Chelonii: Overview

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Meiolanoidea
         `--+--Pleurodira
            |--Paracryptodira
            `--+--Protostegidae
               |--Plesiochelyidae
               `--+--Angolachelonia
                  `--+==Xinjiangchelyidae
                     `--+==Sinemydidae
                        |--Trionychoidea
                        `--+--+--Chelonioidea
                           |  |--Chelydridae
                           |  `-
-Kinosternoidea
                           `--Testudinoidea
```

Contents

The gigantic Late Cretaceous marine turtle *Archelon ischyros* (Testudines - Casichelydia - Cryptodira - Eucryptodira - Protostegidae - Protosteginae. This impressive animal, which inhabited the Cretaceous inland sea of central North America, had a shell 3 meters long, and snout to tail tip length of some 5 meters

illustration by Nobu Tamura (*Wikipedia*), Creative Commons Attribution-Share Alike

Introduction

The humble turtles, or more properly *Chelonii* or *Testudines* (terminology), are among the most ancient groups of reptiles on Earth. yet these strange and highly specialised animals are often taken for granted or ignored in the history of life, eclipsed by their larger and more exotic looking but also shorter lived contemporaries such as sauropods, brontotheres, and so on. This means that few realise how truely strange these animals are. They are, for example, the only vertebrates to have their shoulder girdle inside their ribcage, an astonishing evolutionary transition achieved through a small developmental shift in their embryonic stage. They have no clear ancestors, occuring suddenly in the fossil record during the Late Triassic, a time when many important new groups, such as crocodiles, dinosaurs, pterosaurs, lepidosaurs, and mammals were also appearing, along with shorter-lived but also for their time important clades such as phytosaurs and aetosaurs. They evolved into a diverse range of forms, populating land, rivers, swamps, and the open sea, survived several mass extinctions, and continue to this day.

One of the problems with determining both the origin and the evolutionary famnily tree of turtles is that in both cases there are a number of mutually contradictory hypotheses, each persuasive to some extent, but none of which able to explain all the data.

Originally, taxonomic classifications placed the Chelonia in the Anapsida, a group that originally included all reptiles that lacked temporal skull openings. This is now considered an artificial grouping, the lack of temporal fenestra being a primitive (plesiomorphic) feature retained in many lineages. We have used Anapsida in a more restricted but phylogenetically valid sense to refer to one of the three major clades of amniotes (the alternative popular term "parareptiles" is confusing if turtles, which are reptiles, are anapsids). The other two clades are Synapsids (mammal-like reptiles and mammals) and Eureptiles (Diapsids and their immediate ancestors)). The origin of turtles in the evolutionary tree is no longer clear, if it ever was. At least seven or eight competing hypotheses have been proposed over the years, each with its own problems, and some now discarded. The three main alternatives of anapsid origin from early amniotes ("parareptiles") and lepidosaur and archosaur ancestry among the higher Diapsida, have been proposed in the light of cladistic morphology and molecular phylogeny. The contradiction between Anapsid and Diapsid origins arose because whilst several cranial characters suggest a parareptilian/anapsid origin, some appendicular (limb and limb girdles) characters suggest a lepidosauromorph affinity, and molecular analysis uniformly supports an archosaurian origin (or stem-archosaur, e.g. archosauriforms or archosauromorph (Lyson & Gilbert 2009)). The Reptiliomorph, Eunotosaur, Captorhinid, Procolophonoid, and Pareiasaur origin theories are all variants of the traditional hypothesis that Testudines are Anapsida and the sister-group to Diapsida (i.,e. to all other extant reptiles), which is why and that they retain various primitive amniote characters such as an unfenestrated skull. The Sauropterygian and Ledidosaur hypotheses argue on morphological cladistic grounds for a Diapsid origin, whilst the archosaur origin finds almost no morphological support, but is strongly supported by molecular phylogeny. Other cladistic studies support an Anapsid (Parareptilia) origin, and embryology seems to do likewise.

Moreover, even within the testudine family tree itself, it is no longer clear which groups of chelonians evolved from which. The established view is that very primitive chelonians evolved into pleurodire and cryptodire, according to how they withdraw their head and neck into their shell (Romer, 1966, Gaffney and Meylan, 1988, Carroll, 1988). This has been rejected in view of new discoveries and cladistic analyses which show a range of intermediate forms, while molecular studies sometimes give confirming, and sometimes conflicting, results as regards traditional subgroups established through morphological analysis.

The situation is made even more confusing by the fact that turtle evolution seem to exhibit frequent homoplasy (parallel evolution). Thus for example the Cretaceous Protostegid sea turtles like the great *Archelon* shown at the top of the page, were morphologically extremely similar to the Cenozoic leatherback turtles (the largest extant turtles) but actually evolved from much earlier and more primitive ancesors. As they lived a very similar lifestyle, natural selection resulting in their evolutionarily converging into a very similar form (the classic example is the similarity of form between the shark, tuna, ichthyosaur, and dolphin, all living a very similar ecological lifestyle of large fast-moving marine preditors). Other examples can be given as well (e.g. (Rabi & Joyce, 2012, which shows that phylogeny is anything but parsimonious.

But this is nothing next to the problem of incompatability between morphological and molecular phylogeny. If morphology is correct then both first occurance in the fossil record and molecular phylogeny are often completely unreliable and misleading. If molecular phylogeny is correct then there would be unparalleled convergent evolution between the soft-shelled turtles (Trionychoidae) and the mud turtles (Kinosternoidea); two groups unanimously united on morphological cladistic evidence, which renders cladistics, the "gold standard" of modern phylogenetic studies, more or less irrelevant. If molecular phylogeny and paleontology are correct soft-shelled and the common ancestor of all hard-shelled cryptodire turtles diverged during the early Late Jurassic (Danilov & Parham, 2006); far less ghost lineages and a more reliable fossil record, but a degree of homoplasy that is verging on the ridiculous. Stratocladistics may throw much needed light on this problem, but as this is a methodology that lies outside the current paradigm, this is unlikely in the near or even intermediate future.

In view of all this, the "traditional" account presented in the previous (2002) version of Palaeos has been revised and replaced by a more radical presentation, including a range of alternative interpretations, as shiown by the alterative placement of several taxa in the unit dendrogram. The Anapsid/Parareptile, the Lepidosaur/Sauropterygian, and the Archosaur origin theories are for different reasons equally plausible, but as the first of these remains persuausive the chelonia are listed on Palaeos com next to the early Anapsida, although the expanded coverage and ambiguities regarding their phylogenetic position meansd they deserve a separate unit; hence these new pages. MAK101015

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Chelonii - *Odontochelys*

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--o Testudines with full shell
   |--Proganochelys
   |--Chinlechelys
   `--+--Proterochersis
      `--+--Meiolanoidea
         `--+--Pleurodira
            |--Paracryptodira
            `--+--Protostegidae
               `--+==Xinjiangchelyidae
                  `--+==Sinemydidae
                     |--Trionychoidea
                     `--+--+--Chelonioidea
                         |  |--Chelydridae
                         |  `--Kinosternoidea
                         `--Testudinoidea
```

