
EVOLUTION OF TURTLE

Author:- Dr. Shashi Kanta
Associate Professor, Department of Zoology
S.S.M. College, Dinanagar (Gurdaspur)

INTRODUCTION

The tale of all turtles really starts here, in South Africa - albeit in a totally different world. Around quite a while back, on the shores of the old Karoo ocean, among hills and bushes of a semi-dry Gondwana, carried on with a little reptile called *Eunotosaurus africanus*.

Eunotosaurus africanus.

This little reptile had a one of a kind trademark: its ribs bended in reverse and were particularly thick, framing a defensively covered vault under its skin. Eunotosaurus didn't have a clue about this, yet it was to turn into the predecessor of all turtles, ocean turtles and reptiles.

Relatives of Eunotosaurus are called pantestudines, of which current turtles are a part. In any case, we actually have far to go before we arrive at today...

For what reason did the shell develop?

Around 40 million years after the fact another reptile, called *Odontochelys semitestacea* (signifying "toothed turtle with a portion of a shell"), had developed along the shoreline of shallow seas in what is today China.

Odontochelys semitestacea.

Odontochelys was nothing similar to the turtles we know and love today. It had teeth, not a nose. It had paws, however not flippers. Furthermore, most perceptibly, it didn't have an upper carapace. In any case, it had developed one thing that is normal for turtles: a plastron - its base shell.

It is intriguing that the lower covering of the turtle developed before its top carapace, yet it checks out assuming you ponder the sort of hunters that would have gone after the early turtles - sharks and other trap hunters striking from underneath.

Enter Proganochelys. This animal, called the "monster turtle" strolled the deserts of the old mainland of Laurasia, between current Thailand and Germany. Like its predecessor Odontochelys, it had the base plastron shield plates, however as a land tenant, it required protective layer from a higher place - particularly as the world it meandered was presently occupied by dinosaurs.

Proganochelys advanced upper covering to safeguard itself from these dinosaurs. It had hard neck spikes, protected leg plates and heavily clad spikes on its tail that it could swing like a club. Yet, it had likewise developed highlights that actually stay in most current turtles - a strong, hard carapace and an innocuous, curved mouth.

These turtle-like precursors are classified "stem turtles", the gathering that separated into the turtle, reptile and ocean turtle bunches we perceive today. This advancement was driven by the separating of the old supercontinents and the confinement of the seas and their flows.

Placodonts - the turtles that weren't turtles

During the Triassic, simultaneously as the early turtle precursors were being conceived, a "bombed try" of development happened. These animals were called placodonts - and albeit not connected with turtles, they truly do assume a part in their story.

Their developmental way is like that of turtles. Placodonts began as marine reptiles, for example, Placodus, which were like the present marine iguanas. Their enormous size was sufficient to forestall predation by early sharks.

As additional hunters arose, placodonts started developing shielded plates, however not made of bone as a turtle's shell is. Types of placodont, as Psephoderma, had thick shielded plates and chased little molluscs in shallow waters. Others, as Henodus, created teeth that permitted channel taking care of as found in the present baleen whales.

Placodonts didn't endure the Triassic-Jurassic termination occasion around quite a while back, a volcanically-prompted time of environmental change that brought about the eradication of a portion of the world's species and permitted the dinosaurs to turn into the predominant land

creature. The elimination of the placodonts opened their shallow-water specialty, and permitted present day turtles to thrive.

The first turtles

As the antiquated mainland of Laurasia split up, the southern piece of what we would today perceive as the USA was low-lying, to a great extent canvassed in bitter, pungent marshes. Around a long time back, the land-staying stem turtles began to carry on with semi-oceanic lives, ultimately developing into completely sea-going freshwater and saltwater turtle species.

A large portion of these turtles would keep on fostering the protective layer plating of their Proganochelys precursor, smoothing out it. They lost the neck and tail defensive layer, yet their plastron reinforcement created to safeguard them from marine hunters, covering their necks and keeping them from withdrawing their heads like a turtle can.

Their appendage defensive layer was lost, and their paws and appendages advanced into the flippers we see today - all things considered, they at this point not expected to stroll ashore. The most established fossil of an animal varieties that scientistss concur is a "ocean turtle" and not a "stem turtle" is *Desmatochelys padillai*, the most established realized ocean turtle.

Desmatochelys padillai - the primary realized ocean turtle.

The old leatherbacks

In the shallow oceans that covered quite a bit of North America a long time back, a goliath had developed. This goliath was called Archelon, and at 4m long with a flipper range of 4.9m it was by a wide margin the biggest turtle species that has at any point lived.

Archelon was a Dermocheloid or a "skin-shelled turtle". It had a structure of hard plates, areas of strength for and muscles - a blend that would permit it to be quick and sufficiently able to chase goliath squid.

Predecessors of Archelon emanated across the globe, and for a period they were the predominant huge creature of the sea. These Dermocheloids expanded, exploiting the holes left in biological

systems toward the end-Cretaceous termination (correct, the one that killed the dinosaurs) and started to possess specialties in the climate that we don't ordinarily connect with ocean turtles today - *Alienochelys* had wide, smashing plates that it used to crush shellfish and squid (a similar taking care of procedure utilized by many beams today), and *Ocepechelone*, which had a long cylinder molded jaw that it utilized for pull hunting (very much like a Knysna seahorse).

Recreation of *Ocepechelone bouyai*.

As marine warm blooded creatures, similar to dolphins and whales, advanced around quite a while back, the delicate shelled Dermocheloid turtles were completely pursued or outcompeted to elimination. All with the exception of one - the leatherback turtle (*Dermochelys coriacea*). The leatherback's interesting way of life of benefiting from jellyfish, an extremely supplement unfortunate food source, avoided them with regards to the transformative contest and assisted them with getting by - the quick digestion systems of enormous well evolved creatures couldn't blossom with jellyfish alone.

Antiquated hard-shells

While the old progenitors of the leatherback were differentiating - different gatherings of stem turtles kept on idealizing a shielded shell, at last adjusting to a smoothed out body plan where the plastron and carapace were areas of strength for both light.

Ctenochelys acris, a 80 million-year-old species from the southern USA, is a probable progenitor to all current ocean turtles, aside from the leatherback. It has attributes of current ocean turtles and freshwater snapping turtles - for instance it had enormous back flippers which would have been utilized for drive, something present day ocean turtles don't have.

The first "valid" shelled ocean turtles arose around quite a while back. These turtles are called Chelonian turtles - basically signifying "shelled turtles". This reinforcement permitted them to endure savage marine hunters, including sharks, lepidosaurs and in the end warm blooded creatures. This talent for endurance is the reason we actually see six Chelonian species alive today, while pretty much every other kind of ocean turtle has become terminated. The turtles that arose in this time are basically the same as the species alive today.

Around a long time back, the earth went through an environmental change occasion called the Eocene-Oligocene Transition where the world went from extremely warm to very cool, with the ice covers transforming. The progenitor of current green ocean turtles (*Chelonia mydas*) right now was probable a generalist omnivore, however limited changes in environment impacted its food source, so we see specific taking care of procedures developing: green growth brushing green turtles and savage, ocean cucumber-hunting flatback turtles (*Natator depressus*). Both these turtles are still practically omnivores, however their conduct directs their eating regimen.

The other four present day ocean turtles - blockheads (*Caretta*), hawksbills (*Eretmochelys imbricata*), olive ridleys (*Lepidochelys olivacea*) and Kemp's ridleys (*Lepidochelys kempii*) - are firmly related, reasonable originating from a savage normal precursor that firmly looked like the blockhead turtle. Like the green and flatback turtles, the distinctions in diets and taking care of techniques utilized by these four species proposes that speciation was because of natural changes that impacted their food sources.

Every one of the four of these ocean turtles are "actually" omnivores, albeit truly they stick to rather unbending weight control plans. Blockheads have strong jaws and noses for squashing molluscs and shellfish, hawksbills can live on the whole off of ocean wipes and olive ridleys feed on a mix of jellyfish, fish eggs, echinoderms and shrimp. Kemp's ridley turtles might be the main really omnivorous ocean turtle, benefiting from molluscs, jellyfish, fish and kelp, yet adolescents have unique variations for hunting crabs.

Current ocean turtles

In the beyond 3 million years, the substance of the earth has changed. Elevating of Central America - already completely lowered under the ocean, removing populaces of turtles in the Pacific and Atlantic seas - and upwellings of cold flows at the Cape of Good Hope and *Tierra del Fuego* (southernmost tip of South America) forestall a significant number of these glow dependant creatures from adjusting the tips of the mainlands. This disengagement of the seas, while not far enough in that frame of mind to cause speciation, has impacted the worldwide ocean turtle genetic stock.

With the Palaeogene period 2.5 quite a while back, ice ages started. This cooling of polar waters and the synchronous shutting of a considerable lot of the maritime interfacing courses segregated turtle populaces..

