diversity of their sister taxon, the cryptodires (hidden-necked turtles) (Turtle Taxonomy Working Group 2017). Nevertheless, the fossil record shows that ancient pleurodires had greater ecological and phenotypic diversity, with at least four morphologically-distinct lineages present by the end of the Early Cretaceous, a great radiation of podocnemidoids during the Campanian-Maastrichtian, and two independent marine invasions, leading pleurodires to occupy all continents except Antarctica (Romano et al. 2014; Ferreira et al. 2015, 2018; Nicholson et al. 2015; Joyce et al. 2016).

Ecologically, extant pleurodires exhibit few feeding strategies, being either aquatic herbivores or generalist carnivores (with a few exceptions, e.g. *Chelus fimbriatus*; Lemell et al. 2002), differing from several groups of specialized cryptodires (e.g. Meylan 1988; Lindeman 2006). As such, this issue has received more research in the latter lineage. Nevertheless, bothremydids and stereogenyines (two extinct clades of Pelomedusoides) evolved a remarkable range of triturating surface morphologies, which suggests they may have been adapted to different diets in relation to their extant relatives (Gaffney et al. 2006; Ferreira et al. 2015). Here we employ a 3D geometric morphometrics approach using CT-scan data of pleurodiran turtles aiming to address (i) if clades are well differentiated, suggesting phylogenetic constraints on pleurodire feeding apparatus, and (ii) if there was convergent evolution towards similar morphologies among the clades, which could indicate similar ecologies between distantly related taxa.

We sampled CT- and μ CT-scan data of 21 pleurodires (10 extant and 11 extinct), in order to depict the group diversity, and nearly all main clades were represented (i.e. Chelidae, Pelomedusidae, Podocnemidoidae, and Bothremydidae). The landmarks were based on those used by Ferreira et al. (2015), in addition to six series of semilandmarks placed sliding along the labial ridge of the maxilla and the outline of the triturating surfaces on the palate in order to capture the three-dimensional shape of the palate. Generalized Procrustes analysis followed by a principal-component analysis (PCA) were employed to produce a set of geometric variables that describe the deformations of the upper jaws compared to their mean shape (Webster & Sheets 2010). All analyses were conducted using the geomorph package (Adams & Otárola-Castillo 2013) in R environment software (R Core Team 2017).

The first two PCs explained 65% of the total variation in shape among the analysed taxa. The main variation (PC1 = 46.5%) is related to the depth of the labial ridge and to the overall shape of the palate, almost completely separating podocnemidoids from the remaining pleurodires (i.e. chelids and pelomedusids). Podocnemidoids exhibit mainly a ‘V-shaped’ labial ridge, whereas chelids and pelomedusids have it more ‘C-shaped’. In its turn, PC2 (18.5%) accounted for the variation of width of the triturating surfaces, separating taxa with narrow caudal edges (e.g. *Labrostocheilus*) from those with a very widened caudal portion of the triturating surfaces, such as *Bothremys* ssp. and stereogenyines, variation which has been interpreted as an adaptation to durophagy (Claude et al. 2004; Ferreira et al. 2015).

This is a preliminary survey on the shape of the turtle palate, and ongoing sampling of more taxa (which will include data of pan-cryptodires and stem-turtles too will likely enhance it. Although

the palate seems to be a good proxy to assess diet aspects, other features such as the height of the skull or the degree of both anterolateral and posterodorsal emarginations might also be useful. Further analyses will help us to illustrate a more complete scenario and lead us to a better understanding of the relationship between morphology and ecology regarding the evolution of the turtle skull.

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Evolutionary origin of the turtle shell accompanied with the loss of the sternum

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The bony shell structure of the turtles represents an evolutionary novelty, whose evolutionary derivation had been unclear until recently. In this presentation, we will introduce our recent discoveries and discuss future perspectives about the evolution of the turtle shell.

The carapace of the turtle is contiguous with the axial skeleton, but underlies just beneath the scutes or skin unlike the axial skeletons of typical amniotes. Accordingly, the evolutionary origin of the turtle carapace had been a matter of controversy, in particular regarding an involvement of the dermal bones (or, osteoderms). Upon this problem, we conducted a detailed observation of the embryonic development of the carapace in the Chinese soft-shelled turtle, *Pelodiscus sinensis* (Hirasawa *et al.*, 2013). At the developmental stages before the onset of bone formation, the cartilaginous ribs were enclosed with an embryonic connective tissue medial to the dermis, with a clear boundary between them. Between the adjacent cartilaginous ribs, the anlagen of intercostal muscles developed temporarily, but subsequently became degenerated. Then, the periosteum surrounding each rib was expanded craniocaudally, within the subdermal connective tissue layer, where the intercostal muscle anlagen had been extended. Corresponding to this expansion of the periosteum, at the bone formation, bony trabeculae developed at both cranial and caudal edges of the periosteal bone collar of the rib. Such bony trabeculae were observable minutely also in the chicken embryo, indicating that the bony trabecula of rib is not turtle-specific. In the turtle embryo, the bony trabeculae of the ribs continued to develop extensively, eventually filling the intercostal spaces as the costal plates of the carapace. In the same way, the neural pates develop from the bony trabeculae of the neural spines within the subdermal connective tissue. Therefore, from the developmental point of view, the turtle carapace consists purely of endoskeletal elements. In the other paper, we designated the turtle carapace as an "exposed endoskeleton" (Hirasawa & Kuratani, 2015).

The stem-turtle *Odontochelys semitestacea* from the Upper Triassic possessed ribs with plate-like expansions, which likely developed through the expansion of bony trabeculae of ribs. Although the ribs of *O. semitestacea* were not incorporated into a solid carapace, the morphology of the costovertebral joints is suggestive of that the ribs were almost fixed laterally with the vertebrae (*i.e.*, synarthroses), thereby forming a structure comparable to the extant turtles' carapace (Hirasawa *et al.*, 2013).

The phylogenetic relationships among diapsid clades diversified until the Middle Triassic have remained unsolved, especially in the case including ichthyosaurs as OTUs, but recent phylogenetic analyses have accumulated results supporting that sauropterygians along with Middle Triassic marine reptile *Sinosauropsphargis yunguiensis* comprise a sister group of the turtle. *S. yunguiensis* possessed ribs with plate-like expansions, which almost filled the intercostal spaces. Based on the costovertebral articulations of *S. yunguiensis*, the ribs were laterally held with only limited movability. These features indicate that the ribs of *S. yunguiensis* formed an endoskeletal carapace, but this species possessed numerous osteoderms above the carapace unlike turtles. This condition represents a paleontological evidence of that the carapace evolves independent of the exoskeletal components (Hirasawa *et al.*, 2013).

In the turtles, the ribs are not extended ventrally, due to the "axial arrest" of ribs during embryonic development. Correspondingly, the sternum, which is formed at the ventral part of the ribcage in the other amniotes, does not develop in the turtle. These conditions are present also in the sauropterygians and *S. yunguiensis*, thereby likely representing a synapomorphy of the clade

including the turtles and sauropterygians (Hirasawa *et al.*, 2013; 2015). One parsimonious explanation for the evolution of laterally-held ribs is the relaxation of body support function of ribs in the secondary aquatic adaptation. In addition to the loss of the sternum, the ventral part of the pectoral girdle had received major modifications in the evolution of the turtle-sauropterygian clade. In plesiosaurs, or a derived subgroup of this clade, the interclavicle was folded medially to the coracoid, likely due to a transformation of the body wall during embryonic development (Hirasawa *et al.*, 2016). While in terrestrial amniotes, the pectoralis muscle is connected laterally to the sternum and interclavicle contributing to the body support, in the plesiosaurs the pectoralis was clearly not connected to these skeletal elements. Similarly, in the turtle, the pectoralis muscle is not connected to the interclavicle (entoplastron), but to the hyo- and hypoplastrons (equivalent to the gastralia). Such skeletal connections of the pectoralis muscle perhaps had evolved during the secondary aquatic adaptation of their ancestors.

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Limb morphology of the genus *Bothremys* (Bothremydidae; Pleurodira) from the Late Cretaceous of Morocco, Northern Africa

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Family Bothremydidae is an extinct group of side-necked turtles (Pleurodira) from the Early Cretaceous to Paleogene around the Atlantic Ocean, including North and South America, Africa, Western Europe, and India. This group has very unusual oral morphology and is mainly occurred from the shallow marine sediments. However, as postcranial skeleton of bothremydids, especially limb bones, was virtually unknown, paleoecology of this group has been largely obscured.

A new specimen of the genus *Bothremys* (WUSILS RHg 548) from the Late Cretaceous (Maastrichtian) of Qued Zem of Morocco, northern Africa, is reported here. This includes skull (24 cm long), lower jaw, cervical vertebrae, partial shell, and well articulated right fore limb bones from ulna and radius to unguals. Each finger, especially metacarpal and ungual, is rather elongate as in aquatic turtles, whereas proximal phalanxes are short and have well developed movable articulations. This unique feature of fore limb of *Bothremys* suggests they were shallow sea bottom walker with limited swimming ability.



Figure 1. Right fore limb of *Bothremys* sp. (WUSILS RHg 548) in dorsal view.

“*Carteremys*” *pisdurensis* and *Piramys auffenbergi*, two poorly understood pleurodires from India

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“*Carteremys*” *pisdurensis* is based on a partial skull from the Late Cretaceous (Maastrichtian) Lameta Formation exposed near Pisdura, Maharashtra, India. As presented in the type description, this taxon is characterized by a highly apomorphic morphology, including pterygoids that almost fully separate the palatines, an elongate basisphenoid, and opisthotics that contact the pterygoids on the ventral skull surface. Three partial shells and associated limb bones were subsequently referred to this taxon from nearby Dongargaon, Maharashtra, India. These too were described to exhibit a highly unusual morphology, including a nuchal that does not contribute to the anterior margin of the carapace, hexagonal neurals that equally contact the neighboring costals, and a first vertebral that contributes to the anterior margin of the shell. The taxon was originally referred to the purported pelomedusid genus *Carteremys*, then assigned to the pan-podocnemidid genus *Shweboemys*, but most recently identified as an indeterminate pan-podocnemidid. *Piramys auffenbergi*, by contrast, is based on a well-preserved skull from Mio/Pliocene sediments exposed on Piram Island, Gujarat, India. In the type description, this taxon was interpreted as a representative of Emydidae, but no characters were provided to support that assessment. This taxon has virtually been ignored by all subsequent workers.

Recent study of all available material of “*Carteremys*” *pisdurensis* and *Piramys auffenbergi* yielded numerous insights into the morphology of these rare Indian turtles. The skull of “*Carteremys*” *pisdurensis* more strongly resembles other pleurodires, in particular pelomedusoids, by having a short basisphenoid, pterygoids with a relatively short midline contact, large palatines with a broad midline contact, and a lateral contact of the basioccipital with the quadrate, not the opisthotic. The shell also resembles that of other pelomedusoids by having a rectangular first neural followed by hexagonal neurals with short anterior sides and a nuchal that contributes to the margin of the shell. The skull of *Piramys auffenbergi* similarly resembles pelomedusoids by exhibiting well-developed processus trochlearis pterygoidei, a deep median groove that runs between the orbits, a cleft palate, and by lacking nasals. Preliminary taxonomic and phylogenetic analyses confirm the validity of “*Carteremys*” *pisdurensis* and suggest relationship with the bothremydid clade Kurmademydini, not the podocnemidid lineage. This is biogeographically parsimonious, as Kurmademydini is currently known from the Late Cretaceous of India only. *Piramys auffenbergi*, on the other hand, is preliminarily confirmed to be valid as well, but to be a representative of the podocnemidid clade Stereogenyina. This too is biogeographically parsimonious, as this clade is already known to have inhabited the Indian subcontinent during the early Neogene.

A large soft-shelled turtle from gravity flow deposits of the Upper Cretaceous Nakaminato Group in Ibaraki Prefecture, Japan

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Soft-shelled turtles (Family Trionychidae) are a successful group of aquatic turtles. The oldest fossil record of trionychids is known in the Lower Cretaceous of eastern Asia. Nowadays, more than thirty extant species are living in freshwater environments of Africa, North America, and Asia, although some species can adapt to brackish areas.

Three shell fragments of a large trionychid were newly collected from the Upper Cretaceous Isoai Formation of the Nakaminato Group in Ibaraki Prefecture, Japan. The left eighth costal and two costal fragments suggest that the carapace length of this trionychid turtle might be over 80 cm long.

The Isoai Formation consists of sandstone-dominated interbedding of sandstone and mudstone, occasionally intercalated with conglomerate layers. This formation is divided into 8 units (Is1 to Is8). Two of the trionychid specimens were excavated from Is3 and the other one was obtained as a beach boulder, which seems to be derived from Is3. The geologic age of Is3 is estimated to be early Early Maastrichtian by ammonite and inoceramid biostratigraphy.

Although the Isoai Formation is interpreted as turbidite and debris-flow deposits, hitherto it yields several disarticulated vertebrate skeletons such as a mosasaur caudal vertebra, a pterosaur scapula, and shark teeth.

Therefore, the trionychid materials suggest that large trionychids had inhabited in rivers and/or brackish areas and their some remains were transported and disarticulated from their habitat into the offshore basin.

Relationship between inner ear morphology and ecological habitats in extant turtles: possible application to fossil taxa

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The relationship between the inner ear morphology and the ecological habitats has been extensively investigated in mammals and squamate reptiles. However, it is hardly known whether this relationship exists in turtles. This study aims to understand the relationship between the inner ear morphology and the ecological habitats among terrestrial and aquatic turtle taxa using three-dimensional geometric morphometrics. We analyzed 40 species from 12 families of terrestrial and aquatic turtles. Principal component and canonical variates analyses indicate that the inner ear morphology is statistically different between the terrestrial and aquatic taxa. Specifically, the aquatic taxa tend to exhibit 1) a low ratio of cochlea length to the whole inner ear height, 2) a broad lateral semicircular canal, and 3) a small angle between vestibular region and cochlea region. The small angle between vestibular region and cochlea region is also evident by linear measurements in aquatic taxa, suggesting it is robustly related to the aquatic adaptation. This vestibular-cochlea angle could be used as a reference to reconstruct the ecological habitat of fossil turtles based on the analysis of the inner ear morphology.

A foundational framework for the study of turtles in archaeological sites in China

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Introduction

The earliest widely known socio-cultural connections between societies in China and turtles date back to the sacrificial remains from Jiahu (6500-5500 B.C.E.). Later, but perhaps better known because of their association with the origins of Chinese writing, turtles used as oracle bones are an important component of archaeological remains from the late Shang Dynasty site of Anyang (1350-1046 B.C.E.). That being said, turtle remains from other archaeological sites all over China demonstrate a presence of turtles beyond ritual contexts at least since the early Neolithic. Unfortunately, apart from a few studies at both Jiahu and Anyang, there is a dearth of in-depth analysis of the role of turtles in the cultural developmental history of China. This constitutes a considerable impediment to our understanding of the role of anthropogenic processes on changes in turtle ecology and how this in turn affected human societies. In this paper, we discuss the problems concerning the study of turtles in Chinese zooarchaeology and emphasize the need for methodological integration of archaeology and biology to systematically study human-turtle relationships through history. We use the archaeofaunal collections from four archaeological sites in Anhui and Guangdong provinces to demonstrate the application of new and existing methodologies to the study of turtles. We argue that the results can provide datasets to help formulate new research questions related to the understanding of not only the fluid role that turtles played in the development of ancient societies in China, but also the relationship between humans and their ecological environments.