Contents

Taxa on This Page

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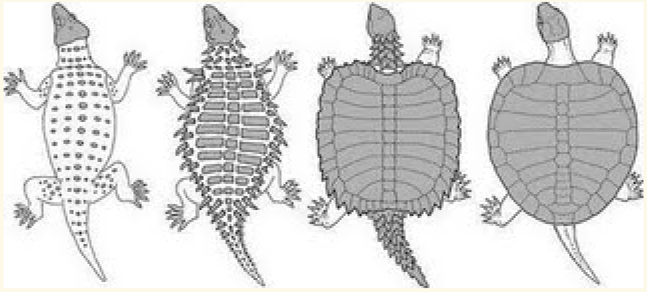
1. Chelonii
2. *Odontochelys* X

The Mystery of Chelonian Origins

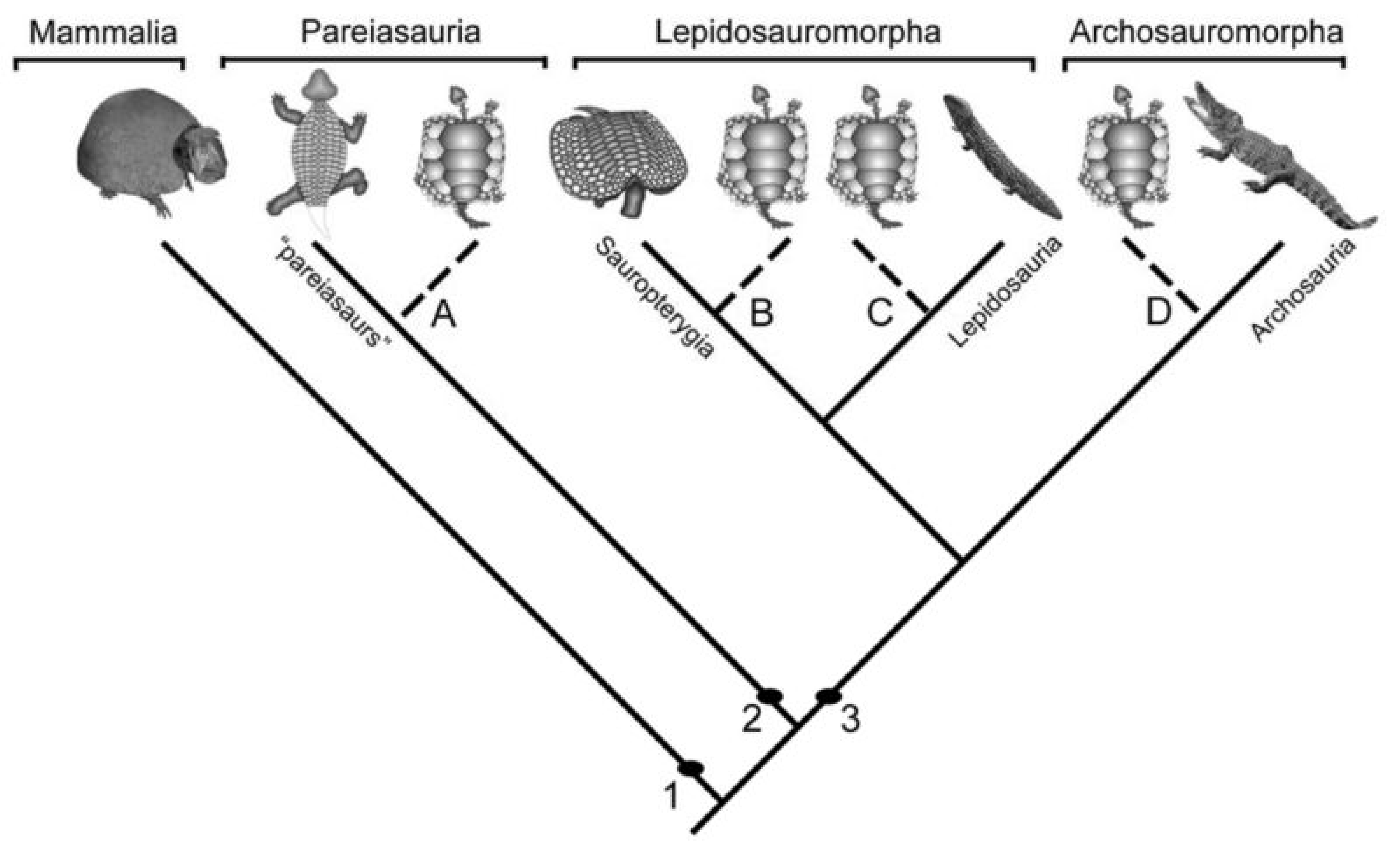
This *or* *this?*



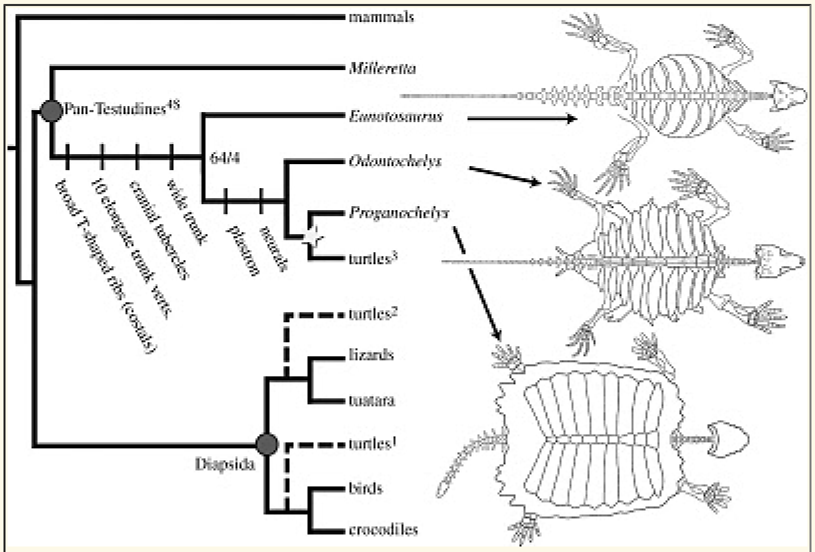
Above: Hypothetical sequence of events leading to the modern chelonian shell, in which dermal scutes expand to form the carapace (upper shell). The two animals on the left are speculative. The third one from the left is *Proganochelys*, and the far right is *Chinlechelys*. This sequence supports the theory that chelonians evolved from a procolophonid or pareiasaur-like ancestor (Joyce & Gauthier, 2004)
Right: the proto-chelonian *Odontochelys*. This animal would seem to support the idea that turtles evolved from aquatic, sauropterygian-like ancestors.

Graphics from "A Carapaceless Turtle" link/link(mirror postings)

The origin of turtles and tortoises (Chelonia) from ancestral reptiles is still unclear. There are many different rival theories of where Chelonians fit on the evolutionary tree, each supported by various arguments and with each there are also objections. "Turtles are very derived. Inevitably, they have convergently evolved derived characters with other groups. Which hypothesis we trust depends on which characters we value." - John Merck. . These hypotheses can be summarised briefly as follows:



A few alternative chelonian origins: hypothesis A) chelonians are parareptiles and deeply nested within pareiasaurs; hypothesis B) chelonians are derived diapsids most closely related to sauropterygians; hypothesis C) chelonians are derived diapsids most closely related to lepidosaurs; hypothesis D) chelonians are derived diapsids most closely related to archosaurs. For source of data on phylogenetic hypotheses of chelonians see text. 1= Synapsida; 2= Parareptilia; 3= Diapsida. Diagram from Scheyer 2007 p.10



The position of chelonians based on molecular (***1***: e.g. Hugall et al. 2007) and morphological (***2***: e.g. deBraga and Rieppel 1997) data sets, and as parareptiles descended from *Eunotosaurus* (***3***). Star indicates complete shell. From Lyson et al 2010