Blockhead turtles have been generally impacted - today there are a few hereditarily unmistakable populaces of blockheads, most outstanding while contrasting Pacific and Atlantic blockheads - we are watching the beginning phases of speciation. Green turtles are likewise pursuing a comparative direction, one that is more noticeable because of their similarly more different shell markings. Albeit green turtles are perceived as one animal groups, a fast hunt uncovers the discussion encompassing them and the names "Agassizi turtle", "dark ocean turtle" and "Galápagos green turtle" all show up as proposed subspecies.

In later times, people have been the critical main thrust in the hereditary qualities of ocean turtles, because of enormous scope hunting and assortment of turtle eggs for food.

Why Turtles Evolved Shells: It Wasn't for Protection

The hard designs began framing before the long rule of the dinosaurs, and they did as such for a particular reason.

Turn back the clock to quite a while back, not long before the beginning of the dinosaur time. Excursion to what is presently South Africa, and advance toward a stream bank. Then, at that point, stand by. In the event that you're fortunate, you could see a little, hand-sized animal jabbing its head out of the mud. It seems to be a fat reptile, with swelling flanks and stocky legs. However, assuming you figured out how to snatch it and flip it over, you'd observe that its flanks are swelling on the grounds that its ribs are particularly wide, expansive, and level, building up its undersides. It's practically similar to the little animal has a portion of a shell.

It was found in 1892 and overlooked for very nearly 100 years. In any case, by concentrating on the numerous fossils of this mysterious reptile, Tyler Lyson from the Denver Museum of Nature and Science has conceived an entrancing novel thought regarding turtle starting points. He believes that their famous shells advanced not really for safeguard, but rather for digging. They

moored the strong arm strokes expected to move soil and sand. Before turtles became invulnerable strolling posts, they were proficient burrowers.

For very nearly a really long period, scientists squabbled over how turtles got their shells — a discussion nearly as sluggish and trudging as the actual animals. Scientists generally contended that the shells advanced from hard scales called osteoderms, which are likewise answerable for the covering of crocodiles, armadillos, and numerous dinosaurs. These scales basically extended to combine with the ribs and spine, making a strong covering. However, formative scientists conflicted. By concentrating on current turtle incipient organisms, they derived that the shell advanced from ribs, which expanded out and ultimately joined together.

It didn't help that for quite a while, the most established realized turtle was an animal called Proganochelys, which previously had a completely evolved (and extremely spiky) shell, meaning it couldn't inform us anything concerning how that structure originally emerged.

Everything changed in 2008, when Chinese scientists found a 220-million-year-old turtle with a shell that covered only its paunch and not its back. They called it *Odontochelys semitestacea* — in a real sense, the "toothed turtle in a half-shell." It was as lovely a moderate fossil as they might have expected. Furthermore, strikingly, it had no osteoderms by any stretch of the imagination. It did, notwithstanding, have exceptionally expansive ribs.

The fossil record of early stem-turtles

In this segment, we audit the fossil record of early stem-turtles, continuing from the putative Permian stem-turtle Eunotosaurus to different Triassic taxa that are progressively more firmly connected with the crown-bunch Testudines (Joyce et al. 2004; Lyson et al. 2010; Joyce 2015; Schoch and Sues 2015). Phylogenetic investigations found Eunotosaurus, Pappochelys, Eorhynchochelys and Odontochelys as progressive sister-taxa to Testudinata as characterized by Joyce et al. (2004).

Eunotosaurus

Eunotosaurus africanus is an up to 30 cm long reptile from the center Permian (Capitanian; c. 259-265 Ma) Tapinocephalus Assemblage Zone of South Africa and most likely corresponding layers in Malawi. It has a proportionately little, short-snouted skull and a foreshortened, transitionally wide trunk encased by anteroposteriorly expanded, marginally covering ribs. In his unique portrayal of *Eunotosaurus*, Seeley (1892) currently looked at the stretching of its dorsal vertebrae and its wide trunk ribs in to the comparing highlights in turtles yet wondered whether or not to construe a cozy relationship. Watson (1914) first unequivocally theorized *Eunotosaurus* as a turtle forerunner. He referred to the low number (nine) of dorsal vertebrae, the extension of their centra, and particularly the unmistakable trunk ribs, which he contrasted with the widened ribs in the undeveloped organisms of surviving turtles. Cox (1969) restudied generally material then, at that point, alluded to *Eunotosaurus* and excused the skeletal similitudes to turtles as 'simply united.' Gow (1997) detailed extra examples that gave significant new physical information, particularly on the skull. He speculated parareptilian affinities for *Eunotosaurus*. Later examinations more specifically put *Eunotosaurus* either in Millerettidae (Cisneros et al. 2004) or as the sister-taxon of that clade (Gow 1997; Tsuji and Müller 2009). Lyson et al. (2010, 2013, 2014,) and Bever et al. (2015) restudied the skull and postcranial pivotal skeleton of *Eunotosaurus* utilizing microCT checking and histological examination of postcranial bones.

Nine dorsal vertebrae. Aside from undisputed stem-turtles and crown-turtles, *Eunotosaurus* is the main reptile known to date with a similar low number of dorsal vertebrae. (The quantity of dorsals in *Pappochelys* stays obscure.)

Centra of dorsal vertebrae over two times as long as tall.

Trunk ribs expanded anteroposteriorly, with rib like front and back augmentations of the rib-shaft, which is T-formed in cross over area.

As opposed to these common determined characters in the postcranial pivotal skeleton, the cranial construction of *Eunotosaurus* varies significantly from that of other referred to Triassic stem-turtles as well as most diapsids. Despite the fact that there is an enormous ventral

emargination of the cheek that probably addresses a lower fleeting opening (Gow 1997), it is lined posteriorly by the quadratojugal instead of the squamosal (Bever et al. 2015, fig. 2). This determined condition, wherein squamosal and quadratojugal have changed positions, is somewhere else present just in some parareptiles, for example, owenettids (Reisz and Scott 2002; Cisneros et al. 2004; MacDougall and Reisz 2014). In Eunotosaurus, the squamosal is a swagger as opposed to a four-rayed component as in Pappochelys, Odontochelys and most saurians, and the jugal is wedge-formed, without the back (quadratojugal) process present in numerous diapsids and stem-turtles (Pappochelys, Eorhynchochelys). Bever et al. (2011, 2012) detailed upper worldly openings in an adolescent of Eunotosaurus and deciphered an unpredictable little hole between the parietal, postorbital and squamosal bones of the skull rooftop in a grown-up person as a similar opening. In any case, the opening is covered by an enormous supratemporal in the grown-up and intently looks like unpredictable holes between bones in the transient district of some development phases of millerettid parareptiles (Gow 1972). In the sense of taste, an enormous suborbital fenestra between the ectopterygoid and palatine describes all saurians, including turtles and their Triassic stem-taxa. In Eunotosaurus, these palatal components are in expansive contact, with the obscure proof of a minuscule cut on the left half of the noggin, which was distinguished by Bever et al. (2015) as a suborbital fenestra.

To summarize, the skull of Eunotosaurus, as well as certain postcranial bones, for example, the ilium, more intently look like those in parareptiles than those in stem-turtles or basal diapsids. Regardless of whether Eunotosaurus is viewed as a stem-turtle, its cranial construction couldn't be thought of as tribal to the turtle condition in many regards (worldly district, expansive average rooftop).

The phylogenetic investigation by Bever et al. (2015) found Eunotosaurus at the foundation of Pan-Testudines, the all out clade containing turtles and their stem-taxa (Joyce et al. 2004). In the examinations by Lyson et al. (2013) and Schoch and Sues (2015), Pan-Testudines was put nearest to sauropterygians and lepidosauromorphs. Later examinations by Bever et al. (2015) and Schoch and Sues (2013) recuperated Pan-Testudines in an unsettled polytomy with other significant clades of diapsid reptiles.

Pappochelys

Pappochelys rosinae is a 25-30 cm long reptile from the upper Middle Triassic (Ladinian; c. 237-247 Ma) Erfurt Formation (Lettenkeuper) of Baden-Württemberg (Germany) (Schoch and Sues 2015,). It is known from a few halfway skeletons and various secluded bones. Pappochelys imparts different inferred highlights to testudinatanans including:

Vomer anteriorly curved, outlining huge front fenestra and posterolaterally choked, coming about in a medially extended choana (as in Proganochelys).

Vomers melded along the midline (imparted to crown-bunch turtles yet missing in Proganochelys).

Scapula tall and swagger like (as in Odontochelys and Proganochelys), with adjusted acromial 'process' less noticeably evolved than in Odontochelys and more determined turtles.

Humerus with raised proximal head.

Diminished number of dorsal vertebrae. Pappochelys most likely had eight to ten dorsal vertebrae, tantamount to the condition in Eunotosaurus and in Odontochelys and more determined turtles.