Methods

Current literature concerning the study of turtles is reviewed to define suitable methodologies for the study of turtle remains from archaeological sites in China. The methodologies include taxonomic and elemental identification, quantification, the reconstruction of caloric and nutritional values, taphonomy, and anthropogenic modifications. By evaluating and modifying these current methodologies, we apply suitable ones to the turtle remains from the following four archaeological sites:

1. Xiaosungang, Anhui Province (ca. 7200-6800 BP)
2. Taijiashi, Anhui Province (3500-3200 BP)
3. Guye, Guangdong Province (5800-4000BP)
4. Lujingcun, Guangdong Province (4000-3500BP)

In order to reconstruct the different human-turtle relationships and their significance in these ancient Chinese societies, the results are analyzed together with other archaeofaunal materials, including mammals and fish, and discussed in the context of the archaeology of the sites. We evaluate how the results can expand the repertoire of zooarchaeological research in China by comparing our results to the available turtle remains from other archaeological sites.

Results

We provide a foundational framework for future attempts to study turtles from archaeological sites, particularly in China and elsewhere in East Asia. Based on the availability, reliability, and accessibility of modern comparative collections, we initiated a database for amassing data useful for zooarchaeologists and herpetologists in identifying and analyzing turtle skeletal remains in China. Primary data based on turtle morphology and ecology from the four archaeological sites are also added to the database to assess the potential of applying identification standards to turtle remains in other archaeological sites in China. Our research demonstrates the possibility of forming and answering new research questions related to the roles of turtles in ancient subsistence strategies and economies, seasonality of human activities and site occupation, cultural utilization of natural resources, and anthropogenic activities on animal ecology. In addition, we re-evaluate and revise the taxonomic classification of turtles and observe species, for example *Rafetus swinhoi* and *Mauremys mutica*, that are currently not discussed, inaccurately categorized, or undermined in published Chinese zooarchaeological site reports.

Conclusions

Zooarchaeology in China traditionally focuses on the study of mammals to reconstruct ancient subsistence economy, environment, and cultural patterns. While recently there is an increase in concern for the roles that non-mammals played in ancient societies in China, turtles as an important cultural resource are relatively understudied. Better studied aspects of turtle use relate to oracle bones and thus to their carapaces and plastrons. Other bony elements are seldom discussed, and the life history of turtles including choice of species, procurement, processing, consumption, and discard is relatively unknown for most archaeological sites in China. This is caused by both the dearth of accessible comparative specimens and standards and by the sampling methods employed in archaeological sites. Our exercise in assessing the difficulties and devising possible solutions for zooarchaeologists in the study of turtles is intended for both zooarchaeologists and biologists so that they can reconsider the fundamental requirements for the study of animals and their roles in human societies, and also to discuss “non-mainstream” animals beyond noting only their presence at archaeological sites.

Development and evolution of the turtle shell

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The dorsal part of the turtle shell, or the carapace, is made of modified ribs and the vertebral column. The carapace represents an example of evolutionary novelties because the topographical relationships between the ribs and scapula is reversed as compared to that in other amniotes. Folding theory assumes that the turtle-specific body plan was achieved through a sequential series of developmental changes that proceeded in a stepwise manner, among which shortening of the ribs played a significant role for the translocation of the shoulder girdle. The rib-shortening process is called the axial arrest; the turtle rib anlagen never grow into the lateral body wall, confined in the axial part of the embryo. Through peripheral growth of the carapacial anlage along the ridge called the carapacial ridge (CR), the turtle ribs can grow over the shoulder girdle. The CR is characterized by turtle-specific expression of genes known to be involved in the canonical Wnt signaling pathway, and functions in the marginal growth of the carapacial primordium, resulting in the fan-shaped pattern of the ribs. A fossil animal, *Odontochelys*, assumed to have been in an ancestral lineage of the modern turtle, exhibited a morphology resembling the embryo of modern turtles before the folding, consistent with the folding theory. To evaluate the novelty of the shell, coupling and decoupling of developmental modules will be discussed.

At the interplay of developmental conservativeness and adaptive plasticity: Form and function in chelonian lungs and their value for phylogenetic considerations

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The conquest of dry land went hand in hand with an obligatory need for an air-breathing faculty in amniotes. Specialized extraembryonic structures serve in aerial gas exchange during development, whereas lungs are the primary respiratory organ of all terrestrial vertebrates after hatching/birth. The origin of lungs – albeit in detail not fully resolved as of yet (Lambertz & Perry 2015; Lambertz 2017) – has to be dated long before the origin of amniotes and was one of the exaptations that eventually permitted the complete terrestrialization. A closer look at amniote lungs reveals an enormous structural diversity among the different lineages, ranging from rather simple and sac-like organs in the majority of squamates over complexly branched bronchioalveolar lungs in mammals to the unique lung-air-sac system in birds. However, regardless of this huge taxon-specific multifariousness in pulmonary anatomy, all amniote lungs share a common *Bauplan* that is characterized by early ontogenetic branching events (Lambertz et al. 2015).

The respiratory apparatus of turtles in its entirety undoubtedly is one of the most remarkable one among amniotes. This is mainly due to the iconic shell, which to a large extent is built through the ontogenetic fusion of the ribs, which eliminates the primary ventilatory motor of the remaining terrestrial vertebrates (Hsia et al. 2013). Paleontological data indicate a very early modification of the chelonian ventilatory system via the recruitment of specific parts of the musculature of the ventral body wall (Lyson et al. 2014; Lambertz 2016).

As much as their ventilatory mechanism is uniquely derived among lung-breathing vertebrates and represents a remarkable adaptation that arose in concert with the general modification of the shelled *Bauplan*, the lungs of turtles appear to have preserved a rather ancestral condition. A recent revision of pulmonary anatomy and evolution among amniotes with their shared branched developmental pattern suggests that the “multichambered” *Bauplan* of turtle lungs actually represents the closest approximation for the air-breathing organ of the first fully terrestrial vertebrates (Lambertz et al. 2015). This in and of itself makes chelonian lungs of great interest for studies aimed at understanding pulmonary evolution, especially of course among amniotes.

Notwithstanding that all chelonian lungs exhibit the above-mentioned principal multichambered *Bauplan*, there is a huge structural diversity of this organ embodied even within this group. Our knowledge about the comparative pulmonary anatomy of turtles, however, primarily still rests on the early studies of Milani (1897) and Gräper (1931). Given that both authors lacked a proper understanding of evolutionary character transformation, a modern systematic revision is long overdue (Perry 1998). In addition, both early authors focused on the adult anatomy only and did so at a time when knowledge about the ontogenetic formation of chelonian lungs still was extremely fragmentary. The seminal studies of Broman (1940a, 1940b) eventually provided the first and so far only complete developmental sequences of pulmonary formation in a small number of species. As a matter of fact, they revealed several inaccuracies in the morphological interpretations of Milani (1897) and Gräper (1931) and highlight the importance of knowledge about pulmonary ontogeny for understanding the adult condition. The high degree of anatomical diversity in chelonian lungs, however, makes them a potential source of information for phylogenetic inferences.

Indeed, based on a combination of information on the developmental and adult anatomy of the respiratory system, one long-lasting controversial issue in chelonian systematics recently received the first morphological support for the robust molecular-based consensus topology. The sole extant representative of the Platysternidae, the Asian big-headed turtle *Platysternon megacephalum* Gray, 1831, shows an intrapulmonary branching pattern that strongly resembles that of the Testudinoidea rather than that of the Chelydridae (Lambertz et al. 2010). This is in full agreement with the molecular data concerning the placement of *P. megacephalum*, but contradicts the osteology-based morphological evidence.

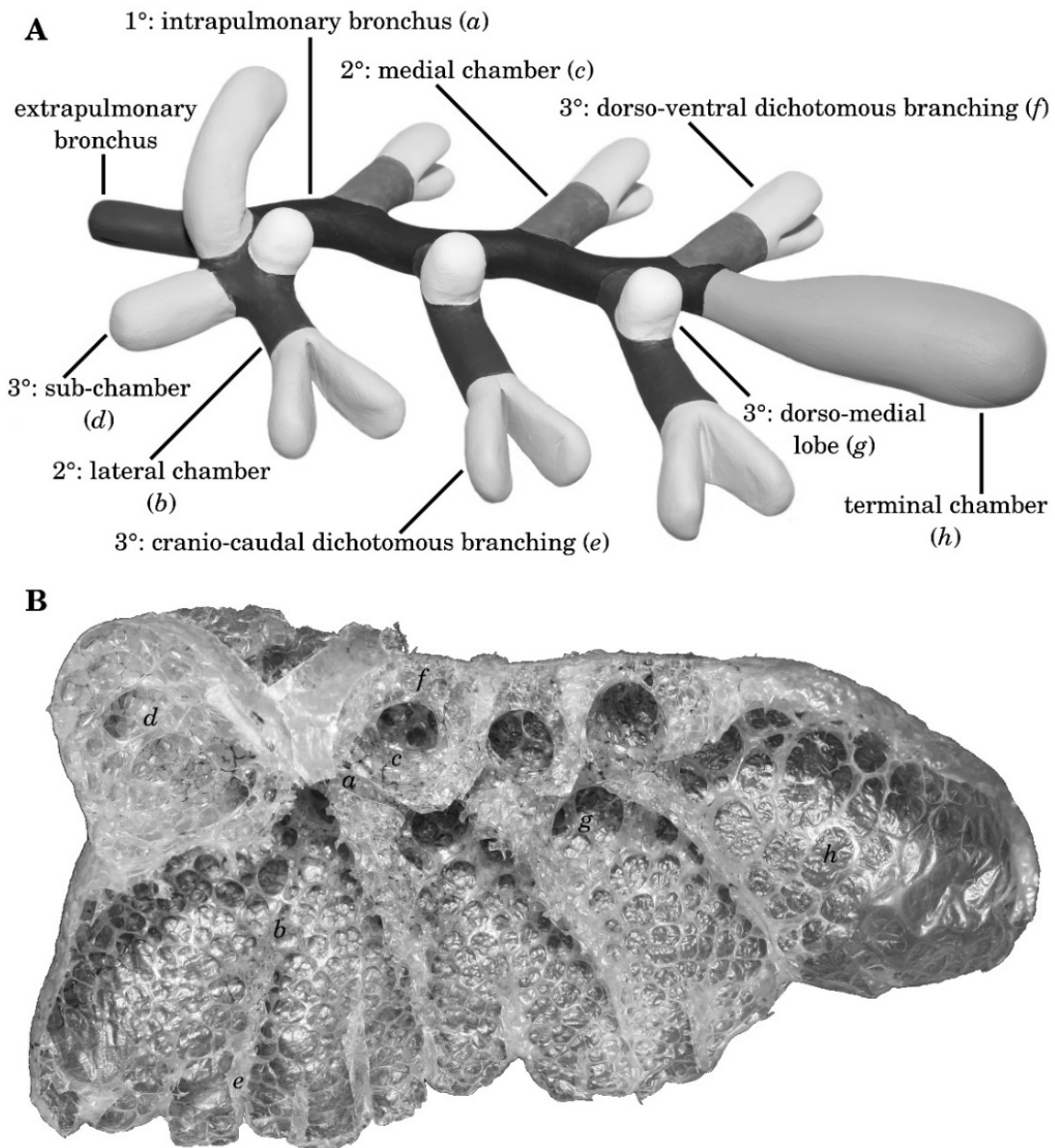


Figure 1. **A.** Dorso-lateral view of the schematic cryptodiran intrapulmonary branching pattern. Note that different third-order (3°) branching patterns can be observed. The parenchyma has been omitted here and would line the different second- and third-order branches. **B.** Ventral view of a dried right lung of *Trachemys scripta* (Thunberg in Schoepff, 1792). The ventral wall of the lung has been removed revealing the internal structures. The edicular parenchyma lining the different chambers appears in a honeycomb-like fashion. Note its heterogeneous distribution. Labeling follows that of panel A.

The question remains as to whether the observed branching patterns are truly as conserved as they appear among the different lineages and thus truly phylogenetically informative or whether there is any variability, and if so, what kind of variability. The recent discovery of a remarkable pathological snapping turtle, *Cheelydra serpentina* (Linnaeus, 1758), actually allowed intriguing insights into the developmental conservativeness and adaptive plasticity of chelonian lungs. Snapping turtles are probably the best studied species of turtle in terms of normal pulmonary development and anatomy. This particular pathological specimen exhibited only one lung, which appeared hypertrophied, but showed no differences in terms of the principal branching pattern known from normal individuals. The hypertrophy rather could be explained by a more pronounced degree of branching in the terminal parenchymal regions, while maintaining the snapper-specific hierarchy of intrapulmonary organization. As a result, the surface area of the lung was increased by 14.3% per unit volume if compared to a normal snapping turtle, which can be interpreted as an adaptive plasticity that at least partly compensated for the lack of the second lung (Schachner et al. 2017).

Comparative data covering the majority of mud and musk turtle species (Kinosternidae) further confirm the phylogenetic applicability of pulmonary morphology. The two sub-clades Kinosterninae and Staurotypinae can unambiguously be separated from each other based on the hierarchical organization of their intrapulmonary branching pattern. Closely related species within these two lineages, however, do have corresponding lungs that are virtually indistinguishable.

In conclusion, the principal branching pattern of chelonian lungs seems to be taxon-specific, highly conserved, and also phylogenetically informative. Figure 1 illustrates the principal hierarchy of intrapulmonary organization in turtles. Adaptive responses and a certain degree of plasticity are evident, but apparently restricted to the most terminal regions of the developing lung that are directly involved in gas exchange. The highest potential value of the differences – or rather the congruence – in the more “upstream” aspects of pulmonary anatomy among the various lineages of turtles seems to lie in establishing hypotheses about the relationships of the higher taxonomic groups. However, the anatomy of the chelonian respiratory system is a yet to be fully explored source of information to achieve phylogenetic congruence in cases that remain conflicting if molecular data are compared to the traditional osteology-based approaches, the latter of which are well known to exhibit a high degree of homoplasy. With this talk I will provide a revised approach of how to address the anatomy of chelonian lungs from a developmental point of view and detail my ongoing research with a pulmonary perspective on turtle systematics.

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High-resolution x-ray tomography of large chelonians: A case study on *Rafetus swinhoei* (Gray, 1873)

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Digital approaches to study animal morphology have become increasingly attractive in recent years. Aside from conventional imaging devices regularly used within a medical/clinical context (mainly computed tomography, CT, and magnetic resonance imaging, MRI), whose spatial resolution usually falls within the range of millimetres, especially the advent of high-resolution approaches extending the resolution down to the level of only a few micrometres (μ CT) made such procedures of great value also for zoologists and paleontologists. One of the main advantages of these digital imaging technologies is their non-destructive nature, which thus also permits the analysis of internal structures in valuable museum vouchers that are not accessible for traditional dissection-based and thereby destructive studies. While the overall popularity and availability of high-resolution μ CT devices has increased, several limitations of their application still persist, the largest of which is specimen size. Commercially available set-ups for μ CT scans usually can accommodate only rather small samples. Depending on the particular system, it is possible to capture objects with a maximum size between a few centimetres and around 25 cm. These values can just be reached by digitally stitching multiple scans, a process that is limited by the dimensions of the x-ray-sealed scanning chamber of conventional μ CT systems. However, a number of vertebrates – including numerous species of turtles – reach body sizes that simply cannot be accommodated by such devices. Non-destructive digital approaches to study the internal morphology of respective specimens hence is forced to rely on clinical tomography systems, which come at the cost of a severely limited spatial resolution of the scans.

For the present study we employed the experimental large-scale and high-resolution x-ray tomography set-up developed and housed at the *Karlsruhe Institute of Technology Institute for Photon Science and Synchrotron Radiation* (IPS, KIT, Germany). This room-sized μ CT facility can accommodate much larger specimens than ordinary set-ups, while still providing digital data at the desired level of fine-scale resolution. In order to demonstrate the advantage of this system, we compared the results of this experimental approach to those obtained via conventional imaging using a clinical device.