Eunotosaurs: The strange Permian reptile *Eunotosaurus africanus* was described by D. M. S. Watson as the ancestor to chelonia, on the basis of the broadly expanded ribs which form a shell-like structure covering its body (Watson, 1914). It was since discovered that the shell of chelonians is made up of narrow ribs covered by dermal bone, not broadly expanded ribs. This, plus the presence of an ectopterygoid bone in the eunotosaur skull, indicate that this creature was not a chelonian ancestor: Interestingly the Eunotosaur ancestry argument has recently been revived (Lyson et al 2010, see illustration at right). The authors suggest that because the ribs of *Eunotosaurus* were not only expanded, but T-shaped in cross section, this suggests that expansion occurred through secondary ossification and the incorporation of dermal (skin armour) components as in true chelonians, which answers the broad rib objection. Unfortunately, this still does not address the "evo-devo" model of the embryonic formation of the chelonian shell and the location of the shoulder girdle inside the ribcage, which is supported by *Odontochelys* (Willmore, 2010). We can safely say therefore that eunotosaurs developed a shell quite independently of chelonians. (also forum discussion of this paper)

Captorhinids: A more common view until fairly recently was that the closest extinct relatives of chelonians were the primitive Permian "cotylosaurian" reptiles of the family, Captorhinidae. Like all chelonians, members of this group lack the ectopterygoid bone and have a large medial process of the jugal bone of the skull. Gauthier *et al*. (1988) argue strongly for close affinities between captorhinids and chelonians. However, no known captorhinid shows any sign of even a partly developed shell. There is also a gap of many millions of years between the last known captorhinid and the earliest known chelonian. This idea has now been pretty much abandoned.