Dorsal vertebral centra prolonged. The centra are equivalent in relative length to those of Odontochelys.

Synapophyses upward adjusted. The blended rib features (synapophyses) on the dorsal vertebrae are upward adjusted, likely limiting rib movement. This element is shared by Odontochelys yet contrasts from the anterodorsally slanted synapophyses in Eunotosaurus (Cox 1969).

Trunk ribs T-formed in cross over segment because of sheet-like expansions foremost and back to the rib-shaft, bringing about a marginally uneven framework in dorsal view (imparted to Odontochelys). Dissimilar to in Eunotosaurus, the ribs don't imbricate.

Trunk ribs more limited and less firmly bended ventrolaterally than in basal amniotes and Eunotosaurus, however more so than in Odontochelys and more determined turtles.

Gastralia vigorous and organized two by two, one for each vertebra and coming up short on an average component. They are boomerang-formed, somewhat unbalanced, and vigorous. Their distal closures need aspects for cartilaginous rib sections, dissimilar to in Eunosaurus. The outside surfaces of the gastralia bear molding made out of equal furrows and edges that end in hard spines distally.

Pubis with unmistakable horizontal cycle. This cycle reached the plastron in Odontochelys, Proganochelys and more determined turtles; it apparently reached the gastralia bin in Pappochelys anteriorly.

The diapsid arrangement of the head of Pappochelys looks like the condition in saurians yet varies from that in more basal diapsid reptiles like Petrolacosaurus and Youngina. The tetradiate setup of the conceivable squamosal is determined comparative with the condition in basal diapsids, similar to its assumed contact with the quadratojugal, the state of the jugal, and the shortfall of a supratemporal bone. These elements are likewise conflicting with recently estimated connections among turtles and parareptiles (Lee 1993; Laurin and Reisz 1997) or among turtles and captorhinid reptiles (Gaffney and Meylan 1988; Gauthier et al. 1988). As in Eunosaurus, all jaw components bear teeth. The accompanying diapsid highlights are available in Pappochelys:

- Squamosal tetradiate, with long slim ventral cycle, as opposed to plate like the squamosal in Captorhinidae or Petrolacosaurus.
- Parietal jumping anteroposteriorly short, oval upper transient fenestra medially.
- Suborbital fenestra advanced.
- Interclavicle cruciform, with huge foremost cycle with adjusted front edge (shared by a few clades of diapsid reptiles).
- Femur with unmistakable fossa between the tibial condyle and the crista tibiofemoralis (shared by turtles).
- Iliac sharp edge with a long back cycle and straight dorsal edge (as in Odontochelys and Proganochelys).

- Metatarsal V unmistakably snared, with a strong average cycle and a little parallel projection (albeit this component has different ontogenetic narratives in saurians and turtles; Joyce et al. 2013a).
- Astragalus and calcaneum fused (as in pareiasaurian parareptiles, lepidosauromorph diapsids, some specimens of Odontochelys, and Proganochelys).

Different creators have deciphered gastralia as antecedents of the more back plastral bones (Jaekel 1915; Goodrich 1930; Romer 1956; Zangerl 1969) however, as of not long ago, there was little proof to help this speculation. Eunotosaurus has sets of slim gastralia lacking horizontal and middle components (Lyson et al. 2013). The cuirass of powerful gastralia in Pappochelys can be deciphered as primarily middle between the matched gastralia in Eunotosaurus and the full grown hard plastron in Odontochelys and more determined turtles.

Eorhynchochelys

Eorhynchochelys imparts some apomorphies to additional determined turtles that are missing in Eunotosaurus and Pappochelys:

- Premaxilla and foremost finish of dentary edentulous, likely covered by a keratinous bill throughout everyday life (as in determined stem and crown turtles).
- Upper transient fenestra missing.
- Brain curves of the storage compartment vertebrae with unmistakably extended apices.
- Trunk ribs broadening horizontally with just slight ventral shape.
- Ischium with a back expansion, looking like the construction where the ischium contacts the hypischium in Odontochelys and more determined turtles.
- Puboischiadic plate with the ischium and pubis solidly stitched together as opposed to approximately joined to one another as in Pappochelys.
- Acromion on scapula more unmistakable than in Pappochelys however not quite as particular as in Odontochelys.

The presence of 12 dorsal vertebrae in *Eorhynchochelys* contrasts from the condition in *Eunotosaurus*, *Odontochelys* and the completely shelled Late Triassic stem-turtles, all of which have less than 10 dorsals. The quantity of dorsal vertebrae in *Pappochelys* can't be laid out in that frame of mind of explained segment yet was most likely somewhere in the range of 8 and 10 (Schoch and Sues 2015). Notwithstanding the shortfall of an upper worldly fenestra, determined elements of the noggin of *Eorhynchochelys* incorporate the combination of the frontals, the proportionately short back locale of the skull table, and the shortfall of a ventral cycle on the squamosal. The unmistakably extended apices of the dorsal brain spines conceivably upheld brain components in life yet these are not safeguarded in the main known example. An elective understanding of these extensions is that they filled in as points of connection for advanced epaxial muscles and tendons between the brain spines.

Odontochelys

Odontochelys semitestacea is additionally from the Upper Triassic (Carnian; c. 227-237 Ma) Wayao Member of the Falang Formation of Guizhou (China) yet was recuperated from a skyline around 7.5 m over the layer yielding *Eorhynchochelys*. The distributed material contains three superbly safeguarded examples that together record the vast majority of the skeleton (Li et al. 2008). Sadly, these significant fossils still can't seem to be portrayed exhaustively.

Odontochelys has a completely evolved plastron (with the exception of a thin middle fontanelle in the holotype of *O. semitestacea*; Fig. 5A) however misses the mark on carapace. Grooves on the plastral components show that these bones bore keratinous scutes. The hyoplastra, hypoplastra and mesoplastra all have along the side anticipating, spine-like cycles. The pelvis incorporates a solidified hypoischium. The dorsal ribs of *Odontochelys* are widened anteroposteriorly and T-formed in cross over segment. They broaden along the side and dorsally as opposed to horizontally and ventrally as in more basal stem-turtles. In spite of the fact that looking like those of *Eunotosaurus*, the ribs don't cover, leaving holes between progressive components, as in *Pappochelys* and *Eorhynchochelys*. Contra Hirasawa et al. (2013), they are not intertwined to the vertebrae, in view of the photos distributed by Li et al. (2008). *Odontochelys* has tight, rectangular hard plates upheld by its dorsal brain spines. Albeit presumably

homologous to the neurals in turtles, these components were not melded to the brain spines and became dislodged after death (Li et al. 2008).

Odontochelys is obviously more determined than Pappochelys, and it imparts the accompanying inferred highlights to Testudinata:

Plastron completely created, involving five sets of plate-like components (hyoplastra, hypoplastra, xiphiplastra and two sets of mesoplastra) as well as the completely incorporated interclavicle (entoplastron) and clavicles (epiplastra). Its bones are thick, level and solidly stitched to one another. The presence of two sets of mesoplastra has somewhere else been recorded exclusively in the basal testudinatan *Proterochersis* (Szczygielski and Sulej 2013).

The entoplastron has advanced anterolateral features for the contact with the epiplastra, which are adjusted upward as in the basal testudinatan *Proganochelys*.

Forelimb extraordinarily longer and more hearty than the rear appendage. The front and rear appendages in *Eorhynchochelys* are pretty much equivalent long.

A hardened hypischium is connected to the back closures of the ischia, as in *Proganochelys* and more determined turtles.

Pubis and ischium structure an inflexible hard plate.

Proterochersis

Proterochersis robusta, from the lower part of the Upper Triassic (Norian; c. 208-227 Ma) Löwenstein Formation of Baden-Württemberg (Germany) (Fraas 1913), is the most seasoned known and most basal testudinatan. Szczygielski and Sulej (2013) distinguished two extra taxa, *Proterochersis porebensis* from the Upper Triassic (Norian) Zbaszynek Beds of Poland and *Keuperotesta limendorsa* from the lower part of the Upper Triassic (Norian) Löwenstein Formation of Baden-Württemberg. Both contrast from *P. robusta* in highlights of the carapace. Joyce (2014) synonymized *Keuperotesta* with *Proterochersis* however held its sort species as substantial.

Proterochersis is as of now known exclusively from its hard shell and pelvic support. The shell accomplished a length of around 40 cm and is exceptionally domed, in contrast to the dorsoventrally to some degree smoothed shell of Proganochelys and similar to the condition in surviving turtles with overwhelmingly earthbound propensities. The epiplastral processes don't contact the nuchal bone of the carapace dorsally. The carapace of Proterochersis incorporates a nuchal bone and fringe components. Its plastron has two sets of mesoplastra, as in Odontochelys yet dissimilar to in Proganochelys. The pelvic bones are suturally connected to the shell, a condition that developed freely in pleurodiran turtles (Joyce et al. 2013b).