As the subject for our case study we chose the Red River Softshell Turtle *Rafetus swinhoei* (Gray, 1873) (Testudines: Trionychidae). It is the largest species of freshwater turtle and simultaneously the rarest one in the world. It is currently assessed as critically endangered (ATTWG 2000) but potentially even extinct in the wild, with as of now only three specimens known to be alive in captivity. Similarly desperate as the situation concerning living specimens is the one concerning those preserved in scientific collections. Worldwide, there are only a small number of partial specimens available for study and only a singular full-body individual exists (Fig. 1A). This extreme rarity of museum vouchers makes non-destructive approaches to study the morphology of this enigmatic species not only elegant, but rather absolutely mandatory. This latter specimen (NHMW 30911) is housed at the *Naturhistorisches Museum Wien* (NHMW, Austria) and was described by Farkas (1992) after its unexpected and fortunate re-discovery. We loaned NHMW 30911 and subjected it to a number of different scans.

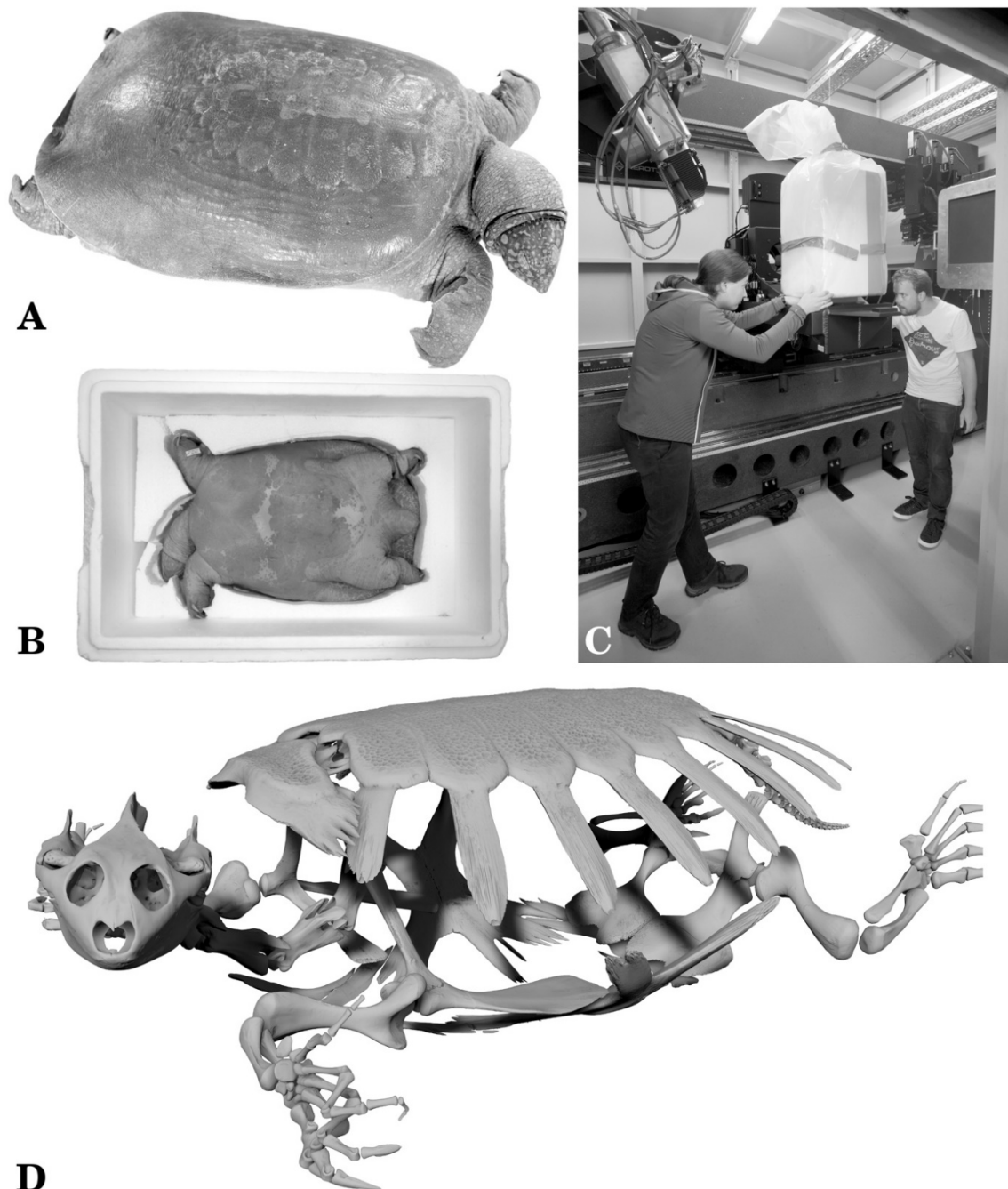


Figure 1. **A.** Dorsolateral view of the exclusively known preserved full-body specimen of *Rafetus swinhoei* (NHMW 30911). **B.** Tailor-made styrofoam casing for the specimen, designed to prevent movements and desiccation during the scanning procedure. Note that the upper layers of styrofoam sheets as well as the lid are removed here. **C.** Coauthors M.Z. (left) and P.T.R. (right) adjusting the specimen within the scanning chamber of the large-scale and high-resolution x-ray tomography set-up at the *Karlsruhe Institute of Technology*, Germany. **D.** Three-dimensional reconstruction of the skeleton of NHMW 30911.

In order to achieve optimal scanning results and last but not least to prevent damage from this invaluable specimen in the form of desiccation, we designed a tailor-made styrofoam casing (Fig. 1B). We used a conventional styrofoam cold box (approximate dimensions 59x39x36 cm) and added multiple layers of styrofoam sheets, which were carved out according to the specimen's body

contour. This guaranteed that the specimen could not move within its box during the scanning process, which is essential for an accurate reconstruction of the individual x-ray images into a virtual image stack. Numerous ethanol-soaked (70% v/v) tissues were placed between the different sheets of styrofoam and a spray bottle was used to further vaporize ethanol into the box in order to generate an alcohol-saturated atmosphere so that the wet specimen could not desiccate. In addition, a plastic foil was wrapped around the entire styrofoam casing to provide further sealing that helped to prevent desiccation, but also protected the μ CT device from any excess ethanol dripping out of the container.

The sealed styrofoam casing was placed into the μ CT device (Fig. 1C) and six individual scans together covering the entire body of NHMW 30911 were performed over night. For each individual scan, 4096 projections over an angular range of 360° were acquired. Each projection was exposed for 0.4s. The X-ray tube (XWT-225 tungsten anode, X-RAY WorX) was operated at 120kVp with a target power of 90W, and a flat panel detector (XRD 1621 CN14 ES PerkinElmer), featuring a pixel pitch of 200 μ m, was employed. The separate scans were stitched together and reconstructed into a digital image stack suitable for further analysis of the three-dimensional morphology. The obtained scanning data have a voxel size of 88.6 μ m, which is about an order of magnitude superior to those achievable with conventional medical imaging devices. In addition, we performed a separate scan of the specimen's head region only, which resulted in a dataset with a voxel size of even 66.9 μ m. Based on the resulting high-resolution digital morphological data for NHMW 30911 (Fig. 1D), we are currently preparing the first full descriptive account of the osteology of this enigmatic turtle.

Conventional medical imaging devices remain valuable apparatuses for the high-throughput acquisition of data, preliminary studies, or the analysis of living specimens. However, their limited spatial resolution puts severe restrictions on the in-depth analysis of morphological structures. Our study thus once again emphasizes the importance of interdisciplinary collaborations. The experimental set-up at the KIT was not primarily designed for addressing such biological research questions, but proved to be an exceptionally valuable system for the morphological analysis of large specimens that otherwise are bound to be examined via medical tomography systems. The large capacity of this set-up did not only allow for the accommodation of the entire specimen for a full-body scan at a so far unmatched resolution, but its huge degree of spatial freedom provided furthermore the opportunity to selectively scan specific subregions such as the head of the specimen at an even higher resolution.

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Comments on the cranial morphology of *Heckerobelys romani* Sukhanov, 2006, a basal turtle from the Middle Jurassic of European Russia

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Heckerobelys romani Sukhanov, 2006 from the Middle Jurassic of European Russia is one of few basal turtles, represented by rather complete and undeformed material, and close to the Cryptodira/Pleurodira divergence. In spite of being only briefly described (Sukhanov, 2006), it is constantly used in phylogenetic analyses (Sterli, 2008; Anquetin et al., 2009; Anquetin, 2010; Sterli and Fuente, 2010; Joyce, 2017; Joyce et al., 2016; see also Danilov et al., 2017 for review). The material of *H. romani* contains isolated or partially articulated skeletal elements, including incomplete disarticulated skulls of two individuals (for complete list of material see Table 1). Here we present scorings of cranial characters of *H. romani* in the global character matrix of Joyce et al. (2016; see Appendix 1) based on examination of all available material, comment on some of these characters, and perform a new phylogenetic analysis.

The following codings of *H. romani* are new or different from those given in Joyce et al. (2016; see Appendix 1):

- Nasal B and C. Although nasal is not available in the material, its characteristics can be determined based on morphology of prefrontals and frontals. Thus, it can be concluded that the nasals contacted one another medially along their entire length and had large dorsal exposure.
- Prefrontal D and E. The prefrontal has a reduced exposure and does not have sculpturing of prominences and bosses.
- Parietal C, E and G. Morphology of the inferior process of the parietal is similar to *Kayentachelys aprix*; it forms only the posterior margin of the foramen nervi trigemini and does not participate in the foramen stapedio-temporalis.
- Jugal B. The jugal does not participate in the upper temporal rim.
- Quadratojugal B and C. The maxilla has no contacts with the quadratojugal. The squamosal has no contact with the quadratojugal below the cavum tympani.
- Squamosal B, C and E. The squamosal has no contact with the supraoccipital and has no posterolateral protuberances. Its contact with the quadrate is tightly sutured.
- Postorbital A. The postorbital has no contact with the palatine.
- Supratemporal A. The morphology of the parietal and squamosal excludes presence of the supratemporal.
- Premaxilla B, D and E. The premaxillae are not fused, not excluded from the aperture narium externa, and do not form a distinct premaxillary hook.
- Maxilla A, C, D and E. The maxillae do not contact each other in ventral view, do not form a secondary palate; their triturating surfaces have only labial ridges.
- Vomer E. The vomer has no ventral crest.
- Quadrate D and G. The quadrate has no precolumnellar fossa and does not form a processus trochlearis oticum.

- Antrum postoticum A and B. The antrum postoticum is fully developed and large, but not enclosed laterally, similar to “*Sichuanchelys palatodentata* and *Mongolochelys efremovi* (see Joyce et al., 2016).

Table 1. Skull materials of *Heckerochelys romani*. Designations: + – element is available; - – element is not available; dex – right element; sin – left element. Abbreviation: PIN, A.A. Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

| Bones | PIN 4561-2 | PIN 4719-34 | Collection PIN 4719 |
|----------------|--------------|--------------|---------------------|
| Premaxilla | + (dex) | - | - |
| Maxilla | + (dex, sin) | + (dex, sin) | - |
| Vomer | + | - | - |
| Palatine | - | - | - |
| Pterygoid | + (dex) | + (dex) | + (4 specimens) |
| Basisphenoid | + | + | - |
| Basioccipital | - | + | - |
| Prootic | + (sin) | + (dex) | - |
| Opisthotic | - | + (dex) | - |
| Exoccipital | - | + (dex, sin) | - |
| Quadrate | + (sin) | + (dex) | - |
| Nasal | - | - | - |
| Prefrontal | + (dex) | - | - |
| Frontal | + (dex) | - | - |
| Postorbital | + (sin) | + (dex, sin) | - |
| Parietal | + (sin) | + (sin) | - |
| Supraoccipital | - | + (dex) | - |
| Jugal | + (sin) | - | - |
| Quadratojugal | - | - | - |
| Squamosal | - | + (dex, sin) | - |
| Dentary | + (dex, sin) | + (dex, sin) | - |
| Articular | | | + |
| Angular | | | + |
| Surangular | | | + |
| Splenial | | | + |

- Pterygoid F and H. The foramen palatinum posterius is present and partially formed by the pterygoid.
- Supraoccipital B. The supraoccipital does not have a large exposure on the dorsal skull roof.
- Exoccipital A. The exoccipitals have no medial contact dorsal to the foramen magnum.
- Basioccipital A. The basioccipital has two ventral tubercles.
- Prootic A. The prootic has a large dorsal exposure.
- Basisphenoid B. Paired pits on the ventral surface of the basisphenoid are present.
- Stapedial artery A, B and C. The stapedio-temporal canal is positioned anterior to fenestra ovalis between quadrate and prootic. The foramen stapedio-temporalis is relatively large and located in the dorsal part of the otic region and points dorsally.
- Fenestra perilymphatica A. The fenestra perilymphatica is large.
- Teeth A. Teeth are absent on premaxilla, maxilla and dentary.
- Upper temporal fenestra A. The upper temporal fenestra is absent.
- Dentary A. The medial contact of the dentaries’ is fused.
- Jugal/quadrate contact. The jugal/quadrate contact is absent.

In the modern global phylogenetic analysis of turtles (Joyce et al., 2016), *H. romani* was scored for 47 (41%) of 115 cranial characters. Our study increases this value to 91 (79%) of cranial

characters. Our phylogenetic analysis was performed using TNT, following Joyce et al. (2016) in all parameters, and resulted in 10000 most parsimonious trees (overflow) with 969 steps. The strict consensus tree resulted from it does not differ noticeably in tree topology from those of Joyce et al. (2016: Additional file 3A), i. e. *H. romani* is placed in a big polytomy with *Condorchelys antiqua*, *Eileanchelys walmani*, *Kayentachelys aprix*, and some other taxa and clades. After pruning wild-card taxa (*Chengyuchelys*, *Indochelys spatulata*, *Patagoniaemys gasparinae*, and *Spoorchelys ormondea*) from the consensus tree, *H. romani* is placed in polytomy with *E. walmani* and a clade of more advanced turtles, one step above *C. antiqua* and two steps above *K. aprix*.

Thus, our study confirms previously revealed similarity of *H. romani* with *E. walmani* (Anquetin et al., 2009). Further resolution of relationships of *H. romani* requires reexamination of its postcranial material and detailed comparison with related taxa.