Procolophonids: During the early 90s, it was proposed by Robert Reisz and one of his students Michel Laurin that the Triassic herbivorous anapsids called Procolophonids are the closest relatives of chelonians. A study by (Reisz & Laurin 1991 of the basal procolophonoid *Owenetta*, revealed a number of characters unique to procolophonoids and chelonians (see Procolophonoidea: Morphology). Most notable is the tympanic notch (the ear). Chelonians lack a tympanum (a thin membrane like the skin of a drum that enables the reception of airborne vibrations, hence, "ear drum") but instead have a layer of skin over their tympanic notch or opening. This unique arrangement is alos found in Owenetta, but not in other reptiles. However, there is again a gap in time (although not as great as with the Captorhinids between *Owenetta* and its relatives and the chelonia. Once again, no known procolophonid shows any tendency of even a partly developed shell.

Pareiasaurs: . Beginning in 1993 (Lee 1993), Michael Lee has argued that the large armoured herbivorous Permian pareiasaurs are the closest known relatives of chelonians, rather than the small procolophonids proposed Pareiasaurs as a sister taxon. Pareiasaurs and chelonians share a number of traits, including a thickened braincase floor, acromian process, dermal armour, a shortened vertebral column and four presacral ribs, among many other features. Cladistically speaking, chelonians are therefore a type of specialised dwarf pareirasaur that survived the end Permian extinction (Lee 1996; Lee 1997). This is the same as birds as specialised dinosaurs. Lee coined the wonderful term *Hallucinocrania* to refer to the clade that includes pareiasaurs and chelonians (with reference to the bizarre form of the pareiasaur skull bones) This theory, which became for a while the established one, is supported by the fact that towards the end of the Permian some pareiasaurs became reduced in size, and some, such as the smallish genus *Anthodon* (left) developed a chelonian-like pattern of bony plates from the dermal armour (osteoderms) embedded in their skin, forming a rigid covering over the entire back, and of flattened, expanded ribs. The discovery of *Chinlechelys* (Joyce, et. al. 2008) supports the argument for an osteoderm-bearing (pareirasaur-like) terrestrial ancestor.

Despite the plausablity of this hypothesis, it is not without problems. The biggest problem is that chelonian carapace ('dermal armour') does not develop from dermal plates in the skin as with pareieasaurs. It, is a complex structure formed through fusion of vertebrae and ribs to interlocking plates beneath the skin and growth of horny scutes above the skin (Cherepanov 1997; Rieppel and Reisz 1999), without parallel in the animal kingdom. Moroever, the ancestral chelonian could not have been a terrestrial animal. The unique chelonian morphology, in which the limb girdles and shoulder blades develop within the rib-cage, rather than outside as in all other vertebrates, mean that the ribs would somehow have had to lose their function of supporting respiration and locomotion Rieppel and Reisz 1999), and hence implies an aquatic ancestry, exactly what we find with *Odontochelys*. Hence the Sauropterygia (Triassic aquatic) origin theory.

There are more technical objections as well. Derived chelonians have lost the basipterygoid joint, as have pareiasaurs, but early forms such as *Odontochelys* and *Proganochelys* retain it. *Odontochelys* teeth are simple cones, very different from the leaf-shaped teeth of pareiasaurs (David Marjanovic DML post). Then there is the recent discovery of what seem to be cleithra in the stem chelonian *Kayentachelys*, and even stem-pleurodires and stem-cryptodires (Joyce et al 2006) (I am not sure if it has been identidfied in *Odontochelys*). Cleithra are a primitive element of the shoulder girdle that are present in stem synapsids and many anapsid reptiles, but absent in all diapsids, as well as in pareiasaurs. This favours a parareptile ancestry, but not a pareiasaur or diapsid origin.

Sauropterygia: The turtles and placodonts (aquatic animals with broad wide shells) show superficial similarities in anatomy, and according to Broom that chelonians and placodonts were related, although in many morphological respects they are very different. This idea has recently been revived by Olivier Rieppel (Rieppel 1995, Rieppel and deBragga 1996, deBraga and Rieppel 1997). Rieppel and deBraga pointed out that previous phylogenetic studies had been too narrowly focused, being based on the assumption that turtles were anapsids. Once they broadened their analysis to include other groups they discovered, that testudines nested within the diapsids, and more specifically inside the Euryapsida (placodonts and sauropterygia), a group of marine reptiles that was established by Romer. Shared features include jaw adductor muscles, temporal (cheek) bone ossification, the shape of the jugal, and the presence of a centrale among the carpal (wrist) bones instead of a radiale (forarm). This was the first cladistic analysis to move chelonians out of their until then universal position within the Anapsida, to the diapsids. This means that chelonians are not derived from an extinct anapsid group but diapsids (and more specifically lepidosauromorphs, as the authors consider sauropterygia and lepidosauria sister groups) that secondarily closed their temporal fenestrae and lost their impedance-matching ear in reverting to the basal amniote condition. Synapomorphies include a hooked fifth metatarsal and an astragalus-calcaneum complex (Lyson & Gilbert 2009). They found that testudines nested particularly close, and even within the sauropterygia, especially placodonts. Rieppel and Reisz 1999 hypothesized a marine origin for the ancestral chelonian, that it most likely had dorsally located ribs, and the plastron developed first in order to protect the soft underbelly. And while the plastron might be derived from gastralia, the sauropterygian pectoral and pelvic girdles form expanded, nearly flat plates meeting along the ventral midline, and this could be another way in which the plastron developed (blog comment). Because Sauropterygia are common and well established in the Triassic, it would certainly explain why chelonians are unknown in the fossil record until the late Triassic.