Proganochelys

Baur (1887) first named *Proganochelys quenstedti* in a reference based on a characteristic shape of the inside surface of a shell from the Upper Triassic (Norian) Löwenstein Formation (Stubensandstein) of Baden-Württemberg (Germany). Quenstedt (1889) later portrayed a similar example under the name *Psammochelys keuperina*. Jaekel (1914, 1915-16) depicted significantly more complete skeletal remaining parts from the reciprocal Arnstadt Formation close to Halberstadt in Saxony-Anhalt (Germany) under the name 'Stegochelys' (engrossed and later renamed Triassochelys) *dux*. Besides, extra examples of *Proganochelys quenstedti* were recuperated from the Löwenstein and Trossingen arrangements of Baden-Württemberg. In light of a monographic correction of every accessible fossil, Gaffney (1990) alluded the whole material to a solitary taxon, *Proganochelys quenstedti*. Skeletal remaining parts of firmly related stem-turtles from the Upper Triassic (Norian) Huai Hin Lat Formation of Thailand (*P. ruchae*; de Broin 1984) and the Upper Triassic (Norian) Fleming Fjord Formation of East Greenland have likewise been alluded to *Proganochelys* (Joyce 2014). Fragmentary bones of a stem-turtle, *Chinlechelys tenertesta*, were accounted for from the Upper Triassic (Norian) Bull Canyon Formation of New Mexico (Joyce et al. 2009). Later Joyce (2014) synonymized *Chinlechelys* with *Proganochelys* yet held its sort species as legitimate.

Proganochelys has a completely evolved hard shell with the carapace and plastron associated by a hard extension on one or the other side. Its shell is more leveled dorsoventrally than that of *Proterochersis*, and the pelvic support isn't stitched to it. *Proganochelys* needs negligible teeth however its vomer and palatine bear denticles. It holds a lacrimal bone. The pterygoid misses the

mark on cross over rib, not at all like in *Odontochelys*. The basicranial joint between the basisphenoid and pterygoid is open, as in more basal stem-turtles and most different reptiles however dissimilar to in more determined testudinans. The storage compartment ribs articulate between centra as opposed to on them as in more basal stem-turtles and different amniotes.

Palaeochersis

Palaeochersis talampayensis is known from one genuinely complete skeleton and other skeletal remaining parts from the Upper Triassic (Norian; 213-227 Ma) Los Colorados Formation of La Rioja area (Argentina) (Rougier et al. 1995; Sterli et al. 2007; Joyce 2012). It has a completely evolved hard shell, which achieved a length of 50 cm. The epiplastral processes most likely comprehensively reached the carapace. Albeit the skull of *Palaeochersis* looks like that of *Proganochelys* in the maintenance of lacrimal and supratemporal bones, it contrasts from that of the previous in different determined highlights, for example, the shortfall of denticles on the vomer, the combination of the basispterygoid joint, and the tight contact between the paroccipital cycle and the quadrate and squamosal. The shell of *Palaeochersis* contrasts from that of *Proterochersis* within the sight of foremost supramarginals and the shortfall of postanal scutes. The quantity of mesoplastra in *Palaeochersis* is dubious.

Advancement of the turtle body plan

During the last 10 years, the disclosures of the Triassic stem-turtles *Pappochelys*, *Eorhynchochelys* and *Odontochelys*, alongside reconsideration of the center Permian *Eunotosaurus*, have archived different morphological stages in the arrangement of the turtle body plan. Following Lyson et al. (2013, 2014), *Eunotosaurus* is utilized as the underlying stage in this groundbreaking grouping. In late many years, transformative situations have gotten a lot of analysis for their absence of exact thoroughness. By and large, specialists frequently neglected to make a reasonable qualification between recreating the developmental history of a gathering of life forms and creating adaptationist stories to make sense of the morphological changes saw inside that gathering. Nonetheless, Gans (1989) contended that painstakingly planned situations are useful for figuring out the developmental history of organic peculiarities. He noticed that situations should supplement cladograms, which give a testable verifiable structure and subsequently should be grown first. Fossils are innately fragmented archives of wiped out living

things and should be deciphered considering surviving creatures. Formative information on the last option give an amazing asset to assessing transformative situations. In this part, we analyze elements of the body plan of terminated stem-turtles with embryological data on the development of homologous designs in surviving turtles.

Carapace

Embryological proof

The carapace of turtles is exceptional among amniotes in the two its construction and improvement. It contrasts even from the surprisingly turtle-like dermal trunk protection in the Late Triassic placodont reptile Henodus where the vertebrae, ribs and gastralia were probably ligamentously connected to yet are not coordinated into the carapace (Westphal 1975).

The overall situation included the development of the carapace in turtles through combination of dermal hard plates (osteoderms) to the hidden ribs (Versluys 1914; Lee 1993, 1996; Joyce et al. 2009; see Rieppel (2015) for a magnificent verifiable review). It conjured a turtle forerunner with a thick front of dorsal reinforcement components, which solidified in the dermis (named 'Spotted Ancestor' by Rieppel). Lee (1993, 1996, 1997) contended that such a forerunner could be found among the center to late Permian pareiasaurian parareptiles, which he viewed as the clade containing turtles. The dorsal osteoderms of the 'Spotted Ancestor' would ultimately meld into bigger plates that thusly became intertwined to the fundamental ribs. The phylogenetic examinations by Lee (1997) and Tsuji (2013) without a doubt propose an expansion in the intricacy and degree of the dorsal dermal protection from basal pareiasaurs, for example, Bradysaurus to determined ones like Anthodon. Nonetheless, this speculation doesn't make sense of how the dermal covering became intertwined to the hidden ribs. It likewise doesn't represent the place of the shoulder support inside the shell in turtles as opposed to outside the rib confine as in different amniotes. This drove Watson (1914) and others to hypothesize a regressive shift of the shoulder support during ontogeny. In any case, Ruckes (1929) and Burke (1991) noticed that the general place of the shoulder support doesn't really change during ontogeny however that the creating trunk ribs develop over the shoulder support.

Once fully developed, ossification of the cartilaginous rib precursors commences with the deposition of a sleeve of periosteal bone. Anterior and posterior extensions expand from, and remain continuous with, the periosteal sleeves of the ribs. Thus, the costal plates develop as extensions of the perichondral ossification of the ribs, not dermal bones. Similarly, the neural plates grow from the perichondral bone surrounding the dorsal neural arches. Thus, the neurals and costals are entirely endoskeletal in origin (Hirasawa et al. 2013).

In the stem-turtle *Odontochelys*, the trunk ribs do not fan out anteroposteriorly (as they do in many derived turtles) but converge slightly toward the mid-trunk region (Li et al. 2008). Nagashima et al. (2007) observed that experimental destruction of the carapacial ridge in embryos of extant soft-shelled turtles suppresses the fanning of the ribs. However, this procedure did not affect the lateral growth of the ribs. Based on these data, the authors argued that the carapacial ridge induces the fanning of the trunk ribs (flabellate pattern) only late in ontogeny and that this developmental step was not yet present in *Odontochelys*.

This work, along with new data on muscle development, led Kuratani et al. (2011) to propose the ‘folding theory’ for the origin of the carapace in turtles. The first developmental step is the axial arrest of the trunk ribs in which the carapacial ridge suppresses the growth of the ribs into the lateral plate domain. As a result, the ribs are proportionately shorter than in other reptiles. The carapacial disc grows independent of the ribs while the body wall is folded underneath it. This infolding of the body wall leads to the ribs extending anteriorly over the shoulder girdle and results in changes in the arrangement of muscles attached to the scapula, which acquire new sites of attachment (Nagashima et al. 2009; Kuratani & Nagashima 2012).

Rice et al. (2015) demonstrated that the processes of carapace development and costal formation differ considerably between extant hard- and soft-shelled turtles. In both groups, however, the carapacial ridge prevents the ribs from extending ventrolaterally into the body wall. Rice and her colleagues underscored the role of this ridge as a signaling centre as a key evolutionary innovation of turtles.

The nuchal, the anteromedian bone of the carapace, develops separately in a two-stage ossification process from all other carapacial elements in extant turtles (Gilbert et al. 2007). It is

now considered homologous to the paired cleithra in more basal amniotes (Lyson et al. 2013), after Vallén (1942) had originally homologized the nuchal with supracleithra, which, however, are elements of osteichthyans that are not present in tetrapods. The nuchal is never lost in turtles; it is even present in the leatherback sea turtle (*Dermochelys coriacea*), which otherwise lacks carapacial elements (Völker 1913). The trapezius muscle originates along the anteroventral surface of the nuchal, providing additional anatomical evidence for homologizing this shell element with the cleithra in other amniotes (Lyson et al. 2013).