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Appendix 1

Characters coded for *Heckerochelys romani* and added to the matrix of Joyce et al. (2016; new codings are bolded): Nasal A, 0; Nasal B, **0**; Nasal C, **0**; Prefrontal A, 0; Prefrontal B, 0; Prefrontal C, ?; Prefrontal D, **1**; Prefrontal E, **1**; Lacrimal A, 1; Frontal A, 1; Frontal B, 0; Parietal A, 0; Parietal B, **1**; Parietal C, -; Parietal D, 0; Parietal E, **1**; Parietal F, -; Parietal G, **0**; Parietal H, 0; Jugal A, 1; Jugal B, **0**; Quadratojugal A, ?; Quadratojugal B, **0**; Quadratojugal C, **0**; Squamosal A, 0; Squamosal B, **0**; Squamosal C, **0**; Squamosal D, 0; Squamosal E, **0**; Postorbital E, **0**; Supratemporal A, **0**; Premaxilla A, 1; Premaxilla B, **0**; Premaxilla C, ?; Premaxilla D, **0**; Premaxilla E, **0**; Maxilla A, **0**; Maxilla C, **0**; Maxilla D, **0**; Maxilla E, -; Vomer A, 1; Vomer B, ?; Vomer C, 1; Vomer D, ?; Vomer E, **0**; Palatine A, ?; Quadrate A, 1; Quadrate B+C, 2; Quadrate D, **0**; Antrum postoticum A, **2**; Quadrate F: incisura columella auris, 1; Quadrate G, **0**; Quadrate H, ?; Quadrate I, 0; Epipterygoid A, ?; Pterygoid A, 1; Pterygoid B, 1; Pterygoid C, 0; Pterygoid D, 0; Pterygoid E, 0; Pterygoid F, **0**; Pterygoid G, 0; Pterygoid H, **0**; Pterygoid I, 1; Pterygoid G, 0; Pterygoid K, 0; Supraoccipital A, 0; Supraoccipital B, **0**; Supraoccipital C, -; Exoccipital A, **0**; Basioccipital A, **0**; Prootic A, **0**; Opisthotic A, 1; Opisthotic B, 0; Opisthotic C, 1; Opisthotic D, 2; Basisphenoid A, 0; Basisphenoid B, **1**; Basisphenoid C, 0; Hyomandibular nerve A, ?; Stapedial artery A, **1**; Stapedial artery B, **0**; Stapedial artery C, **0**; Recessus scalae tympani A, 1; Foramen jugulare posterius A, 1; Foramen jugulare posterius B, -; Foramen nervi hypoglossi (XII), 0; Canalis caroticum F, 0; Fenestra perilymphatica A, **0**; Cranial scute A, ?; Cranial scute B, ?; Cranial scute C, ?; Cranial scute D, ?; Cranial scute E, ?;

Cranial scute F, ?; Cranial scute G, ?; Cranial scute H, ?; Cranial scute I, ?; Cranial scute J, ?; Cranial scute K, ?; Cranial scute L, ?; Cranial scute M, ?; Cranial scute N, ?; Cranial scute O, ?; Cranial scute P, ?; Teeth A, **1**; Upper temporal fenestra A, **1**; Dentary A, 0; Carotid canal entry, 0; Pterygoid extension, 0; Carotid canal split, 0; Antrum postoticum, **1**; Jugal/quadrato contact, **0**; Parabasisphenoid decorated by ridges, 0; Secondary pair of basioccipital tubercles formed by pterygoid, 0.

The re-emergence of the Aldabra Atoll during the Late Pleistocene – community structure and trophic interactions

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Introduction

Remote marine islands are considered as ideal places to study evolution, biodiversity and ecological community dynamics, because these islands are considered simplified systems compared to more complex mainland systems (Gillespie et al., 2008). One such remote island is Aldabra Atoll, the largest atoll in the Indian Ocean, lying about 400 km northwest of the tip of Madagascar and more than 600 km east of the African continent. It is today home of the largest population of giant tortoises, *Aldabrachelys gigantea*, with about 100.000 individuals distributed over the four main islands of the atoll. Besides being home to the giant tortoises, the atoll is also the habitat of more than 400 endemic species and it was declared a UNESCO World Heritage Site in 1982 (UNESCO, 2018).

The atoll, although officially being part of the far away granitic Seychelles, consists of a massive reef limestone and palaeosol complex, which today rises to about 8 m above sea level, surrounding a shallow central lagoon (Braithwaite et al., 1973). The coralline limestone layers were deposited on a submarine volcano, rising approximately 4000 m high above the seafloor (e.g., Stoddart et al., 1971), and range from the Late Pleistocene to Recent in age (Braithwaite et al., 1973). At least two marine incursions led to complete inundation of the sediments of the atoll, and subsequent sub-aerial exposure led to cementation of the limestone but also to solution and karstification of the landscape (Braithwaite et al., 1973; Taylor et al., 1979). The latest deposition of massive limestones on the atoll, known as the Aldabra limestone, is dated to about 125.000 years before present. Fossiliferous sediments infilling karst and pipe holes and pits in the Aldabra limestone are therefore necessarily younger, being deposited in a time interval between ca. 125.000 and 90.000 years (Braithwaite et al., 1973).

The Late Pleistocene fossils from Aldabra have been partially studied in the 1970s by different authors (e.g., Arnold, 1976: reptile fossils; Harrison and Walker, 1978: bird fossils). Taylor et al. (1979) were the first to provide an overview of all the known Pleistocene fauna on the atoll, consisting of the reptile fossils (giant tortoises virtually identical to the modern form, small-sized crocodylian remains, and six different lizard species), three known bird species, and a rich mollusc fauna, including terrestrial, freshwater and littoral fringe forms.

Methods

All specimens have been studied osteologically, and fossils have been compared with extant taxa.

Results

Additional fossils from Late Pleistocene Aldabra limestone infillings have recently been recovered by our team, and are currently under study, thus adding to the already known fauna, and

our understanding of an early stage colonization community structure of a remote island. These fossils include well-preserved isolated giant tortoise shell, skull and endoskeletal postcranial material, larger-sized crocodylian cranial and postcranial remains, vertebrate coprolites, and marine fish remains (i.e., shark and teleost teeth), the latter indicating at least occasional (partial) flooding of the low relief parts of the atoll. Several of the tortoise bones show bite marks that are interpreted to have been inflicted by crocodylians and, indeed some of the newly recovered larger crocodylian remains indicate one or more animals with a cranial skull length of 40–50 cm, corresponding to a total body length of approximately 290–370 cm (Scheyer et al., 2018). This provides direct evidence for trophic interactions between the crocodylians and giant tortoises, the former either actively preying upon or scavenging on the latter. This level of trophic interaction is unknown today as the giant tortoises are the largest animals remaining on the atoll, while larger predatory species are completely absent.

Conclusions

The recovery of larger, well-preserved material (in the case of a large nuchal bone), associated bones (i.e., pelvic girdle of a giant tortoise), and even articulated specimens (crocodylian cranial remains) is furthermore important, because previous environmental interpretations by Taylor et al. (1979, p. 60) noted the “lack of even partial articulation” of the fossil finds. This fact, together with local high concentrations of bone fragments were then used to argue against larger animals such as the giant tortoises and the crocodylians falling into and then dying within open pits within the Aldabra limestone. Our new finds thus make it again reasonable that empty pits can act as death traps for these larger animals, and that the previous absence of articulated material represented rather a sampling bias.

The predator-prey interactions between the crocodylians and the giant tortoises was likely a very generalised one, as many crocodylians have a wide and ontogenetically variable prey spectrum including fishes, amphibians, lizards, birds and invertebrates, specifically crustaceans (also brackish taxa; e.g., Mohd Sah and Stuebing, 1996; Nifong and Silliman, 2013), but also spiders and aquatic and terrestrial insects (which, due to lower potential to fossilise are thus so far unknown from the Pleistocene Aldabran fossil record), the latter constituting important food sources especially for juvenile crocodylians (e.g., Platt et al., 2006). We can therefore speculate that the successful colonisation of crocodylians on Aldabra could have been independent of whether or not the giant tortoises were already present on the atoll. However, a presence of such a considerable and stable additional food source for these predators might well have been a determining factor that maintained or allowed the evolution of the generally large body size.

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A new nanhsiungchelyid from the Upper Cretaceous in Jiangxi, China

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The Family Nanhsiungchelyidae is middle to large sized terrestrial turtles of pan-trionychia. Eight genera and thirteen species are hitherto known in the fossil record during the Cretaceous of Asia and North America. Most of species of the Nanhsiungchelyidae occurred in Mongolia and North America. Only two species, *Nanhsiungchelys wuchingensis* and *Jiangxiichelys ganzhouensis*, were known from China.

Here, we report new materials that discovered from the Upper Cretaceous Nanxiong Formation at Ganzhou City in Jiangxi Province, China. The two individuals are stored in Zhejiang Museum of Natural History. ZMNH M9069 has a nearly complete carapace with a skull. The carapace length is 76 cm, and the width is 47 cm in maximum. ZMNH M30036 is also preserved nearly complete carapace and skull. The carapace is 120cm in length and 80 cm in width. Skulls of ZMNH M9069 and M30036 is 12cm and 23 cm long respectively as exposed. The skull of ZMNH nanhsiungchelyid is roughly trapezoidal in shape. The snout, the distance between orbit and nostril, is long with elongated prefrontals and maxillae. The surface of skull roof and shell are covered with the sculpture of irregular pits and grooves. This type of sculpture is characteristic for nanhsiungchelyid turtles. Nuchal notch formed by nuchal and first peripherals. The first vertebral scale is trapezoidal and the anterior side is constricted in contact with cervical only. Skull and shell morphology of ZMNH nanhsiungchelyid is most similar to *N. wuchingensis*. However, it differs from *N. wuchingensis* in having no sulci on the skull, and the trapezoidal skull. Phylogenetic relationships of nanhsiungchelyid turtles were analyzed using the data matrix of Sukhanov et al. (2008) by PAUP*4.0b. ZMNH specimens were included in the same clade of *N. wuchingensis* and *Anomalochelys angulata*. These new ZMNH materials indicate that the diversity of nanhsiungchelyid in the latest Cretaceous of the southern China was higher than expected, and shed new light on the evolution on the skull morphology of nanhsiungchelyid turtles.

Phylogeographic studies about the freshwater turtles in the Japanese main islands

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We investigated genetic diversities of freshwater turtle species in the Japanese main islands (Suzuki and Hikida 2011, 2014; Suzuki et al. 2011, 2014). The Japanese pond turtle, *Mauremys japonica* (Temminck and Schlegel, 1835), which is an endemic species in Japan, was studied by analyzing the variation in two mitochondrial DNA sequences. The analyses suggest that *M. japonica* comprises two major lineages and they are distributed in east and west regions, respectively. Microsatellite marker analysis supported the result of the mitochondrial ones. Reeves' pond turtle, *M. reevesii* (Gray, 1831), is distributed in East Asia, Korea, China, Taiwan, and Japan. The Japanese population has generally been considered to be native, but some studies raised possibility of artificial origin. To clarify the origin of the Japanese population of *M. reevesii*, we investigate the mitochondrial DNA sequences and compare them to the individuals of neighboring countries. We observed three distinct lineages in the Japanese population. Within each lineage, the genetic diversities were quite low. On the other hand, the sequences of the lineages almost identical with some haplotypes from the Korean, Chinese and Taiwanese samples. Furthermore, the nuclear marker analysis revealed some individuals captured in the wild habitats in Japan were hybrid between *M. japonica* and *M. reevesii* (Fig. 1), and it also shown some hybrids seemed F2 or backcross ones. This result indicates the possibility of introgression between two species. Finally, we investigated the mitochondrial DNA variations of the soft-shell turtle of the genus *Pelodiscus* in Japan. The Japanese populations were comprised two species, *P. sinensis* and *P. maackii*. It seemed that the former is nonnative and the latter is native to Japan. While the Japanese soft-shell turtle was originally described as *Trionyx stellatus* var. *japonica* by Temminck and Schlegel (1835), *P. maackii* was later described as *Trionyx maackii* Brandt 1857. Then, the binomen *Pelodiscus japonicus* (Temminck and Schlegel, 1835) should be applied instead of *P. maackii* to refer to the native soft-shell turtles of Japan.

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Figure 1. Hybrid individual between *Mauremys japonica* and *M. reevesii*.

Shell variability and sexual dimorphism in the earliest turtles

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Generally conservative turtle shells tend to exhibit a substantial normal and abnormal variability of the number and layout of keratinous scutes and underlying bones (e.g., Zangerl 1969; Cherepanov 2016). Moreover, sexual dimorphism is frequently observed within the shell (e.g., Pritchard 2008). Unfortunately, still very little is known about the variability, abnormalities, ontogeny, and dimorphism of fossil turtles. The Triassic taxa are especially enigmatic in this regard due to scarcity and frequently poor state of preservation. Among Triassic turtles, thus far only *Proganochelys quenstedti* Baur 1887 provided some data about the intraspecific variability (Gaffney 1990). A growing collection of the Norian basal turtles representing the family Proterochersidae, however, gives new insight into the ancestral variability and development of the turtle shell.

All the available shell remains of *Proterochersis robusta* Fraas 1913 (Löwenstein Formation, Germany – 13 specimens) and *Prot. porebensis* Szczygielski & Sulej 2016 (Grabowa Formation, Poland – over 260 specimens) were studied morphologically in order to identify any ontogenetic changes, intraspecific variability, sexual dimorphism, and shell abnormalities. To test the inferred sexual dimorphism, geometric morphometric techniques were performed for the anal region of the plastron. We analyzed the shape of caudal processes and scutes of seven individuals of *Prot. porebensis* and three specimens of *Prot. robusta*. A set of six landmarks and four semilandmarks was digitalized from the photographs of the specimens in ventral view. In order to remove the effects of size and rotation the Procrustes Analysis was performed. Then, to visualize the differences between the shape, we used the Principal Component Analysis (PCA) and Canonical Variates Analysis (CVA).

Proterochersis spp. is represented by specimens of varied sizes and ontogenetic age. Both the average and maximal sizes of *Prot. robusta* are lower than those of *Prot. porebensis*. Based on some fragmentary specimens, *Prot. porebensis* could have reached up to 80 cm in carapace length. A large variability is observed within the carapace and plastron of both species, some of which may be attributed to ontogeny or sexual dimorphism. Ontogenetic changes include size increase of gulars, extragulars, caudals, and marginals, and disappearance of middorsal keel on the carapace. Old individuals tend to exhibit more pronounced scute growth marks and radial striation, and have wider, more undulating scute sulci. The geometric morphometric analysis of dimorphism shows a shape difference of the caudal processes which is independent of size and is therefore proposed to be a sexually dimorphic. Abnormalities observed in the available material include atypical layout of scute sulci, unusual morphologies of vertebral scute areas (apparent medial split in younger regions of the scute), an additional pair of plastral scutes, and extraordinarily pronounced, likely pathological, growth rings on the carapace.

Despite the plesiomorphic structure of their bony shell, the scute anatomy and growth of Proterochersidae apparently did not differ much from those of modern turtles, and the scutes exhibited similar degree and types of abnormalities as extant species. Based on the layout of growth marks, it is evident that the scutes grew asymmetrically (non-centrally – e.g., the older parts of pleurals were located in the posterodorsal section of each scute area, the older parts of vertebrals were close to their posterior borders, etc.). It may be assumed that the developmental program of scute formation of the earliest Testudinata was already comparable to that observed in crown group turtles.

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Osteodermal mosaic in the carapace of the earliest turtles

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Despite the intensive research and numerous new discoveries during the last three decades, the composition (number and layout of elements) of the Triassic turtle bony carapaces remains a mystery. Although the appearance and subsequent evolution of the plastron and costal bones is relatively well understood thanks to developmental, histological, and paleontological data, most notably the Middle Triassic (Ladinian) *Pappochelys rosinae* Schoch & Sues 2015 and the Late Triassic (Carnian) *Odontochelys semitestacea* Li et al. 2008, the shells of the earliest true turtles (Testudinata) from the Norian are typically fully ankylosed and thus usually provide no data about the dermal components of the carapace (nuchal, peripheral, suprapygals and pygal bones). For that reason, despite the complete lack of evidence, the composition of the carapace in the first turtles, such as *Proterochersis* spp. and *Proganochelys quenstedti* Baur 1887, was conservatively thought to be the same as in the more derived forms, i.e., to include a ring of peripheral bones, a single nuchal, and a single row of suprapygals and pygal.

A detailed study of the new and historical material of the oldest (Norian) and most basal testudines belonging to the species *Proterochersis robusta* Fraas 1913 (Löwenstein Formation, Germany) and *Prot. porebensis* Szczygielski & Sulej 2016 (Grabowa Formation, Poland) was performed. All the osseous shell material of these turtles was studied in detail macroscopically, microscopically, and (in case of two most interesting specimens) utilizing computed tomography in search of sutures. The topology of the phylogenetic tree was confirmed using the matrix of Joyce et al. (2016) with the modifications introduced by Pérez-García & Codrea (2017), and added eleven new characters and three new taxa (*Pappochelys rosinae*, *Proterochersis porebensis*, and *Chinlechelys tenertesta* Joyce et al. 2009 – the latter scored either as having complex cervical osteoderms or complex posterior region of the carapace). The character mapping option of TNT was used to check whether the newly observed characters are plesiomorphic for Testudinata.