The discovery of *Odontochelys* adds weight to the Sauropterygia origin theory (Li et al 2008; Reisz & Head 2008), although this strange form also arises more questions than it answers , and it could equally be used to argue for a parareptilian ancestry, either eunotosaur (Lyson et al 2010) or procolophonoid (David Marjanovic blog comment). In any case even in this very primitive turtle there is no trace of temporal fenestration such as would characterise it as a diapsid, in contrast to all other specialised aquatic Triassic reptiles.

There is a problem however with placodonts. Although extremely turtle-like, they developed their shell by fusing osteoderms - bony armor plates that develop from the skin. Whereas the chelonian shell is a unique combination of dermal and endochondral (skeleton) bone. So the placodont connection has the same problem the pareirasaur one has. In each case, the structure, and indeed the microstructure of the armour is quite different to turtles and tortoises (Scheyer 2007). And whilst *Priscochelys hegnabrunnensis*, based on a fragmentary piece of shell from the Muschelkalk of Germany was originally believed to represent the most ancient chelonian, and a transitional form between placodonts and testudines (Karl, 2005), it was later shown to be a cyamodontoid placodont (Scheyer 2008).

The analysis used has been criticised (Lee, 1997a), and the sauropterygian-chelonian theory is only weakly supported and based on characters that are homoplastic on the tree as a whole (Rieppel and Reisz, 1999), with only a small increase in tree length needed to return turtles to the Parareptilia (Wilkinson et al. 1997). There is also the matter of taxon sampling. Turtles appear as diapsids, and the sister clade to, or even nested within, the sauropterygians in the analyses including euryapsids; without euryapsids, the same analysis supports a parareptile affinity for turtles (Brochu

2001, pp.1190, 1192), while adding additional characters and taxa mak them the sister group of the lepidosaurs (Hill, 2005).

One thing *Odontochelys* does do is conclusively refute the pariesaurian hypothesis. Quoting Adam Yates (Closing in on turtle origins):

> Of the synapomorphies linking pareiasaurs, or derived subclades within pareiasaurs, to turtles a good many of them are missing in *Odonotochelys*. These include: basal tuberae (ventral swelling of the braincase) midway between the occipital condyle and the basipterygoid processes (where the palate attaches to the braincase); acromial process on the scapula, closure of the spaces between the ribs (it is debatable wether or not any turtle actually has this condition); fewer than twenty caudal vertebrae; and body covered in united osteoderms. Note that although it appears to support a diapsid origin for turtles the skull of Odontochelys lacks any trace of temporal openings so perhaps we can't quite rule out other anapsid sister groups just yet.

Lepidosaurs: although there are no transitional forms known between the lizard and lizard-like lepidosaurs (a group that includes lizards and snakes and the sphenodontia (tuatura), and seems to be allied to the Sauropteerygia) and testudines, there is a decent amount of cladistic evidence that argues for their close relationship. Of course, these may just be parallels, but the lepidosaur origin, while not as popular as the pareiasaur, sauropterygian, or now archosaur orgin, still has supporters and cladistic evidence (Müller, 2003.; Hill, 2005, the latter, using much larger taxonomic and character sampling, arriving at the rather surprising finding that Lepidosaurs and Crown group Archosaurs (to the exclusion of basal archosauromorphs) are also sister taxa, which goes against the entire Diapsid phylogenetic consensus).

Archosaurs. Yes, archosaurs! Beginning in 1997, molecular phylogenetic analyses, both mitochondrial and nuclear gene analyses, consistently and unanimously places suggests that testudines are related to archosaurs, or even that they *are* derived archosaurs. (Zardoya and Meyer 1998; Hedges & Poling, 1999 (review); Kumazawa & Nishida, 1999; Janke et al. 2001; Zardoya and Meyer 2001; Meyer and Zardoya 2003; Rest et al 2003; Hugall et al. 2007; Shedlock & Edwards, 2009). Although one early findings (of Hedges & Poling, 1999) rather disconcertingly also placed *Sphenodon* (the tuatura) among the archosaurs, this was not reported in the later paper by Rest et al 2003, who however confirm the testudine-archosaur sister relationship.