Ossification centres of peripherals first occur along the anterior margin of the carapace and, during further growth, appear more posteriorly. These bones form the periphery of the carapace and expand laterally and internally during their growth (Gilbert et al. 2001). The pygal forms as the last peripheral and thus last bony element of the carapace.

Fossil evidence

Unlike *Eunotosaurus*, the stem-turtles *Pappochelys*, *Eorhynchochelys* and *Odontochelys* probably retained limited mobility of the trunk ribs based on the position and structure of the synapophyses and the presence of intercostal spaces. The intervertebral position of the synapophyses typical of turtles is first observed in the basal testudinatans *Proganochelys* and *Proterochersis*, in which the costal plates are already fully.

The costal plates of the carapace in *Proganochelys* and more derived turtles have a layer of cancellous bone sandwiched between an external and an internal layer of cortical bone (Scheyer & Sander 2007). This structural pattern is absent in the broadened ribs of *Pappochelys*; the conditions in *Odontochelys* and *Eorhynchochelys* are still unknown.

A nuchal is first identifiable in *Proterochersis* and *Proganochelys*. Lyson et al. (2013) noted that the dorsal migration of the cleithra and their eventual fusion into the nuchal, along with the loss of the scapular rami of the clavicles, led to a wide separation of these originally closely associated bones and reconfiguration of the shoulder girdle in turtles. Finally, Szczygielski & Sulej (2015) hypothesized that the peripherals, suprapygals and the pygal are most likely to be osteodermal in origin.

Plastron

Embryological evidence

Like the carapace, the plastron is a particularly determined element of turtles. The presence of a full grown hard plastron in *Odontochelys* exhibits that the improvement of the plastron went before that of the carapace in turtles (Li et al. 2008). It is fascinating to take note of that hardening of the carapace lingers behind that of the plastron in surviving turtles (Rieppel 1993) despite the fact that the beginning of the ontogenetic improvement of the two parts of the turtle shell corresponds (Rice et al. 2014). Clark et al. (2001) showed that the plastral bones are shaped by intramembranous solidification of cells got from the brain peak.

The foremost part of the plastron comprises of a couple of anterolaterally arranged epiplastra and the anteromedial entoplastron. Following Parker (1868), most creators have homologized the epiplastra with the clavicles in different tetrapods and the entoplastron with the interclavicle in the last option. Lyson et al. (2013) offered convincing help for this speculation by taking note of that the sternocleidomastoideus muscles join to the epiplastra and entoplastron, similarly as they connect to the clavicles and interclavicle in other surviving tetrapods. The entoplastron and epiplastra are quick to harden during the ontogenetic improvement of the plastron (Rieppel 1993; Gilbert et al. 2001). Bone buildups with various hard spicules structure along the horizontal edges of the ventral mesenchyme and develop medially, ultimately framing hard plates. Cuvier (1817) recommended that the plastron of turtles compares to the sternum in different tetrapods. Rice et al. (2014) showed that the relative position and timing of the plastral buildups to be sure matches those of the antecedents of the sternal ligaments in birds and mice. Be that as it may, the buildups in the ventral mesenchyme of turtle undeveloped organisms resolve to bone arrangement and thus stifle the improvement of sternal ligaments.

The plastron of crown turtles coordinates parts of the dermal pectoral support (clavicles and interclavicle, dark) and combined gastralia (dark), which can in any case be followed in the undeveloped organism of *Chelydra serpentina* displayed here. Figure altered from Rieppel (1993). Scale bar addresses 2 mm.

The more back bones of the plastron have for some time been viewed as homologous to the gastralia in different amniotes (Zangerl 1939). Right off the bat being developed, these plastral components are addressed by bunches of hard spicules. Gilbert et al. (2007) gave histochemical proof recommending that the gastralia in the American croc (*Alligator mississippiensis*) are gotten from brain peak cells, similar as the back plastral bones in turtles. Notwithstanding, the gastralia of the gator create inside mesenchyme remotely nearby the stomach muscle structure (Vickaryous and Hall 2008).

Fossil proof

Pappochelys has a ventral arrangement of firmly pressed sets of gastralia. These gastralia are strong, proportionately significantly longer than in different amniotes and there are no average components, in contrast to in different reptiles. Their distal finishes are much of the time bifurcated or brush-like. Histological assessment showed that the gastralia in Pappochelys are single components as opposed to the consequence of combination of more modest, more thin bones (Schoch et al. 2015). Individual gastralia fluctuate impressively in shape. Furthermore, there is territorial separation of these bones, with straightforward pole like gastralia in the front locale of the storage compartment and more back ones that are wound along their long tomahawks.

Li et al. (2014) outlined a couple gastralia in *Eorhynchochelys* that look like those in Pappochelys, yet the game plan of these bones isn't clear as the main known skeleton of this stem-turtle is uncovered in dorsal view.

Odontochelys records the earliest appearance of a total hard plastron in the turtle heredity. It has the full supplement of plastral bones present in additional determined turtles with the option of two sets of mesoplastra. The plastral components structure along the side expanding projections that end in hard spikes.

Adjustment of the storage compartment

In Eunotosaurus (Cox 1969; Lyson et al. 2013, 2014; Joyce 2014) and the Triassic stem-turtles coming up short on a total hard shell, the foreshortening of the storage compartment is related with widened ribs and extended vertebral centra. The ribs are not as expansive anteroposteriorly as the costal plates in the carapace of additional determined turtles with full grown hard shells yet they as of now possess a more dorsal situation than in different amniotes.

Eunotosaurus has 10 dorsal vertebrae (Lyson et al. 2013), in contrast to the larger number (14-30) in most different reptiles (Müller et al. 2010). Pappochelys likely has something like 10 dorsals yet the specific number of its cervical vertebrae is at this point unclear. Odontochelys, Proganochelys, and most more inferred turtles have 8 cervical and 9 dorsal vertebrae. Just Eorhynchochelys is strange in the ownership of 9 cervicals and 12 dorsals.

Odontochelys varies from Pappochelys in having ventrolaterally less bended ribs, bringing about a dorsoventrally more leveled trunk. In Eunotosaurus, the ribs are significantly longer than in any of the Triassic stem-turtles and unequivocally bend ventrolaterally (Cox 1969; Lyson et al. 2014). They are likewise more extended anteroposteriorly than in Pappochelys, Eorhynchochelys and Odontochelys, and, dissimilar to in the last taxa, posteriorly cross-over progressive ribs for a lot of their length, leaving no space for intercostal muscles. The distal closures of the ribs in Eunotosaurus are obtuse and bear features for the connection of cartilaginous costosternal sections as in different reptiles (Lyson et al. 2014), recommending the presence of a probably cartilaginous sternum.

In many amniotes, the ribs and stomach muscles act in show to work with breath and balance out the storage compartment (Brainerd and Owerkowicz 2006). The widening of the storage compartment ribs and attending loss of intercostal muscles in the turtle genealogy dispensed with development and compression of the rib confine for relaxing. All things being equal, turtles developed a one of a kind respiratory framework that includes two sets of opposing muscles, the transversus abdominis muscle and the obliquus abdominis muscle (Gans and Hughes 1967; Landberg et al. 2003). In many amniotes, these muscles embed on the interior (instinctive) surfaces of every dorsal rib. In turtles, be that as it may, they embed just on the front and back

dorsal ribs and not on the mid-dorsal ribs. Lyson et al. (2014) showed that this particular example of addition was at that point present in Eunosaurus.

In Pappochelys, adjustment of the storage compartment likewise elaborate its ventral crate of firmly pressed sets of hearty gastralia, much the same as the condition in sauropterygian reptiles (Robinson 1975). Its gastralia are proportionately significantly longer than in different amniotes. Almost certainly, the gastralia bin in Pappochelys, along with the foreshortening of the storage compartment locale, would have extraordinarily limited stomach adaptability and safeguarded the underside.

Palaeobiology of stem-turtles

The shell in surviving turtles serves overwhelmingly as security for the creature (Zangerl 1969; Magwene and Socha 2012). Rieppel and Reisz (1999) contended that it developed at first in water-abiding stem-turtles since sea-going hunters would likely go after their prey from underneath. Moreover, Rieppel (2013) recommended that the plastron in Odontochelys might have filled in as bone counterbalance for lightness control and that the ventral place of this weight in the storage compartment locale would be hydrodynamically worthwhile for this reason. The event of Eorhynchochelys and Odontochelys in marine layers seems, by all accounts, to be predictable with a sea-going beginning of the turtle shell. The appendage extents of Odontochelys relate to those of present-day turtles that live in stale or little waterways (Rieppel 2015). Notwithstanding, Joyce (2015) contended that the short proximal phalanges of Odontochelys propose that this stem-turtle was more earthly, maybe essentially living in muggy regions. The presence of stays of land plants in the layers from which Eorhynchochelys and Odontochelys were recuperated shows that these stores most likely didn't frame a long way from land. Subsequently, all things considered, these stem-turtles lived along the coast as opposed to in the vast ocean (Li et al. 2008, 2012).