Proterochersis spp. exhibits a complex mosaic of numerous irregular, polygonal bones of varied sizes in the anterior (nuchal) and posterior (pygal) region of the carapace. These bones are separate from the costals and at least in part external to them. Besides the position, there is no clear distinction between these supernumerary bones and peripherals, and no bones clearly identifiable as a suprapygals or a pygal can be observed – it is therefore likely that the dermal carapacial mosaic of *Proterochersis* spp. and the peripherals, the suprapygals, and the pygal of more derived turtles share the same basic homology. The only specimen with preserved sutures of the nuchal reveals that the nuchal was short and paired. Three additional ossifications were observed in the posterior part of the plastron of *Proterochersis* spp., supporting the two caudal and the intercaudal scutes. Considering the position of these bones (behind the pelvis, in contact with the ischium) and their shape (paired, fingerlike projections), they may be interpreted as a modified hypischium. The obtained phylogenetic tree topology is (*Pappochelys rosinae* (*Odontochelys semitestacea* (Proterochersidae (*Proganochelys quenstedti* (*Chinlechelys tenertesta* (Australochelyidae + more derived turtles)))))). Despite its incompleteness, *C. tenertesta* is recovered as crownward to *Prog. quenstedti* regardless if its complex osteodermal spikes (Lucas et al. 2000; Joyce et al. 2009) are scored as cervical osteoderms or posterior part of the shell, supporting its generic distinctiveness. When *C. tenertesta* is removed, the relative positions of the remaining Triassic taxa stay the same and the jackknife support for the clade of *Prog. quenstedti* and more derived turtles exclusive of *Proterochersis* spp. is 75, confirming the basal position of Proterochersidae in the turtle phylogenetic tree (Szczygielski & Sulej 2016).

Beside the complex spikes, *Chinlechelys tenertesta* was recently reported to have supernumerary bones elsewhere in its carapace (Lichtig & Lucas 2016). Given that none of the remaining Triassic

turtles, including *Proganochelys quenstedti*, provides any data about the number of wholly dermal carapacial elements and their layout (the condition of the “carapacial mosaic” character is unknown for them due to suture-obliterating ankylosis), based on the recovered topology two equally parsimonious evolutionary scenarios may be proposed:

1. The complex dermal carapacial mosaic is plesiomorphic for Testudinata and crownward to *Chinlechelys tenertesta* the number of elements was reduced to the derived condition of a single ring of peripherals and a single row of up to three suprapyrgals and a single pygal. This scenario would require the mosaic to be present at least in *Prog. quenstedti* as well.

2. The complex dermal carapacial mosaic is not plesiomorphic for Testudinata but appeared independently in the Norian in *Proterochersis* spp. and *C. tenertesta*.

The first scenario seems to be more probable, based on a phylogenetic bracketing (the condition for *Prog. quenstedti* is unknown, but it is located between two mosaic-bearing taxa) and because the presence of the mosaic is hinted by the unusual, viscerally exposed but externally covered intercostal fontanelles in the pygal region of *Prog. quenstedti* carapace (Gaffney 1990). The paired nuchal bone is likewise probably plesiomorphic – this element in many modern turtles develops from paired primordia and is considered homologous to paired cleithra (Lyson *et al.* 2013). The incorporation of the hypoischium into the plastron is, however, autapomorphic.

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Three-dimensional restoration model of *Anomalochelys angulata* (Nanhsiungchelyidae; Cryptodira)

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Anomalochelys angulata is a Cretaceous non-marine turtle of the family Nanhsiungchelyidae, originally described from the Cenomanian sediment of Hokkaido Prefecture, northern Japan (Hirayama et al., 2001). This turtle has a very unique horn-like structure along its anterior margin of the carapace. Its holotype (HMG 1056) is virtually known from large part of carapace. Hirayama et al. (2009) reported a second specimen of this genus from the Late Cretaceous of Guangdong Province of China. This specimen is a nearly complete shell associated with skull and lower jaw. Limb morphology of this family has been known from the genus *Basilemys* of North America, suggesting their terrestrial ecology like living tortoises of the family Testudinidae (Hirayama et al., 2001). Thus, it is possible to make a composite three-dimensional life restoration model of *Anomalochelys*. Size of this model is 16 cm long, about one sixth of actual specimen from China. This model would be helpful for understanding the functional meaning of unusual morphology of carapace of *Anomalochelys*.

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Turtle assemblages from the Phu Kradung Formation of the Khorat Group, NE Thailand and their stratigraphical and palaeobiogeographical implications

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The Mesozoic non-marine deposits of the Khorat Group in northeastern Thailand have yielded abundant turtle remains (Tong *et al.* 2009a). The turtle assemblages from the Early Cretaceous Sao Khua and Khok Kruat formations (Barremian to Aptian) consist of trionychoids. Those from the basal unit of the Khorat Group, the Phu Kradung Formation, comprise xinjiangchelyids from its lower part and primitive trionychoids from the upper part (Tong *et al.* 2006, 2009a, 2015). This distribution seems to have a stratigraphical and palaeobiogeographical significance.

Geological setting

According to recent stratigraphical reviews, the Khorat Group contains five formations (Racey 2009). They are, from bottom to top, the Phu Kradung, Phra Wihan, Sao Khua, Phu Phan and Khok Kruat formations. It is now generally accepted that most formations of the Khorat Group are of Early Cretaceous age, while the age of its basal unit, the Phu Kradung Formation, is still uncertain. The evidence from vertebrate palaeontology, notably dinosaurs, support a Late Jurassic age for that formation; while on the basis of palynology and detrital zircon thermochronology, it is dated as Early Cretaceous. However, palynological evidence cannot exclude a Late Jurassic age for the lowermost part of the Phu Kradung Formation, because of the absence of key Early Cretaceous marker taxa (Racey and Goodall 2009). The Phu Kradung Formation is composed of sandstones, siltstones and mudstones of mainly fluvial origin. It is rich in vertebrate remains, including freshwater sharks, bony fishes, temnospondyl amphibians, turtles, crocodiles, pterosaurs and various dinosaurs (sauropods, theropods and ornithopods) (see Buffetaut *et al.* 2006; Buffetaut and Suteethorn 2007 and references therein).

Turtle assemblages from the Phu Kradung Formation

The upper part of the Phu Kradung Formation is rich in remains of a basal trionychoid turtle *Basilochelys macrobios* Tong, Claude, Naksri, Suteethorn, Buffetaut, Khansubha, Wongko and Yuangdetkla, 2009 (Tong *et al.* 2009b, a). Several localities in Mukdahan Province (Kham Phok, Huai Sai, Dan Luang, Huai Pai, Dan Kaeng) have yielded abundant material. *Basilochelys* is a large turtle, with a shell length of about 90 cm. Its shell shows some derived characters such as the sculptured shell surface, the wide and large entoplastron, the pectoroabdominal sulcus cutting the entoplastron, the relatively long pygal, the suprapygal contacting the peripheral 10 and the marginals 11-12 extending onto the suprapygal. These features are shared with the primitive trionychoids Adocidae and Nanhsiungchelyidae, thus supporting the trionychoid affinities of the taxon. On the skull, the morphology of the arterial system and related structures appear to be more advanced than in xinjiangchelyids, but close to basal trionychoids such as *Adocus* and

nanhsiungchelyids in some respects. Several morphotypes of large trionychoids are present in these localities, which may correspond to different species, sexual dimorphism or strong intraspecific variation.

Stratigraphically located under the above mentioned localities in the Phu Kradung Formation, two sites have yielded basal eucryptodiran turtles referable to xinjiangchelyids. The most complete material is from Phu Noi, in Kalasin Province. *Phunoichelys thirakbupti* Tong, Naksri, Buffetaut, Suteethorn, Suteethorn, Deesri, Sila, Chanthasit and Claude, 2015 is represented by several incomplete shells, disarticulated shells and isolated shell elements have also been collected. This relatively small turtle has a low and thin carapace. It has a particular sculpture on the shell surface, no cervical notch, a complete neural series and an extremely broad and short cervical scute. The sutured plastron/carapace connection and the marginals covering the lateral end of the second to seventh costals suggest that this turtle may be related to some primitive xinjiangchelyids from the Sichuan Basin, China (Tong *et al.* 2015).

A new and more advanced xinjiangchelyid taxon from Phu Noi locality is currently under study. The material consists of several shells, one of them is associated with a fairly well preserved skull. Several xinjiangchelyid synapomorphies are present on the shell, shared also with *Phunoichelys*, including the lateral marginals extending onto the costal plates, relatively reduced plastron and a longer than wide oval-shaped entoplastron. The new taxon differs from *Phunoichelys* in the more heavily built shell with thickened free margin, the smooth shell surface, the presence of a moderately developed cervical notch, the shape of the nuchal plate and cervical scute, and a reduced neural series. The almost complete skull is low with an oval outline as seen from above. The general morphology of the skull, especially the structure of the arterial system closely resembles that of xinjiangchelyids from China and Mongolia, notably *Annemys*.

Fragmentary shell elements of these two xinjiangchelyids have also been collected from Ban Khok Sanam locality, Kalasin Province. In that locality, a few fragmentary shell elements show the carapace surface covered with fine ridges arranged in a radiating pattern. This is reminiscent of some xinjiangchelyids and macrobaenids from China, although the fragmentary nature of the material prevents a precise systematic assignment.

Discussion

Turtle assemblages from different localities of the Phu Kradung Formation can be gathered in two groups. Those from Phu Noi and Ban Khok Sanam localities in Kalasin Province, corresponding to a relatively lower stratigraphical level of the Phu Kradung Formation, consist of diverse xinjiangchelyids and have close affinities with those from the Late Jurassic of China and Mongolia, which seems to support a similar age for that part of the formation. The upper part of the Phu Kradung Formation has yielded abundant basal trionychoids. These assemblages have no equivalents in mainland Asia, where the turtle faunas are mainly composed of basal eucryptodiran xinjiangchelyids in the Jurassic deposits and sinemydids/macrobaenids in the Early Cretaceous. It is noteworthy that turtle faunas from the upper part of the Phu Kradung Formation, as well as from the overlying Sao Khua and Khok Kruat formations are more comparable with those from the Early Cretaceous Tetori Group of Japan in the presence of various primitive trionychoids, on the basis of which stratigraphical correlations can be made.

From a palaeogeographical point of view, the close affinities of the turtle faunas from the lower part of the Phu Kradung Formation on one hand; and those from China and Mongolia on the other hand, suggest a faunal link between SE Asia and mainland Asia during Late Jurassic times, while distinct turtle assemblages from the upper part of that formation compared with the coeval faunas from mainland Asia seem to suggest that SE Asia became more isolated than before during that time interval.

In conclusion, turtle assemblages from the Phu Kradung Formation provide new insights on the evolution of eucryptodiran turtles during the Late Jurassic - Early Cretaceous, a crucial period

for the early diversification of crown group turtles. Based on the turtle faunas, the lower part of the Phu Kradung Formation can be correlated with the Late Jurassic of mainland Asia, thus supporting a similar age for that part of the Formation. Comparisons between Thai assemblages and those from more northern parts of Asia suggest some faunal exchanges between these areas during the Late Jurassic and a greater isolation of SE Asia during the Early Cretaceous.

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U-Pb dating of turtle fossils from the Upper Cretaceous Tamagawa Formation in Kuji, Iwate, Japan

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The Upper Cretaceous Kuji Group is broadly distributed at the Kuji City of Iwate Prefecture, Japan, which comprises of three formations, Tamagawa, Kunitan and Sawayama formations in ascending order (Ando, 1997). The outcrop of the upper portion of Tamagawa Formation occurs around the Kuji Amber Museum, where plenty of turtle bones were found as sediment on floodplain (Hirayama *et al.*, 2010). Most bones are disarticulated but little deformed. It is necessary to determine the age of fossils for paleontological discussion regarding the turtle fossils.

A lenticular tuff is interbedded above the bone bed in the flood plain. The tuff does not include exogenous matters such as eroded sand and carbonaceous fragments, which reveals that the tuff is mainly made of an autochthonous ash-fall without contamination by long-distance transport. The dating of the lenticular tuff is expected to approximately express the age of fossil-bearing bed.

Uranium-lead (U-Pb) dating is one of most common dating methods applicable to geological materials. The method is utilizing abundance of Pb isotopes produced by U decay. ²³⁸U and ²³⁵U undergo radioactive decay to ²⁰⁶Pb and ²⁰⁷Pb, respectively (Schoene, 2014). Zircon (ZrSiO₄) is most frequently used for U-Pb dating due to its advantages; 1, Zircon is resistant to physical and chemical diagenesis and expected to be a closed system; 2, During formation of the zircon, it relatively aggregates U but does not include Pb as primary components (Schoene, 2014).

We analyzed the ratios of ²⁰⁶Pb/²³⁸U and Pb isotopes in the zircon grains in the tuff sample using SHRIMP IIe installed at NIPR. The dating based on the ratio, 45 of 107 data fell within a single youngest cluster, which represented eruption (\approx deposition) age, indicated 90.51 ± 0.54 Ma (95% confidence, MSWD=0.91). Thus, turtle-bearing bed was deposited nearly in this age.

In some studies based on palynostratigraphy of the Kuji Group, the age of upper Tamagawa Formation including turtle-bearing bone bed has been regarded as the border between the Coniacian and the lower Campanian (ca. 86.3- ca. 80 Ma) (Umetsu and Kurita, 2007). The radioactive dating, in this study, based on the ash-fall tuff could provide more closely true age.

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A total evidence phylogeny of Pan-Testudinidae

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Despite their global distribution, substantial diversity, and rich fossil record, the evolutionary history of Testudinidae (tortoises) is poorly understood. We here present the first total evidence analysis of Pan-Testudinidae combining previous and novel morphological datasets with fossil data and published molecular information. Parsimony analysis of this dataset demonstrates that the conflict between morphological and molecular topologies are largely due to the aberrant taxa, *Malacochersus tornieri* and *Kinixys* spp., indicating that morphology is a powerful tool for phylogenetic reconstruction within extant and extinct Testudinidae. The total evidence topology is congruent with the molecular topology and recovered two clades of crown-Testudinidae: Testudona and Geochelona. The inclusion of fossil species implies that Testudona and Geochelona diverged at latest by the Late Eocene, in agreement with recent molecular estimates. The age of crown *Testudo* is Late Miocene, again in accordance with some molecular dates. Ghost lineage analysis estimates high rates of diversification during the Late Eocene and Miocene onwards and implies no major decline during the Neogene and Quaternary. Phylogenetic placement of fossils demonstrates that giant body size independently evolved in multiple continental mainland taxa and is not linked to insular effect. A somewhat unexpected outcome is the recovery of miniaturization in Testudona (<30 cm carapace length) sometime between the Oligocene and Early Miocene. On the contrary, Geochelona shows great body size disparity including the largest and smallest tortoises ever lived. These patterns appear to be independent of topological changes resulting from homoplasy down-weighting (implied weighting). Future research should focus on expanding taxon and character sample in order to refine body size evolution, diversification, and paleobiogeographic patterns in Pan-Testudinidae.