This unanimous molecular evidence may or may not be the result of factors such as long branch attraction, always a problem with isolated taxa - here molecular evidence for archosaurian affinities of turtles is based on ingroup divergences little older than the Jurassic, whilst available outgroups (mammals and lissamphibians) had diverged by the end of the early Carboniferous (Brochu 2001, p.1190). - but it is unanimous across all forms of molecular analysis (Shedlock & Edwards, 2009 p.376). And while early molecular analyses could be criticized (short sequences, poor taxon sampling, genes with inappropriately fast substitution rates), and molecular phylogeny prior to 2001 tends to suffer from long-branch attraction (citing David Marjanovic post), more recent analyses of long nuclear genes such as the nuclear gene RAG-1 ((Recombination activating gene, a large slowly evolving gene useful for phylogenetic analysis (Krenz et al 2005, p.186.)) still strongly position chelonians as the sister group to archosaurs (Hugall et al. 2007). Although the much slower nucleotide substitution rate in turtles in relation to diapsids might predispose the reptile RAG-1 tree to be rooted in diapsids, there is no difference in substitution rate in the case of mitochondrial genes Rest et al 2003 and studies here also place testudines alongside archosaurs (Lyson & Gilbert 2009). The only disagreement being whether chelonians are closer to birds or to crocodiles, or equally distant from either. It has even been suggested that aëtosaurs are stem-turtles; advanced forms like *Typothorax* and *Paratypothorax* had broad turtle-like bodies, their ventral plating compared to a plastron, and in at least one species the neck spines resemble those of an early turtle (Hedges & Poling, 1999). But these are quite weak arguments, much better explained as homoplasy, and if chelonians do belong on the archosaurian tree it is more likely as basal Archosauromorphs. In any case when both crocodiles and birds are used as outgroups to test intra-testudine phylogeny they come up as more closely related to each other than to testudines (e.g. Krenz et al 2005, see figure here). The problem is, this hypotheses has virtually no morphologic support, and is equally opposed by both the Parareptile origin and Sauropterygian origin camps (Rieppel 2000; Lee, 2001); and it has been argued that even when both morphology and molecules are considered together a parareptile ancestry is still the most plausible (Lee, 2001), There are more recently a few morphological arguments. Comparison of chelonian bone histology with osteoderm-bearing pareiasaurs, mammals, placodonts, archosauromorphs and lepidosaurs, show closest resemblance with archosaurs (Scheyer 2007). And a new paper reports the existence of an archosaurian-like laterosphenoid bone in *Proganochelys* (Bhullar & Bever 2009). There is also analysis that supports Ichthyosauria, Sauropterygia and Chelonia included under the Archosauromorphs (but not Archosauria) rather than Lepidosaurs (Merck, 1997, Borsuk-Bialynicka & Evans 2009 p.230), which would be an interesting way to converge the morphological (Rieppel & Braga's Sauropterygia + Chelonia) and molecular findings. See also *Azendohsaurus*, the early archosauromorph radiation and a new position for turtles for an interesting if speculative approach to this, placing testudine ancestry within the Archosauriforms. And it is worth considering the quite similar problem of the origin of whales, another highly specialised group that did not have clear terrestrial ancestors. Against all expectations, molecular phylogeny nested Cetacea (whales and their relatives) with the Artiodactyla (even-toed hooved animals). This was confirmed by a discovery in 2000 of the distinctive artiodactyl-like double-pulley astragalus (ankle) bones in early archaeocete skeletons (Gingerich et al., 2001, non-technical essay) There are however other isntances where molecular evolution gives much more dubious results, such as grouping monotremes and marsupials together, the Marsupionta hypothesis (Janke et al. 1996). However, unlike the case with turtles, these findings were alter challenged by further molecular research (e.g. Killian et al. 2001; Kullberg et al 2008)

Yet while both cladistic morphological, and molecular phylogeny have been widely employed, and as above mentioned give very different results, a third methodology, embryology, was brought in by Werneburg & Sánchez-Villagra 2009 to examine and test these conflicting phylogenetic hypotheses. They found that the timing of organogenesis events (stages of embryonic development) in the various amniote clades clearly supported a basal position of turtles (i.e. as suister group to Sauria). This implies significant convergence or paralellism in either the molecular/genetic composition, adult morphology, or embryological developmental timing characters, as only one of these alternative solutions can be right. The following presents

Hypothesis:	Eunotosaur origin	Procolophonoid origin	Pareiasaur origin	Sauropterygian origin	Lepidosaur origin	Archosauromorph origin
Gross morphology (excluding *Odontochelys*)	N	Y	Y	Y	Y	N
Odontochelys Li et al 2008	Y	--	N	Y	--	--
Cleithra Joyce et al 2006	Y	Y	N	N	N	N
Shell histology Scheyer 2007	--	--	N	N	N	Y
Molecular phylogeny	N	N	N	N	N	Y
Embryology Werneburg & Sánchez-Villagra 2009	(Y)	(Y)	(Y)	N	N	N

Thus the problem remains unresolved, and the conficting arguments, each persuasive in its own way, make it impossible to identify any ancestral group with confidence. The Eunotosaur and Pareiasaur hypotheses can I believe be discarded. As for the rest, molecular phylogeny and shell histology make a powerful case for the Archosauromorph origin, and gross morphology equally supports anapsid/parareptile and lepidosauromorph origins. But embryology, the presence of cleithra in basal and stem chelonians, and the absense of any trace of temporal openings (on its own not very persuuasive because temporal fenestrae disappear in many diapsid lineages, but perhaps significant in association with the other arguments) even in such a transitional form as *Odontochelys* (the chelonian equivalent of archaeopteryx if ever there was one), all seem to suggest an anapsid ancestor, perhaps a hypothetical aquatic Owenettid-type procolophonoid. Admittedly, the lack of any evidence of such an animal in the fossil record does make this hypothesis a lot less plausible than it otherwise would be. (MAK101013)