The event of Pappochelys in lacustrine sedimentary layers could be deciphered as extra proof for an amphibian beginning of the turtle body plan. Nonetheless, histological work exhibited that bones of this stem-turtle miss the mark on changes (for example pachyostosis) normally connected with an overwhelmingly oceanic method of life (Schoch et al. 2015). Moreover,

fossils of this stem-turtle are tracked down along with the skeletal remaining parts of a significant variety of earthbound tetrapods (Schoch and Seegis 2015). Most examples of Eunosaurus have been recuperated from layers kept on mainland floodplains with transient waterways (Lyson et al. 2012).

Gaffney (1990) recreated Proganochelys as semi-sea-going dependent especially upon the depositional climate in which its remaining parts were saved. Notwithstanding, Joyce and Gauthier (2004) contended that this basal testudinatan was likely earthly in view of the general extents of its forelimbs. The presence of osteoderms on the neck, tail and appendages and the decreased phalangeal includes in the manus and pes of Proganochelys offer extra help for their understanding. Scheyer and Sander (2007) explored the microstructure of shell components of Proganochelys and Proterochersis. They found that these pitifully vascularized bones have advanced outside and inward cortical layers, much as in surviving earthly turtles. This histological picture contrasts from that for shell components in sea-going turtles, which regularly are more vascularized and have diminished cortical layers. Scheyer and Sander (2007) concurred with Joyce and Gauthier (2004) that Proganochelys and Proterochersis were earthly creatures.

Lyson et al. (2015) presented a convincing defense that Eunosaurus was fossorial. The shoulder support and forelimb show highlights predictable with this surmised movement, including the presence of a huge deltopectoral peak on the humerus, the presence of an unmistakable olecranon process on the powerful ulna, and the enormous, spatulate unguis phalanges of the manus. Lyson et al. (2014) deciphered the expanded, covering ribs of Eunosaurus as giving inflexibility to the foreshortened trunk, which would give a steady premise to utilizing the forelimbs for scratch-digging. In his examination of widened ribs in specific surviving types of well evolved creatures, Jenkins (1970) contended that adjustment of the storage compartment is significant for the adequacy of forelimb use during digging and different exercises. The ribs and thick intercostal muscles assist with giving the imperative dependability.

Lyson et al. (2014) recreated Eunosaurus as tunneling to make cover yet fundamentally searching over the ground, tantamount to the propensities for surviving gopher turtles. Moreover, the creators gathered that fossoriality was a significant consider the early development of the

turtle body plan. In view of histological information, Schoch et al. (2013) placed that the Middle Triassic Pappochelys had a land and/or water capable and potentially fossorial method of life. The at present accessible data proposes that the most seasoned completely shelled stem-turtles had overwhelmingly earthbound propensities.

CONCLUSION

New disclosures of early stem-turtles and late investigations of the ontogenetic advancement of the shell in surviving turtles have prompted reexamination of the beginning of the turtle shell, the critical demonstrative component of Testudinata. The earliest stem-turtles actually come up short on carapace and plastron however as of now have foreshortened trunks with expanded ribs and stretch dorsal vertebrae. The Middle Triassic Pappochelys has a ventral crate containing sets of strong gastralia. The early Late Triassic Odontochelys is the most established known stem-turtle with a completely evolved plastron yet misses the mark on complete carapace. The Late Triassic basal testudinatan, best recorded by Proganochelys, have completely evolved hard shells with carapace and plastron. The developmental directions in the arrangement of the shell in stem-turtles intently track the ontogenetic directions in surviving turtles. Late embryological research has shown that the costal and brain plates of the carapace are solely endoskeletal in beginning. The carapacial edge in turtle undeveloped organisms directs the parallel as opposed to ventrolateral development of the storage compartment ribs as well as their regularly fan-formed course of action. The last option brings about the place of the shoulder support inside the carapace in turtles. The nuchal component of the carapace is homologous to the cleithra in different tetrapods. The plastron contains the homologues of the clavicles and interclavicle in different tetrapods anteriorly and plates that are most likely homologous to the gastralia more posteriorly. The fossil record shows that the improvement of the turtle shell occurred in numerous means more than great many years. Almost certainly, this change happened in non-amphibian stem-turtles. The diapsid affinities of turtles, long estimated based on atomic information, have gotten morphological help from the unambiguously diapsid cranial design in the stem-turtle Pappochelys.

REFERENCES

- Baur, G. 1887. Über den Ursprung der Extremitäten der Ichthyopterygia. Jahresberichte und Mitteilungen des oberrheinischen geologischen Vereins, 20, 17– 20.
- Bever, G. S., Lyson, T., Field, D. J. and Bhullar, B.-A. S. 2015. Evolutionary origin of the turtle skull. *Nature*, 525, 239– 242.
- Bever, G. S., Lyson, T., Field, D. J. and Bhullar, B.-A. S. 2014. The amniote temporal roof and the diapsid origin of the turtle skull. *Zoology*, 119, 471– 473.
- Bhullar, B. A.-S. and Bever, G. S. 2009. An archosaur-like laterosphenoid in early turtles (Reptilia: Pantestudines). *Breviora*, 518, 1– 11.
- Bojanus, L. H. 1819–21. *Anatome Testudinis Europaeae*. Zawadski, Vilnius, 178 pp.
- Brainerd, E. L. and Owerkowicz, T. 2006. Functional morphology and evolution of aspiration breathing in tetrapods. *Respiratory Physiology & Neurobiology*, 154, 73– 88.
- Broin, F. DE 1984. *Proganochelys rucha* n.sp., chélonien du Trias supérieur de Thaïlande. *Studia Palaeocheloniologica*, 1, 87– 97.
- Burke, A. C. 1989. Development of the turtle carapace: implications for the evolution of a novel Bauplan. *Journal of Morphology*, 199, 363– 378.
- Burke, A. C. 1991. The development and evolution of the turtle body plan: inferring intrinsic aspects of the evolutionary process from experimental embryology. *American Zoologist*, 31, 616– 627.
- Carroll, R. L. 1988. *Vertebrate paleontology and evolution*. W. H. Freeman, New York, 698 pp.
- Carroll, R. L. 2013. Problems of the ancestry of turtles. 19– 36. In D. B. Brinkman, P. A. Holroyd and J. D. Gardner (eds). *Morphology and evolution of turtles*. Springer, 577 pp.
- Chiari, Y., Cahais, V., Galtier, N. and Delsuc, F. 2012. Phylogenomic analyses support the position of turtles as the sister group of birds and crocodiles (Archosauria). *BMC Biology*, 10, 65.
- Cisneros, J. C., Damiani, R., Schultz, C., Da Rosa, Á., Schwanke, C., Neto, L. W. and Aurélio, P. L. P. 2004. A procolophonoid reptile with temporal fenestration from the Middle Triassic of Brazil. *Proceedings of the Royal Society B*, 271, 1541– 1546.

- Clark, K., Bender, G., Murray, B. P., Panfilio, K., Cook, S., Davis, R., Murnen, K., Tuan, R. S. and Gilbert, S. F. 2001. Evidence for the neural crest origin of turtle plastron bones. *Genesis*, 31, 111– 117.
- Cohen, K. M., Finney, S. C., Gibbard, P. L. and Fan, J.-X. 2013, updated. The ICS International Chronostratigraphic Chart. *Episodes*, 36, 199– 204.
- Cox, C. B. 1969. The problematic Permian reptile *Eunotosaurus*. *Bulletin of the British Museum (Natural History), Geology*, 18, 165– 196.
- Crawford, N. G., Faircloth, B. C., McCormack, J. E., Brumfield, R. T., Winker, K. and Glenn, T. C. 2012. More than 1000 ultraconserved elements provide evidence that turtles are the sister group of archosaurs. *Biology Letters*, 8, 783– 786.
- Cuvier, G. 1817. *Le règne animal distribué d'après son organization, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Vol. 2: Contenant les reptiles, les poissons, les mollusques, et les annélides.* Deterville, Paris, France, 588 pp.
- deBraga, M. and Rieppel, O. 1997. Reptile phylogeny and the affinities of turtles. *Zoological Journal of the Linnean Society*, 120, 281– 354.
- Field, D., Gauthier, J. A., King, B. L., Pisani, D., Lyson, T. R. and Peterson, K. J. 2014. Toward consilience in reptile phylogeny: miRNAs support an archosaur, not lepidosaur, affinity for turtles. *Evolution & Development*, 16, 189– 196.
- Fraas, E. 1913. *Proterochersis, eine pleurodire Schildkröte aus dem Keuper.* *Jahreshefte der Gesellschaft für Naturkunde in Württemberg*, 69, 13– 90.
- Gaffney, E. S. 1985. The shell morphology of the Triassic turtle *Proganochelys*. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 170, 1– 26.
- Gaffney, E. S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History*, 194, 1– 263.
- Gaffney, E. S. and Meylan, P. A. 1988. A phylogeny of turtles. 157– 219. In M. J. Benton (ed.). *The phylogeny and classification of tetrapods. 1. Amphibians, reptiles, birds.* Clarendon Press, Oxford, 377 pp.
- Gans, C. 1989. Stages in the origin of vertebrates: analysis by means of scenarios. *Biological Reviews*, 64, 221– 268.