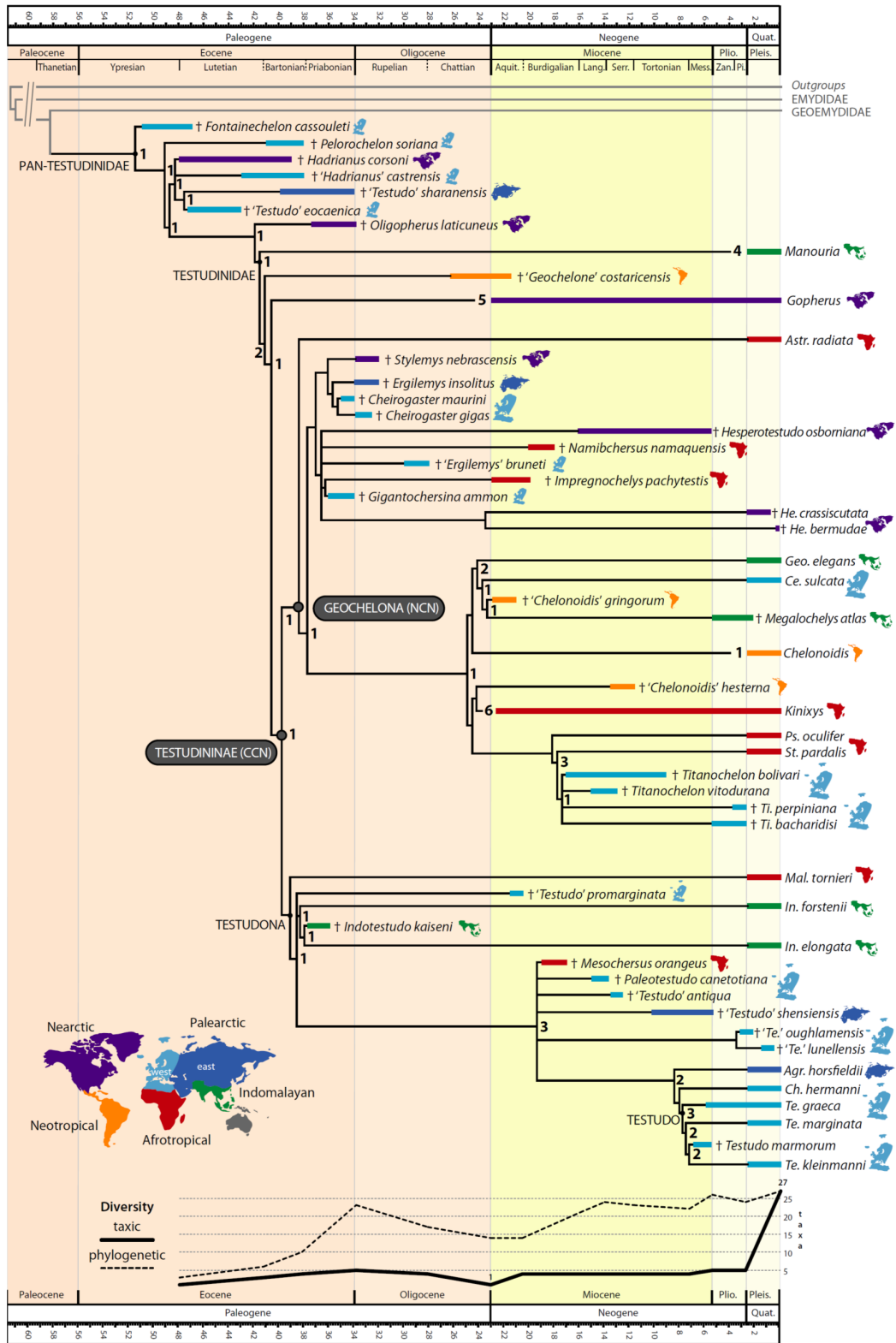


Figure 1. Simplified time-calibrated phylogeny of Pan-Testudinidae based on the strict consensus tree of the total evidence analysis under equal weights. Bremer support values are in bold. Extinct taxa are marked with a cross. Results of ghost lineage analysis are shown in the diagram below the tree including taxonomic diversity (as raw counts of taxa; solid line) and phylogenetic diversity (dashed line).

Considerations on the development of the akinetic skull in pleurodire and cryptodire turtles

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Extant turtles are characterized by an akinetic skull (Werneburg 2012), whereas several stem Testudines plesiomorphically had a basicranial articulation (Gaffney 1986, 1990; Joyce 2007; Rabi et al. 2013). We demonstrate, discussing three character complexes, how the akinetic skull is formed through ontogeny, including (1) the formation of the broad ethmoid area in association with the upper jaw bones (Fig. 1A), (2) the lateral closure of cavum epiptericum, and (3) the fusion of the palatoquadrate cartilage to the neurocranium. Both major clades of modern turtles, Pleurodira and Cryptodira, show strikingly different strategies on how to develop the akinetic construction in the orbitotemporal region. Whereas the ascending process of the palatoquadrate (later ossified as epipterygoid) contributes to the formation of the secondary braincase wall in Cryptodira (Fig. 1B) (Fuchs 1915; Rieppel 1976), only the descending process of the parietal is forming that wall in Pleurodira. Related to that, the latter taxon does not develop an extended ascending process (Eßwein 1993; Werneburg et al. 2009; Werneburg 2011; Paluh and Sheil 2013; Sheil and Zaharewicz 2014). Moreover, whereas the palatoquadrate directly fuses to the braincase with the help of appositional bone (perichondral bone, Zuwachsknochen) in pleurodires, it is bridged by the pterygoid in cryptodires (Fig. 1C) (Eßwein 1993). These diverging patterns could indicate that the last common ancestor of extant turtles, to a certain extent, still had a kinetic skull and that fully akinetic skull constructions independently evolved in pleurodires and cryptodires. The characters are discussed in the context of muscle anatomy, skull dimensions, and fossil record. Mainly embryonic neck muscle activity might cause the detected heterotopic shifts of the palatoquadrate. Side necked retraction in pleurodires redirects the palatoquadrate posterolaterally, whereas hidden-necked retraction in cryptodires pulls the palatoquadrate in a posterodorsal direction through ontogeny. These mechanisms result in differing positions of the palatoquadrate in relation to the braincase and eventually lead to the diverging fusion pattern documented herein.

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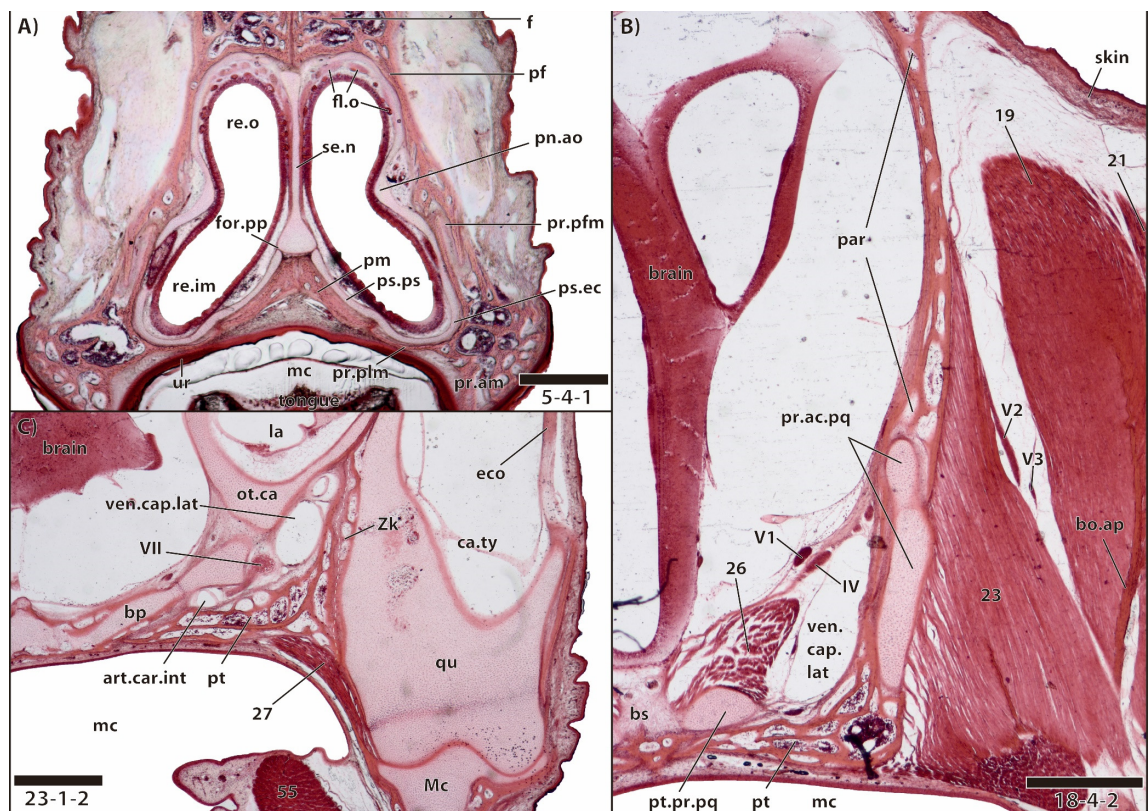


Figure 1. Histological cross sections through the embryonic head of *Chelydra serpentina* (Cryptodira) (Phylogenetisches Museum Jena, Inv.-Nr.: Rept. 1213, crown-rump-length 23 mm, hematoxylin & eosin staining, 30 µm slide thickness). **A)** Nose region in which the nasal capsule broadly aligns to the snout bones, **B)** lateral closure of cavum epipterygium by the descending process of the parietal and the ascendant process of the palatoquadrate [white dashed line indicates the border between pterygoid and the appositional bone (Zuwachsknochen) of the quadrate], and **C)** fusion of the palatoquadrate to the braincase bridged by the pterygoid and appositional bone of the quadrate. **Abbreviations:** bo.ap, bodenaponeurose (coronar tendon); bp, basal plate; ca.ty, cavum tympanicum; eco, extracolumella, f, frontal; fl.o, filia olfactoria; for.pp, foramen prepalatinum (here as fissure); la, labyrinth; mc, mouth cavity; Mc, Meckel's cartilage; ot.ca, otic capsule; pf, prefrontal; pm, premaxilla, pn.ao, planum antorbitale; pr.ac.pq, processus ascendens palatoquadrati; pr.am, processus alveolaris maxillaris; pr.pfm, processus prefrontalis maxillaris; pr.plm, processus palatinus maxillaris; ps.ec, pars entochonialis; ps.ps, pars paraseptale; pt, pterygoid; pt.pr.pq, pterygoid process of the palatoquadrate; qu, quadrate; re.im, region intermedialis; re.o, region olfactoria; se.n, septum nasi; ur, upper ramphotheca; ven.cap.lat, vena capitis lateralis; IV, nervus trochlearis; V1, nervus ophthalmicus trigemini; V2, nervus mandibularis trigemini; V3, nervus maxillaris trigemini; VII, nervus facialis; Zk, Zuwachsknochen; 19, musculus (m.) adductor mandibulae externus Pars profundus; 21, m. adductor mandibulae externus Pars superficialis; 23, m. adductor mandibulae internus Pars pseudotemporalis; 27, m. adductor mandibulae internus Pars pterygoideus posterior. Muscle numbers refer to Werneburg (2011). Bar scales equal 0.5 mm. Numbers below bar scales refer to slide numbers.

Marine turtle remains from the Upper Cretaceous Yezo Group (Hokkaido, Northern Japan) suggest the continuous dispersal of the oldest known sea turtle lineage to Northwest Pacific

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Introduction

A number of fossil vertebrates have been reported from the Upper Cretaceous Yezo Group of Northern Japan. Among them, *Mesodermochelys* (Chelonioidae: Dermochelyidae) have been recognized as one of the dominant marine turtle taxon from Santonian to Maastrichtian in Northwest Pacific Realm. From the Santonian to Maastrichtian, no other marine turtle has been reported. Therefore, the diversity of marine turtles in Northwest Pacific Realm of Late Cretaceous has been considered as rather low. Here, we report the several cervical vertebrae remains of Chelonioidae from Turonian to Campanian of Hokkaido.

Material and methods

OBR-3610-01 specimen is an isolated procoelous vertebra, lacking prezygapophysis and neural spine. The vertebral body is well preserved. The specimen is collected from the Santonian–Campanian Haborogawa Formation of Yezo Group at Obira area, Hokkaido. HMG-1128 specimen is stored in Hobetsu Museum, a series of articulated vertebrae with fragmental bones. It includes 7th and 8th cervical, 1st and 2nd thoracic vertebrae. Dorsal part of vertebrae is damaged but ventral part is well preserved. The specimen is collected from the Lower Cenomanian–Turonian Formation in Hobetsu area, Hokkaido. We compared OBR-3610-01 and HMG-1128 to THU g262 specimen. THU g262 is *Desmatochelys* cf. *D. lowi* from the Turonian Saku Formation, Yezo Group in Oyubari area, and includes the complete cervical series. All the specimens show the shared character on the ventral side of cervical vertebrae.

Results and conclusion

Both OBR-3610-01 specimen and HMG-1128 specimen show the shared character to *Desmatochelys lowi* (Chelonioidae: Protostegidae) in the hypapophysis. The hypapophysis process is not elevated down as in other Chelonioids, but forms two longitudinal ridges and concave surface between ridges. This hypapophysis character is only known in *D. lowi*. Together with the large size of fossil specimens, we assume these newly discovered specimens might be the closer relative of *D. lowi*. In genus *Desmatochelys*, there is the oldest known sea turtle *D. padillai* from the Lower Cretaceous of Columbia. Other fossil records of *Desmatochelys* is mostly known from North America from the Upper Cretaceous Cenomanian to Campanian. These newly found specimens suggest the *Desmatochelys* lineage had dispersed to Northwest Pacific Realm much earlier and survived longer than we had recognized.

Paleogene turtles of Eastern Europe: new findings and reinterpretation of the previous materials

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Paleogene turtles of Eastern Europe (in limits of the European part of the former USSR) are poorly known and represented by remains of cheloniid and dermochelyid sea turtles, trionychids, testudinoids, and indeterminate turtles from 19 localities (Averianov and Yarkov, 2000, 2004; Averianov, 2002; Danilov et al., 2010, 2011, 2017; Zvonok, 2011, 2013; Zvonok et al., 2013a, b; Zvonok and Danilov, 2017). In this communication we present new data and materials on turtles from some of the previously known localities (1–4; see references therein for more data) and new localities (5–11) of the Paleogene of Eastern Europe. The new materials are stored in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZIN PH) and A.A. Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia (PIN).

1) Bakhmutovka and Krasnorechenskoe localities, Luhansk Province, Ukraine; the turtle material comes from the phosphate horizon of the Kiev Formation, rather than from the quartz sand of the Buchak Formation as was reported previously (Averianov, 2002), Lutetian. Collector: N.I. Udovichenko. Previous material from both localities was represented by fragmentary shell remains of cheloniids with sculpturing on the shell surface (Averianov, 2002; Zvonok and Danilov, 2017). New material from Bakhmutovka locality (ZIN PH) includes additional remains (at least one neural, two costals and five peripherals) of the cheloniid with sculpturing. New material from Krasnorechenskoe locality (ZIN PH) is represented by posteromedial part of costal 1 with a small adjacent fragment of the hyoplastron in articulation (Fig. 1A). This specimen is assigned to Geoemydidae indet. based on that the plastral buttress is at least partially attached to the carapace by a connective tissue, and vertebral 1 scute is lyre-shaped, like in many Paleogene European geoemydids (see Hervet, 2004).