Some Links/References used here: John Merck - class notes (On Beyond Dinosaurs: Patterns and Enigmas in Vertebrate Evolution) (includes very good description of Long branch attraction) (updated page with Odontochelys, but some nonloading images). Reptipage - T-U-R-T-L-E Power! Part 2: The weird and wacky origin of turtles (easy to read page, some of this information included here). Turtles all the way down: loggerheads at the root of the chelonian tree - pdf - short and readable academic essay) MAK101030

The proto-chelonian *Odontochelys semitestacea* - Carnian of China

Artworkby Arthur Weasley - Wikipedia

Descriptions

Chelonii Latreille 1800 **:** ancestral and derived turtles (= Testudinata).

Range: from the Triassic (Carnian).

Phylogeny: choose from Procolophonia or Pareiasaurs(Hallucicrania hypothesis) or Neodiapsida or Sauropterygia or Archosauromorpha or other alternatives **:::** * **:** *Odontochelys* +Testudinata

Characters: Axial arrest of ribs, plastron. For derived forms see Testudinata.

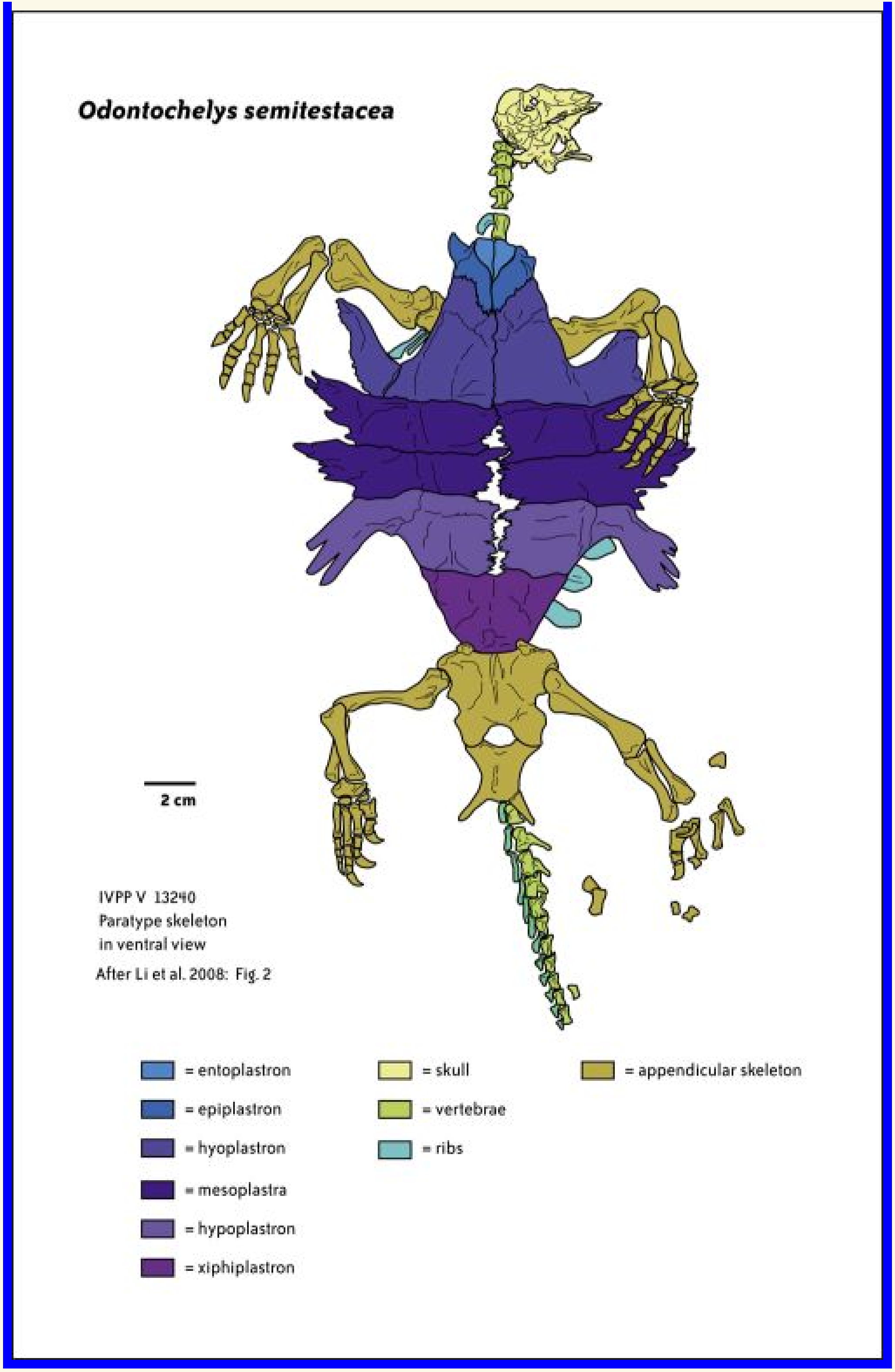
Notes: Usually Chelonia, Testudines, or Testudinata. However Dubois & Bour 2010 argue that none of these names are viable. For example, although "Testudines" has been credited to Linnaeus, the term as originally used was a plural referring to the members of the genus *Testudo*, not a family-series or class-series nomen. Both Chelonii and Chelonia are latinisations of Chéloniens Brongniart, 1800. Chelonia was first used in 1802, after Chelonii (1800), and moreover can lead to confusion because of homonymy with the generic name *Chelonia* Brongniart, 1800. Testudinata is a valid name coined by Oppel, in 1811, Chelonii of Latreille, which dates to 1800, has priority over the former, as well as over Chelonia Ross & Macartney, 1802 (Dubois & Bour 2010, pp. 152-3). Testudines and Chelonia(ns) can still be used as informal names. MAK121222

Odontochelys: most primitive known chelonian. *O. semitestacea* Li et al., 2008

Range: Late Triassic (Carnian) of China.