- Gans, C. and Hughes, G. M. 1967. The mechanism of lung ventilation in the tortoise *Testudo graeca* Linné. *Journal of Experimental Biology*, 47, 1– 20.
- Gauthier, J., Kluge, A. G. and Rowe, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics*, 4, 105– 209.
- Gilbert, S. F., Loredó, G. A., Brukman, A. and Burke, A. C. 2001. Morphogenesis of the turtle shell: the development of a novel structure in tetrapod evolution. *Evolution & Development*, 3, 47– 58.
- Gilbert, S. F., Bender, G., Betters, E., Yin, M. and Cebra-Thomas, J. A. 2007. The contribution of neural crest cells to the nuchal bone and plastron of the turtle shell. *Integrative & Comparative Biology*, 47, 401– 408.
- Goodrich, E. S. 1916. On the classification of the Reptilia. *Proceedings of the Royal Society B*, 89, 261– 267.
- Goodrich, E. S. 1930. *Studies on the structure & development of vertebrates*. Macmillan, London, 837 pp.
- Gow, C. E. 1972. The osteology and relationships of the Millerettidae (Reptilia: Cotylosauria). *Journal of Zoology (London)*, 167, 219– 264.
- Gow, C. E. 1997. A reassessment of *Eunotosaurus africanus* Seeley (Amniota: Parareptilia). *Palaeontologia Africana*, 34, 33– 42.
- Hedges, S. B. and Poling, L. L. 1999. A molecular phylogeny of reptiles. *Science*, 283, 998– 1001.
- Hill, R. V. 2005. Integration of morphological data sets for phylogenetic analysis of Amniota: the importance of integumentary characters and increased taxonomic sampling. *Systematic Biology*, 54, 530– 547.
- Hirasawa, T., Nagashima, H. and Kuratani, S. 2013. The endoskeletal origin of the turtle carapace. *Nature Communications*, 4, 2107.
- Hugall, A. F., Foster, R. and Lee, M. S. Y. 2007. Calibration choice, rate smoothing, and the pattern of tetrapod diversification according to the long nuclear gene RAG-1. *Systematic Biology*, 56, 543– 563.

- Iwabe, N., Hara, Y., Kumazawa, Y., Shibamoto, K., Saito, Y., Miyata, T. and Katoh, K. 2005. Sister group relationship of turtles to the bird-crocodylian clade revealed by nuclear DNA-coded proteins. *Molecular Biology & Evolution*, 22, 810– 813.
- Jaekel, O. 1913–14. Über die Wirbeltierfunde in der oberen Trias von Halberstadt. *Paläontologische Zeitschrift*, 1, 155– 215.
- Jaekel, O. 1915–16. Die Wirbeltierfunde aus dem Keuper von Halberstadt. Serie II. Testudinata. *Paläontologische Zeitschrift*, 2, 88– 214.
- Jenkins, F. A. JR 1970. Anatomy and function of expanded ribs in certain edentates and primates. *Journal of Mammalogy*, 51, 288– 301.
- Joyce, W. G. 2015. The origin of turtles: a paleontological perspective. *Journal of Experimental Zoology (Molecular & Developmental Evolution)*, 324B, 181– 193.
- Joyce, W. G. 2014. A review of the fossil record of basal Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History, Yale University*, 58, 65– 113.
- Joyce, W. G. and Gauthier, J. A. 2004. Palaeoecology of Triassic stem-turtles sheds new light on turtle origins. *Proceedings of the Royal Society B*, 271, 1– 5.
- Joyce, W. G., Parham, J. F. and Gauthier, J. A. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *Journal of Paleontology*, 78, 989– 1013.
- Joyce, W. G., Lucas, S. G., Scheyer, T. M., Heckert, A. B. and Hunt, A. P. 2009. A thin-shelled reptile from the Late Triassic of North America and the origin of the turtle shell. *Proceedings of the Royal Society B*, 276, 507– 513.
- Joyce, W. G., Werneburg, I. and Lyson, T. R. 2013a. The hooked element in the pes of turtles (Testudines): a global approach to exploring primary and secondary homology. *Journal of Anatomy*, 223, 421– 441.
- Joyce, W. G., Schoch, R. R. and Lyson, T. R. 2013b. The girdles of the oldest fossil turtle, *Proterochersis robusta*, and the age of the turtle crown. *BMC Evolutionary Biology*, 13, 266.
- Kuraku, S., Usuda, R. and Kuratani, S. 2005. Comprehensive survey of carapacial ridge-specific genes in turtle implies co-option of some regulatory genes in carapace evolution. *Evolution & Development*, 7, 3– 17.

- Kuratani, S. and Nagashima, H. 2012. A developmental basis for innovative evolution of the turtle shell. 279– 300. In R. Asher and J. Müller (eds). From clone to bone: The synergy of morphological and molecular tools in palaeobiology. Cambridge University Press, 387 pp.
- Kuratani, S., Kuraku, S. and Nagashima, H. 2011. Evolutionary developmental perspective for the origin of turtles: the folding theory for the shell based on the developmental nature of the carapacial ridge. *Evolution & Development*, 13, 1– 14.
- Landberg, T., Mailhot, J. D. and Brainerd, E. L. 2003. Lung ventilation during treadmill locomotion in a terrestrial turtle, *Terrapene carolina*. *Journal of Experimental Biology*, 206, 3391– 3404.
- Laurin, M. and Reisz, R. R. 1997. A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society*, 113, 165– 215.
- Lee, M. S. Y. 1993. The origin of the turtle body plan: bridging a famous morphological gap. *Science*, 261, 1716– 1720.
- Lee, M. S. Y. 1996. Correlated progression and the origin of turtles. *Nature*, 379, 812– 815.
- Lee, M. S. Y. 1997. Pareiasaur phylogeny and the origin of turtles. *Zoological Journal of the Linnean Society*, 120, 197– 280.
- Li, C., Wu, X.-C., Rieppel, O., Wang, L.-T. and Zhao, L. J. 2008. An ancestral turtle from the Late Triassic of southwestern China. *Nature*, 456, 497– 501.
- Li, C., Fraser, N. C., Rieppel, O. and Wu, X.-C. 2015. A basal Triassic stem-turtle with an edentulous beak. *Nature*, 560, 476– 479.
- Lu, B., Yang, W., Dai, Q. and Fu, J. 2013. Using genes as characters and a parsimony analysis to explore the phylogenetic position of turtles. *PLoS One*, 8, e79348.
- Lyson, T., Bever, G. S., Bhullar, B.-A. S., Joyce, W. G. and Gauthier, J. A. 2010. Transitional fossils and the origin of turtles. *Biology Letters*, 6, 830– 833.
- Lyson, T., Bever, G. S., Scheyer, T. M., Hsiang, A. Y. and Gauthier, J. A. 2013. Evolutionary origin of the turtle shell. *Current Biology*, 23, 1113– 1119.

- Lyson, T., Schachner, E. R., Botha-Brink, J., Scheyer, T. M., Lambertz, M., Bever, G. S., Rubidge, B. S. and Queiroz, K. DE 2014. Origin of the unique ventilatory apparatus of turtles. *Nature Communications*, 5, 5211.
- Lyson, T., Rubidge, B. S., Scheyer, T. M., Queiroz, K. DE, Schachner, E. R., Smith, R. M. H., Botha-Brink, J. and Bever, G. S. 2015. Fossorial origin of the turtle shell. *Current Biology*, 26, 1887– 1894.
- MacDougall, M. J. and Reisz, R. R. 2014. The first record of a nyctiphuretid parareptile from the Early Permian of North America, with a discussion of parareptilian temporal fenestration. *Zoological Journal of the Linnean Society*, 172, 616– 630.
- Magwene, P. M. and Socha, J. J. 2012. Biomechanics of turtle shells: how whole shells fail in compression. *Journal of Experimental Biology*, 319A, 86– 98.
- Müller, J., Scheyer, T. M., Head, J. J., Barrett, P. M., Werneburg, I., Ericson, P. G. P., Pol, D. and Sánchez-Villagra, M. R. 2010. Homeotic effects, somitogenesis and the evolution of vertebral numbers in recent and fossil amniotes. *Proceedings of the National Academy of Sciences*, 107, 2118– 2123.
- Nagashima, H., Kuraku, S., Uchida, K., Ohya, Y. K., Narita, Y. and Kuratani, S. 2007. On the carapacial ridge in turtle embryos: its developmental origin, function and the chelonian body plan. *Development*, 134, 2219– 2226.
- Nagashima, H., Sugahara, F., Takechi, M., Ericsson, R., Kawashima-Ohya, Y., Narita, Y. and Kuratani, S. 2009. Evolution of the turtle body plan by the folding and creation of new muscle connections. *Science*, 325, 193– 196.
- Osborn, H. F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of Diaptosauria. *Memoirs of the American Museum of Natural History*, 1, 451– 519.
- Parker, W. K. 1868. A monograph on the structure and development of the shoulder-girdle and sternum in the vertebrata. Robert Hardwicke, London, 233 pp.
- Pritchard, A. C. and Sues, H.-D. 2014. Postcranial remains of Teraterpeton hrynewichorum (Reptilia: Archosauromorpha) and the mosaic evolution of the saurian postcranial skeleton. *Journal of Systematic Palaeontology*, 17, 1745– 1765