2) Ikovo locality, Luhansk Province, Ukraine; lower Lutetian. Previous material includes the partial skull and postcranial remains of a trionychid “*Trionyx*” *ikoviensis* Danilov et al., 2011, remains of several cheloniids: isolated bones of *Argillochebys* sp., skulls and isolated bones of *Puppigerus nessovi* Averianov, 2005, symphysis of the dentaries of *Eochelone* sp., facial skull region of cf. *Glossochebys* sp. (Cheloniidae gen. indet. 3; Danilov et al., 2017; see new interpretation below), bones of Cheloniidae indet.; and not designated remains of Testudinoidea indet. (Danilov et al., 2011; Zvonok, 2011; Zvonok, 2013; Zvonok et al., 2013b). New materials (ZIN PH) include numerous shell bones of trionychids, and a partial skull of the second trionychid assigned to the clade Plastomenidae, based on a contribution of the parietal to the wall of the orbit, and in that the maxillae form extensive, infolded secondary palate (Fig. 1B; see Joyce and Lyson, 2011). The presence of two skull-based taxa of trionychids in Ikovo raises a problem of association of the skull and postcranial materials. Some of the postcranial specimens previously attributed to “*T.*” *ikoviensis* may belong to the second trionychid taxon. Additional preparation of the facial skull region of “cf. *Glossochebys* sp.” and finding of a new maxilla specimen of the same taxon allow us to reinterpret it as Geoemydidae gen. et sp. nov. (Fig. 1C – E). The new interpretation is based on a combination of morphological characters known only in some geoemydids (i.e. *Geoclemys hamiltonii* (Gray, 1831)): participation of the jugal in the rim of the upper temporal emargination, and wide and not-ridged triturating surface of the upper jaw with participation of the palatine (see Joyce and Bell, 2004). Fragments of peripherals 2 and 3, and xiphiplastron with smooth external surface and shallow sulci may belong to the same geoemydid taxon. The remains of Testudinidae indet. are represented by a large epiplastron similar to those of a testudinid *Pelorochelon soriana* Perez-Garcia et al., 2016 from the

middle Eocene (Bartonian) of Spain (Fig. 1F, G; Perez-Garcia et al., 2016: fig. 5) and a number of thin-walled bones of the shell with a wrinkled outer surface and deep scute sulci.

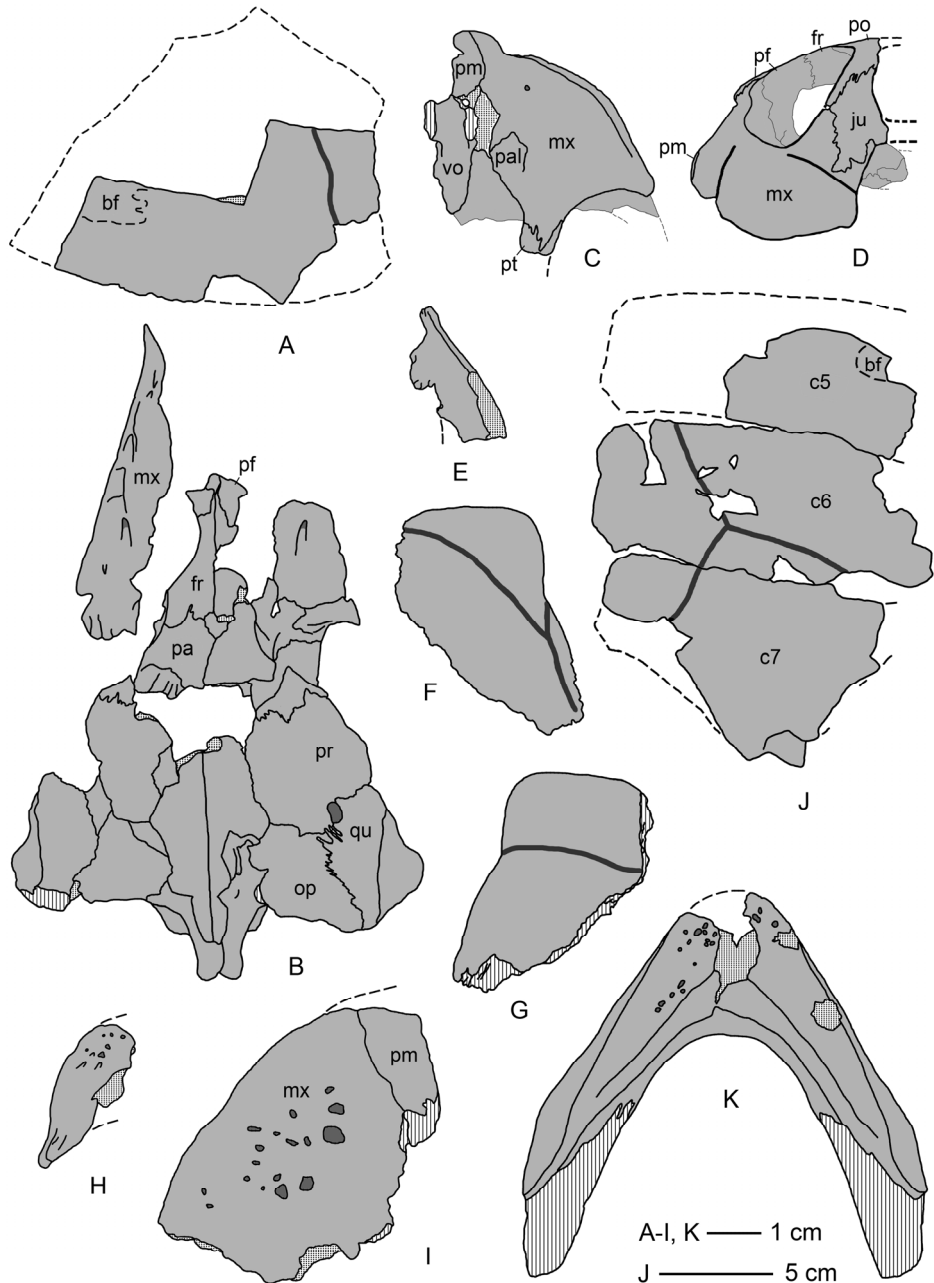


Figure 1. Remains of Paleogene turtles of Eastern Europe: **A** – Krasnorechenskoe locality (1): *Geoemydidae* indet., costal 1 (collection ZIN PH 19) in dorsal view; **B** – **G** – Ikovo locality (2): **B** – *Trionychidae* indet. (*Plastomenidae*), partial disarticulated skull (ZIN PH 51/145) in dorsal view; **C** – **E** – *Geoemydidae* gen. et sp. nov., **C**, **D** – facial skull region (ZIN PH 50/145) in ventral (**C**) and left lateral (**D**) views; **E** – left maxilla (ZIN PH 52/145) in ventral view; **F**, **G** – *Testudinidae* indet., epiplastron (ZIN PH 53/145) in dorsal (**F**) and ventral (**G**) views; **H** – **J** – Bereslavka 2a locality (3): **H**, **I** – *Euclastes wielandi*: **H** – dentary (ZIN PH 21/22) in dorsal view; **I** – ZIN PH 6/22, right maxilla and premaxilla in ventral view; **J** – *Testudinoidea* indet. 1, carapace fragment (ZIN PH 22/22) in dorsal view; **K** – Novoivanovka locality (9): *Argillochebys* sp., symphysis of the dentaries (ZIN PH 1/247) in dorsal view. Sutures are hatched, breakages are stippled. Position of buttresses are shown by dashed lines. Abbreviations: bf – butress fossa; c5 – 7, costals 5 – 7; fr – frontal; ju – jugal; mx – maxilla; op – opisthotic; pa – parietal; pal – palatine; pf – prefrontal; pm – premaxilla; po – postorbital; pr – prootic; pt – pterygoid; qu – quadrate; vo – vomer.

3) Bereslavka 2a (= Karpovka) locality, Volgograd Province, Russia; Syzran Formation, middle Paleocene (Selandian) (see Averianov and Yarkov, 2004 for correct age of the locality). Previous materials include the upper jaw and shell fragments of cheloniids primarily referred to as *Osteopyginae* gen. et sp. indet., and later as “Karpovka *Euclastes?*” and *Cheloniidae* gen. indet. 1 (Averianov and Yarkov, 2000; Lynch and Parham, 2003; Danilov et al., 2017), shell fragments of *Trionychidae* indet. and shell plates of *Testudinata* indet.: genus et species indet. 1 and 2 (Averianov and Yarkov, 2000; see new interpretations below). New turtle materials from this locality (ZIN PH), collected by A.A. Yarkov, include skull bones of cheloniids, which allow assignment of the Bereslavka 2a cheloniid to *Euclastes wielandi* (Hay, 1908) known previously from the Maastrichtian – Thanetian of USA and Maastrichtian of Morocco (Fig. 1H, I; see Parham 2005). The new assignment is based on weakly elongated palatal elements and rounded anterior tip of the skull (see Hirayama and Tong, 2003; Jalil et al., 2009). There is also a carapace fragment (20 cm in length as preserved) composed of costals 5 – 7, of which costal 5 bears a smooth buttress fossa, suggesting a loose plastron-carapace connection (Fig. 1J). This specimen is similar in morphology to some basal testudinoids and referred here to as *Testudinoidea* indet. 1. *Testudinata* indet.: genus et species indet. 1, represented by costal 6(?) (Averianov and Yarkov, 2000), is reinterpreted here as *Testudinoidea* indet. 2, based on wedge-shaped costal, and absence of the rib thickening on its internal surface (both characters are present in problematic testudinoids *Anhuichebys* spp. from the Paleocene of Asia; Tong et al., 2016; IGD’s personal observations). *Testudinata* indet.: genus et species indet. 2, represented by a thick neural with folded external surface (Averianov and Yarkov, 2000), is accomplished by numerous shell fragments, which are characterized, besides mentioned features, by deep and undulating scute sulci. This turtle is similar in bone thickness and deep scute sulci to *Cryptodira incertae sedis* sp. 2, represented by fused epiplastra and entoplastron from the Maastrichtian of Bereslavka 1 locality (Averianov and Yarkov, 2004). The systematic position of this turtle remains unclear and may be among basal turtles or basal cryptodires (see Danilov et al., 2017: *Testudines* subord. indet. 9).

4) Loznoe locality, Volgograd Region, Russia; Kamyshin Formation, upper Paleocene (Thanetian). Previous material includes a phalanx of *Testudines* indet. (Averianov and Yarkov, 2004). New materials from this locality (ZIN PH), collected by A.V. Panteleev and A.A. Yarkov, include shell fragment of *Trionychidae* indet., and shell fragments of *Testudines* indet.

5) Georgievka locality, Lutugino District, Luhansk Province, Ukraine; 48°26' N, 39°19' E; glauconitic sands of the lower part of the Kiev Formation, Lutetian. The material (ZIN PH) is represented by a medial part of the costal of *Testudines* indet. Collector: N.I. Udovichenko.

6) Gorniy Luch locality, Apsheronsk District, Krasnodar Territory, Russia; 44°19' N 39°48' E; shales of the Kuma Horizon, Bartonian. The material (PIN) is represented by a partially disarticulated skeleton of a juvenile cheloniid turtle (*Cheloniidae* indet.) in the matrix. Collector: A.F. Bannikov.

7) Krinichnoe locality, Melovoe District, Luhansk Province, Ukraine; 49°19' N, 40°04' E; phosphate bed, Lutetian (the age is based on bivalves; personal communication of A.A. Berezovskiy). The material (ZIN PH) is represented by two isolated peripherals of *Cheloniidae* indet. Collector: E.A. Zvonok.

8) Malchevskaya locality, Millerovo District, Rostov Province, Russia; 49°03' N, 40°22' E; quartz sands, ?Lutetian stage. The material (ZIN PH) is represented by costal fragment of *Testudines* indet. Collector: A.V. Panteleev.

9) Novoivanovka locality, Millerovo District, Rostov Province, Russia; 48°50' N, 40°23' E; quartz sands, ?Lutetian stage. The material (ZIN PH) is represented by a symphysis of the dentaries of the cheloniid *Argillochebys* sp. (Fig. 1K). Collector: K.S. Benitskiy.

10) Otradnoe locality, Mikhaylovka District, Volgograd Province, Russia; 50°01'N, 43°09'E; phosphate horizon, Priabonian (not to be confused with Otradnaya locality, Krasnodar Region, Russia; ?Eocene, wherefrom undescribed *Cheloniidae* indet. were mentioned (see Averianov, 2002)). The material is represented by a shell fragment of *Cheloniidae* indet. with a distinct

sculpturing similar to those of cheloniids from Bakhmutovka and Krasnorechenskoe localities (see 1). Collector: A.A. Yarkov.

11) Voznesenskiy locality, Morozovsk District, Rostov Province, Russia; 48°22' N, 41°56' E; quartz sands, ?Lutetian. The material is represented by the postorbital, neural, six costals and three peripherals of Cheloniidae indet., and a plastral fragment of Testudines indet. Collectors: A.V. Panteleev and E.V. Popov.

To summarize, our study increases the number of the turtle bearing Paleogene localities of Eastern Europe to 26, of which seven localities are new. The richest among them are the Paleocene (Selandian) Bereslavka 2a and the Eocene (Lutetian) Ikovo localities having each at least five and seven turtle taxa respectively, whereas other localities have usually one or two taxa. The reinterpretation of some previous materials and new findings of turtles from the Paleogene of Eastern Europe, demonstrate presence on this territory of the previously unknown plastomenid trionychids, cheloniids, basal testudinoids, geoemydids, primitive testudinids and basal turtles or basal cryptodires. The plastomenid from Ikovo represents the first true plastomenid outside North America. The attribution of the cheloniid material from Bereslavka 2a to *Euclastes wielandi* expands distribution of this taxon to the eastern part of Tethys. New material from Novoivanovka locality expands distribution of the cheloniid genus *Argillochebys*, and represents the first finding of this genus in Russia. Testudinoidea indet. 1 and 2 from Bereslavka 2a, if our assignment is correct, represent the oldest European testudinoids (see Danilov, 2005). The *Geoclemys*-like geoemydid from Ikovo is one of a few Paleogene geoemydids represented by skull material. Testudinidae indet. from Ikovo is the oldest testudinid known from Eastern Europe. The basal turtle or basal cryptodire from Bereslavka 2a is one of a few such turtles known in the Paleocene of Europe.

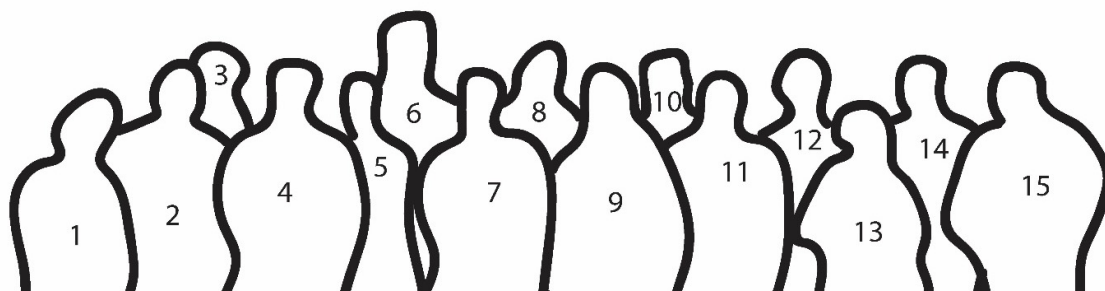
Acknowledgements. The authors thank A.F. Bannikov, K.S. Benitskiy, A.V. Panteleev, E.V. Popov, N.I. Udovichenko, and A.A. Yarkov for providing materials for this study, and A.A. Berezovskiy for the determination of the geological age of the Krinichnoe locality based on assemblage of bivalves. This study was fulfilled under partial support of the Program of the Russian Academy of Sciences Presidium “Evolution of the organic world. The role and significance of planetary processes.”

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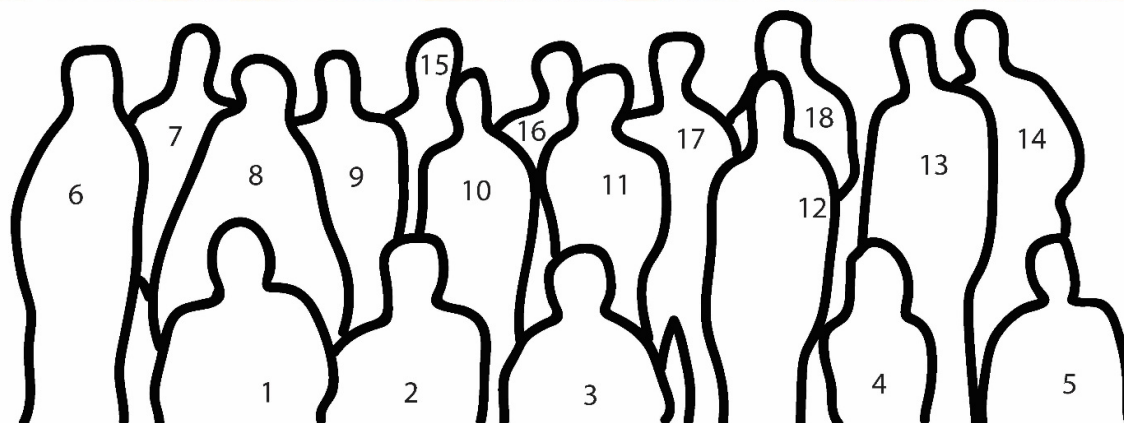
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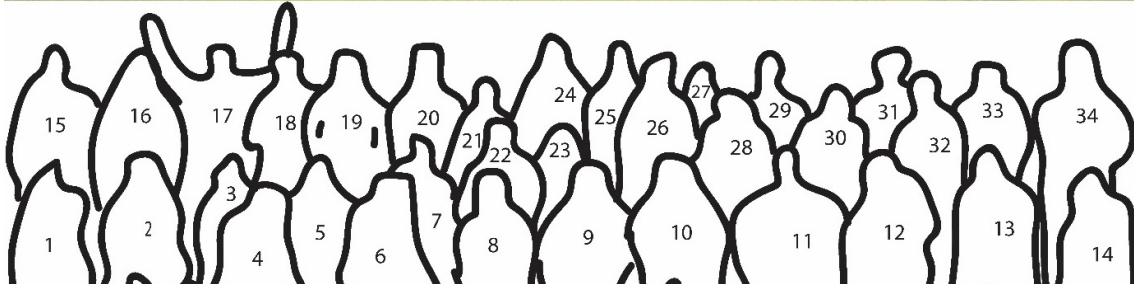
**Conference photos of the past
turtle evolution symposia**



1. International Symposium on Fossil Turtles (Paris, France, October 1983). 1. Ren Hirayama, 2. T. Kotsakis, 3. Roger Wood, 4. Emiliano Jiménez-Fuentes, 5. Marie-Claire Groessens-Van Dick, 6. Peter Pritchard, 7. Marian Mlynarski, 8. Hans-Herman Schleich, 9. M. Moody, 10. Donald Smith, 11. Richard Moody, 12. Peter Meylan, 13. France de Lapparent De Broin, 14. Eugene Gaffney, 15. Roger Bour

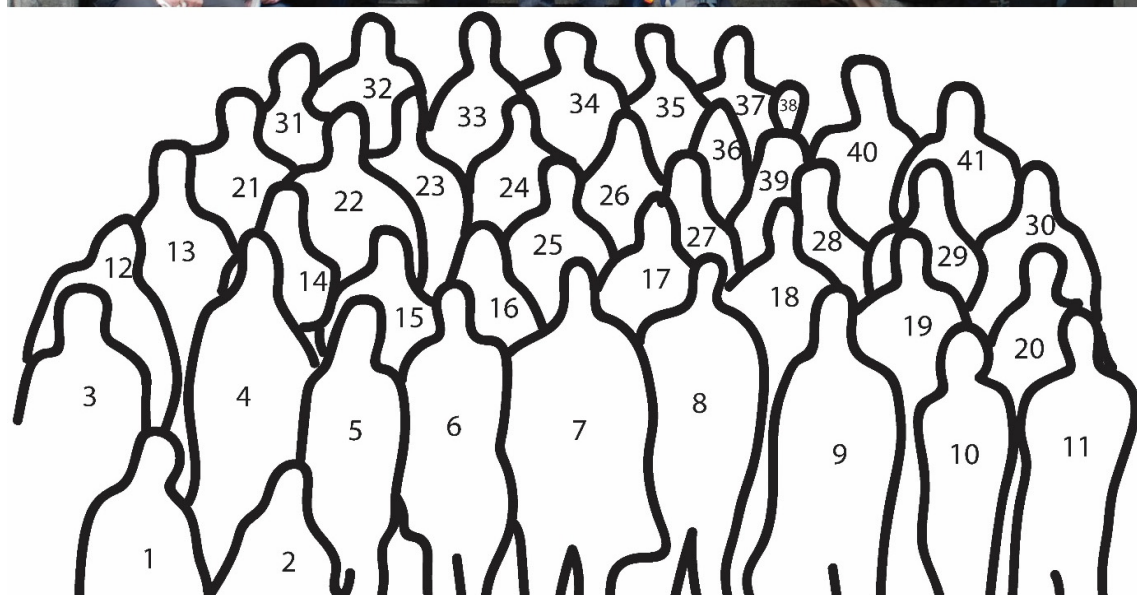


2. Symposium on Turtle Origins, Evolution and Systematics (St. Petersburg, Russia, August 2003). 1. Igor Danilov, 2. James Parham, 3. Ren Hirayama, 4. Yoshie Ohya, 5. Haiyan Tong, 6. Svetlana Krasnova, 7. Julien Claude, 8. Vladimir Sukanov, 9. Gennady Cherepanov, 10. Vera Egorova, 11. Shigeru Kuratani, 12. Sandra Chapman, 13. Oliver Piskurek, 14. Éric Buffetaut, 15. Anton Rezvyi, 16. Donald Brinkman, 17. Walter Joyce, 18. Vincent Gillespie

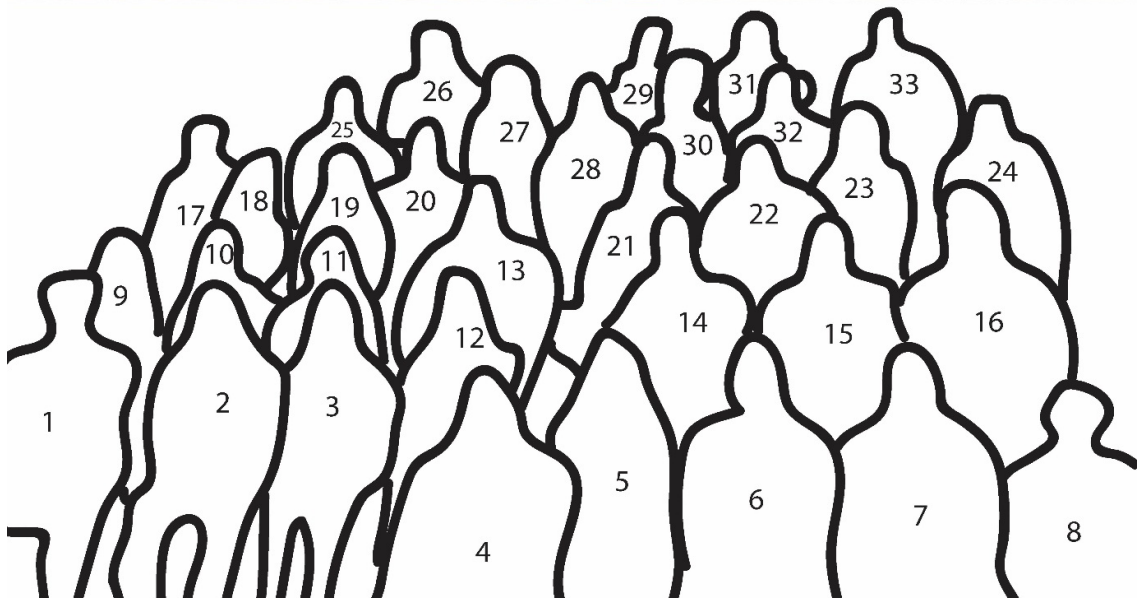


3. Gaffney Turtle Symposium (Drumheller, Canada, 2009). 1. Haiyan Tong, 2. Dennis Braman, 3. Robert Smith, 4. Hiroshi Nagashima, 5. Conrad Wilson, 6. Elizabeth Smith, 7. Adan Pérez-García, 8. Ren Hirayama, 9. Robert Carroll, 10. Pedro Romano, 11. Peter Meylan, 12. Igor Danilov, 13. Donald Brinkman, 14. James Gardner, 15. Éric Buffetaut, 16. David Eberth, 17. Akio Takahashi, 18. Tepei Sonoda, 19. Gustavo Oliveira, 20. Torsten Scheyer, 21. Yvonne Lichtenfelt, 22. Walter Joyce, 23. Georgia Knauss, 24. Dean Pearson, 25. Tyler Lyson, 26. Barbara Gaffney, 27. Diana Vineyard, 28. France de Broin, 29. Robert Weems ?, 30. Elena Syromyatnikova, 31. Brian Cressman ?, 32. Chris Marion, 33. Brandon Strilisky ?, 34. Roger Wood.

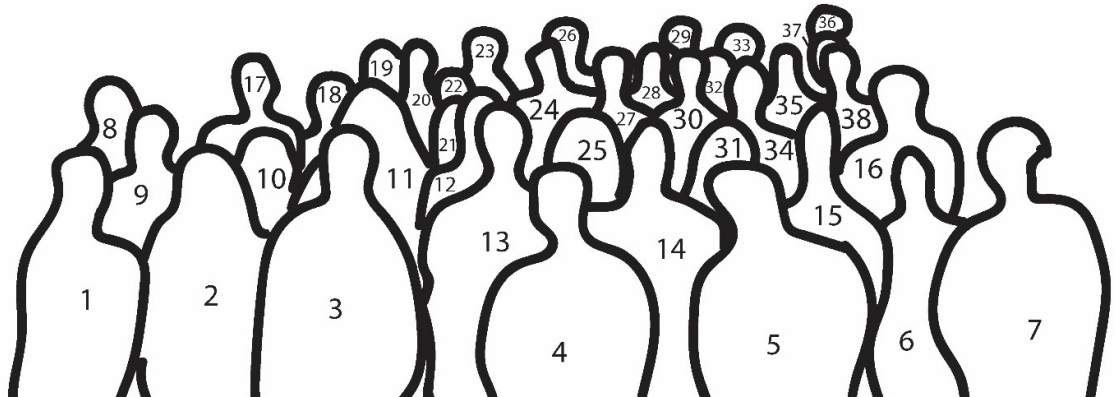
This picture was taken at the field excursion. In addition to the persons seen on the photo, following persons attended the symposium: Alison Murray, Allison Fotheringham, Amanda McGee, Andrew Milner, Andrew Neuman, Barry Peterson, Bill Dean, Brent Noland, Christopher Bell, Christopher Jass, Cory Jones, Darren Tanke, David Lloyd, Dawna MacLeod, Dean Pearson, Derek Larson, Donald Henderson, Edwin Cadena, Edwin Hooks, Gene Gaffney, H. Bradley Shaffer, Hans Peter Schultz, Howard Hutchinson, Jason Anderson, Jason Bourque, Jason Head, Jeff Baltzer, Jennifer Dick, Jessica Theodore, Jim Gardner, Jim McCabe, Joseph Corsini, Joyce Harrod-Dean, Kenneth Angielczyk, Lara Shychoski, Lindsey Nydegger, Marie Tounissoux, Marilyn Laframboise, Mark Mitchell, Masashi Tanaka, Meagan Gilbert, Michael Caldwell, Michael Densmore, Michael Knell, Natasha Vitek, Patricia Holroyd, Patty Ralrick, Paul Sereno, Pete Truch, Rebecca Bavington, Rhian Russell, Richard Fox, Richard Moody, Robert Burroughs, Robert Holmes, Robin Sissons, Roger Benson, Sandra Chapman, Sara ElShafie, Takuya Konishi, Thomas Near, Tim Tokaryk, Tyler Shaw, Vincent Gillespie, Wendy Taylor, Xiao-chun Wu



4. Symposium on Turtle Evolution (Tübingen, Germany, June 2012). 1. Torsten Scheyer, 2. Elena Syromyatnikova, 3. Adan Pérez-García, 4. Joseph Corsini, 5. Wilailuck Naksri, 6. Haiyan Tong, 7. Gustavo Oliveira, 8. Pedro Romano, 9. Gabriel Ferreira, 10. Natasha Vitek, 11. Robert Burroughs, 12. Markus Lambertz, 13. Michael Knell, 14. Walter Joyce, 15. Maren Jansen, 16. Andrea Petričević, 17. Loïc Bocat, 18. Tomasz Szczygielski, 19. Tomasz Sulej, 20. Donald Brinkman, 21. Jake Saylor, 22. Daniel Lawver, 23. Ingmar Werneburg, 24. Jean-Paul Billon-Bruyat, 25. Christian Püntener, 26. Fernanda Deantoni, 27. Ren Hirayama, 28. Massimo Delfino, 29. Martón Rabi, 30. Evangelos Vlachos, 31. Philipe Havlik, 32. Nickolay Natchev, 33. Tyler Lyson, 34. Igor Danilov, 35. Brian Roach, 36. Juliana Sterli, 37. Julien Claude, 38. Sandra Chapman, 39. Ignacio Maniel, 40. Akio Takahashi, 41. Hans-Volker Karl



5. Symposium on Turtle Evolution (Rio de Janeiro, Brazil, July 2015). 1. Gabriel Ferreira, 2. Richard Moody, 3. Zoe Moody, 4. Igor Danilov, 5. Ekaterina Obraztsova, 6. Ren Hirayama, 7. Marcelo de la Fuente, 8. Sandra Chapman, 9. Rafaela Garbin, 10. Isadora Gerheim, 11. Natália Fri, 12. Fernanda Deantoni, 13. Markus Lambertz, 14. Tyler Lyson, 15. Walter Joyce, 16. Daniel Lawver, 17. Natália Benevenuto, 18. Carina Figueired, 19. Jessyca Rezende, 20. Natan Brilhante, 21. Alfredo Holley, 22. Evangelos Vlachos, 23. Juliana Sterli, 24. J. Alfredo Holley, 25. Anieli Pereira, 26. Tomasz Szczygielski, 27. Thiago Fiorillo Mariani, 28. Masataka Yoshida, 29. Edwin Cadena, 30. Tepei Sonoda, 31. Pedro Romano, 32. Vincent Gillespie, 33. Gustavo Oliveira



6. Symposium on Turtle Evolution (Tokyo, Japan, May 2018). 1. Haiyan Tong, 2. Wilailuck Naksri, 3. Donald Brinkman, 4. Ren Hirayama, 5. Shigeru Kuratani, 6. Sandra Chapman, 7. Tatsuya Hirasawa, 8. Taichi Kato, 9. Yoshikazu Hasegawa, 10. Jada Ko, 11. Tomasz Szczygielski, 12. Gabriel Ferreira, 13. Martón Rabi, 14. Walter Joyce, 15. Ekaterina Obraztsova, 16. Hikaru Uno, 17. Teppei Sonoda, 18. Chisako Sakata, 19. Hiroki Tanaka, 20. Hirokazu Tokugawa, 21. Konami Ando, 22. Elena Syromyatnikova, 23. Takashi Oda, 24. Igor Danilov, 25. Rafaela Garbin, 26. Dai Suzuki, 27. Markus Lambertz, 28. Yuichiro Nishioka, 29. Masataka Yoshida, 30. Ingmar Werneburg, 31. Anna Gnetneva, 32. Hideki Endo, 33. Akio Takahashi, 34. Torsten Scheyer, 35. Mohamed Abdel Gawad, 36. Tai Kubo, 37. Yasuhisa Nakajima, 38. Julien Claude