- Quenstedt, F. A. VON 1889. *Psammochelys keuperiana*. Jahreshefte des Vereins für vaterländische Naturkunde Württemberg, 45, 120– 130.
- Reisz, R. R. and Scott, D. 2002. *Owenetta kitchingorum*, sp. nov., a small parareptile (Procolophonia: Owenettidae) from the Lower Triassic of South Africa. *Journal of Vertebrate Paleontology*, 22, 244– 256.
- Rice, R., Riccio, P., Gilbert, S. F. and Cebra-Thomas, J. 2015. Emerging from the rib: resolving the turtle controversies. *Journal of Experimental Zoology (Molecular & Developmental Evolution)*, 324B, 208– 220.
- Rice, R., Kallonen, A., Cebra-Thomas, J. and Gilbert, S. F. 2015. Development of the turtle plastron, the order-defining skeletal structure. *Proceedings of the National Academy of Sciences*, 113, 5317– 5322.
- Rieppel, O. 1993. Studies on skeleton formation in reptiles: patterns of ossification in the skeleton of *Chelydra serpentina* (Reptila, Testudines). *Journal of Zoology, London*, 231, 487– 509.
- Rieppel, O. 2000. Turtles as diapsid reptiles. *Zoologica Scripta*, 29, 199– 212.
- Rieppel, O. 2013. The evolution of the turtle shell. 51– 61. In D. B. Brinkman, P. A. Holroyd and J. D. Gardner (eds). *Morphology and evolution of turtles*. Springer, 577 pp.
- Rieppel, O. 2012. *Turtles as hopeful monsters: origins and evolution*. Indiana University Press, 206 pp.
- Rieppel, O. and Kearney, M. 2007. The poverty of taxonomic characters. *Biology & Philosophy*, 22, 95– 113.
- Rieppel, O. and Reisz, R. R. 1999. The origin and early evolution of turtles. *Annual Review of Ecology & Systematics*, 30, 1– 22.
- Robinson, J. A. 1975. The locomotion of plesiosaurs. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 149, 186– 332.
- Romer, A. S. 1956. *The osteology of the reptiles*. University of Chicago Press, 772 pp.
- Rougier, G. W., DE LA Fuente, M. S. and Arcucci, A. 1995. Late Triassic turtles from South America. *Science*, 268, 855– 858.

- Ruckes, H. 1929. Studies in chelonian osteology. Part I. The morphological relationships between the girdles, ribs, and carapace. *Annals of the New York Academy of Sciences*, 13, 81– 120.
- Rütimeyer, L. 1873. Ueber den Bau von Schale und Schädel bei lebenden und fossilen Schildkröten als Beitrag zu einer paläontologischen Geschichte dieser Thiergruppe. *Verhandlungen der naturforschenden Gesellschaft in Basel*, 6, 3– 137.
- Scheyer, T. M. and Sander, P. M. 2007. Shell bone histology indicates terrestrial palaeoecology of basal turtles. *Proceedings of the Royal Society B*, 274, 1885– 1893.
- Schoch, R. R. and Seegis, D. 2015. A Middle Triassic palaeontological gold mine: the vertebrate deposits of Vellberg (Germany). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 459, 249– 267.
- Schoch, R. R. and Sues, H.-D. 2015. A new stem-turtle from the Middle Triassic of Germany and the evolution of the turtle body plan. *Nature*, 523, 584– 587.
- Schoch, R. R. and Sues, H.-D. 2015. Osteology of the stem-turtle *Pappochelys rosinae* and the early evolution of the turtle skeleton. *Journal of Systematic Palaeontology*, 16, 927– 965.
- Schoch, R. R., Klein, N., Scheyer, T. M. and Sues, H.-D. 2014. Microanatomy of the stem-turtle *Pappochelys rosinae* indicates a predominantly fossorial mode of life and clarifies early steps in the evolution of the shell. *Scientific Reports*, 9, 10430.
- Seeley, H. G. 1892. On a new reptile from Welte Vreden (Beaufort West), *Eunotosaurus africanus* (Seeley). *Quarterly Journal of the Geological Society of London*, 48, 583– 585.
- Sterli, J., DE LA Fuente, M. S. and Rougier, G. W. 2007. Anatomy and relationships of *Palaeochersis talampayensis*, a Late Triassic turtle from Argentina. *Palaeontographica A*, 281, 1– 61.
- Szczygielski, T. and Sulej, T. 2014. Revision of the Triassic European turtles *Proterochersis* and *Murrhardtia* (Reptilia, Testudinata, Proterochersidae), with the description of new taxa from Poland and Germany. *Zoological Journal of the Linnean Society*, 177, 395– 427.
- Szczygielski, T. and Sulej, T. 2015. The early composition and evolution of the turtle shell (Reptilia, Testudinata). *Palaeontology*, 62, 375– 415. Wiley Online Library Web of

- ScienceTsuji, L. A. 2013. Anatomy, cranial ontogeny and phylogenetic relationships of the pareiasaur *Deltavjatia rossicus* from the Late Permian of central Russia. *Earth & Environmental Science Transactions of the Royal Society of Edinburgh*, 104, 81– 122.
- Tsuji, L. A. and Müller, J. 2009. Assembling the history of the Parareptilia: phylogeny, diversification, and a new definition of the clade. *Fossil Record*, 12, 71– 81.
 - Tzika, A. C., Helaers, R., Schramm, G. and Milinkovitch, M. C. 2011. Reptilian transcriptome v1.0, a glimpse in the brain transcriptome of five divergent Sauropsida lineages and the phylogenetic position of turtles. *Evolution & Development*, 2, 19.
 - Vallén, E. 1942. Beiträge zur Kenntnis der Ontogenie und der vergleichenden Anatomie des Schildkrötenpanzers. *Acta Zoologica Stockholm*, 23, 1– 127.
 - Versluys, J. 1914. Über die Phylogenie des Panzers der Schildkröten und über die Verwandtschaft der Lederschildkröte (*Dermochelys coriacea*). *Paläontologische Zeitschrift*, 1, 321– 347.
 - Vickaryous, M. K. and Hall, B. K. 2008. Development of the dermal akeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. *Journal of Morphology*, 269, 398– 422.
 - Völker, H. 1913. Über das Stamm-, Gliedmaßen- und Hautskelet von *Dermochelys coriacea* L. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere*, 33, 431– 552.
 - Wang, Z., Pascual-Anaya, J., Zadissa, A., Li, W., Niimura, Y., Huang, Z., Li, C., White, S., Xiong, Z., Fang, D., Wang, B., Ming, Y., Chen, Y., Zheng, Y., Kuraku, S., Pignatelli, M., Herrero, J., Beal, K., Nozawa, M., Li, Q., Wang, J., Zhang, H., Yu, L., Shigenobu, S., Wang, J., Liu, J., Flicek, P., Searle, S., Wang, J., Kuratani, S., Yin, Y., Aken, B., Zhang, G. and Irie, N. 2013. The draft genomes of soft-shell turtle and green sea turtle yield insights into the development and evolution of the turtle-specific body plan. *Nature Genetics*, 45, 701– 706.
 - Watson, D. M. S. 1914. *Eunotosaurus africanus* Seeley, and the ancestry of the Chelonia. *Proceedings of the Zoological Society of London*, 1914, 1011– 1020.
 - Werneburg, I. 2015. Neck motion in turtles and its relation to the shape of the temporal skull region. *Comptes Rendus Palevol*, 14, 527– 548.

-
- Werneburg, I. and Sánchez-Villagra, M. R. 2009. Timing of organogenesis support basal position of turtles in the amniote tree of life. *BMC Evolutionary Biology*, 9, 82.
 - Westphal, F. 1975. Bauprinzipien im Panzer der Placodonten (Reptilia triadica). *Paläontologische Zeitschrift*, 49, 97– 125.
 - Williston, S. W. 1917. The phylogeny and classification of reptiles. *Journal of Geology*, 25, 411– 421.