Phylogeny: Testudinata **:** *Proganochelys* + (Pleurodira + Cryptodira)) + *.

Description and Comments: from Wikipedia, slightly edited: *Odontochelys semitestacea* ("toothed turtle with a half-shell") is the oldest known chelonian. It is the only known species in the genus



Odontochelys and the family Odontochelyidae. The species was first described from three 220 million year-old specimens excavated in Triassic deposits originating from Guizhou, China. (Li *et al.*, 2008; Reisz & Head 2008)

As a primitive chelonian, *Odontochelys* grossly differed from modern representatives of the group in several ways. Modern chelonians possess a horny beak without any teeth in their mouth. In contrast, *Odontochelys* fossils were found to have had teeth embedded in their upper and lower jaws. One of the most striking features of chelonians, both modern and prehistoric alike, are their dorsal shells, forming an armored carapace over the body of the animal. *Odontochelys* only possessed the bottom portion of a turtle's armor, the plastron. It did not yet have a solid carapace as most other testudines do. Instead of a solid carapace, *Odontochelys* possessed broadened ribs like those of modern chelonian embryos that still have not started developing the ossified plates of a carapace. (Li *et al.*, 2008)

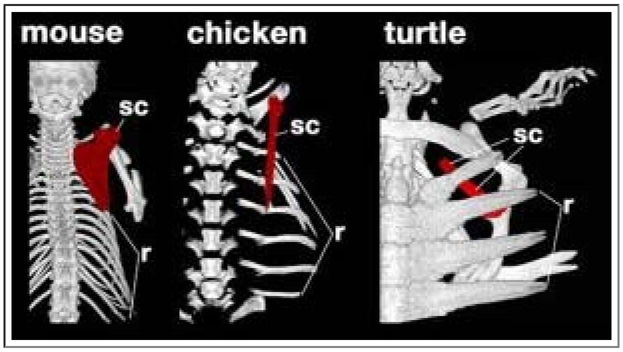
Aside from the presence of teeth and the absence of a carapace, a few other skeletal traits distinguish *Odontochelys* as basal compared to other chelonians, extant and otherwise. The point of articulation between the dorsal ribs and the vertebrae are decidedly different in *Odontochelys* than in later testudines. In a comparison of skull proportions, the skull of *Odontochelys* is far more elongated pre-orbitally (behind the eyes) compared to other chelonians. The tail was proportionally long, and unlike later forms, transverse processes in the tail are not fused. The scapulae of the examined specimens were identified to lack acromion processes. These anatomical differences are all very primitive features, indicating the transitional nature of this species (Li *et al.*, 2008).

It is likely that *Odontochelys* was aquatic, as the fossil specimens were found in marine deposits rife with conodonts and ammonites. It probbaly frequented shallow marine waters close to shore. (Li *et al.*, 2008). In contrast, all other early chelonians were terrestrial until the Mid Jurassic. The aquaticx or semi-aquatic nature of *Odontochelys* supports a Sauropterygian origin for the group

After Li, Wu, Rieppel, Wang & Zhao, 2008 (from Mikko's Phylogeny Archive):

```
<==o Testudines
   |--Odontochelys
   `--+--Proganochelys
      `--+--Palaeochersis
         |--Proterochersis
         `--Testudines crown group
```

The following is paraphrased and slightly modified from Mysteries of the Turtle's Shell (Nature Notes):



Position of scapula (red) and ribs (r) in a mouse, chicken, and turtle. Note that in the turtle the scapula sits *under* the ribs, the only instance of this in the animal kingdom. In *Odontochelys* the scapula occupies an intermediate position, and is not uyet positioned inside the ribcage. Photo © Jamie Wilson / Shutterstock

Turtles are unique not only in the way the shell is formed by the ribs being flattened and fused to the vertebrae, but even more extraordinarily by the placement of their shoulder blades (scapula). Rather than being located on the back, as in other vertebrates, they lie within its ribcage (see image, *left*). This results in the muscles connecting the shoulder blades to the trunk being twisted and folded.

For a long time scientists puzzled over how this bizarre arrangement could have evolved. Until recently, no one really knew. No transitional fossil forms had been found that showed the shoulder blade migrating towards the inside of the ribcage. In the end the new science of developmental biology, or "evo-devo" provided the answer. A team of scientists led by Hiroshi Nagashima from the RIKEN Center for Developmental Biology in Japan compared the embryos of turtles at various stages of development to those of mice and chickens (Nagashima et al. 2009. During the early stages of development, all three embryos have shoulder blades that sit on their back, outside of the ribcage. As the mouse and chicken embryos develop, the shoulder blades remain on the animal's back, while the ribs become embedded in a layer of muscle called the muscle plate. But as the turtle embryo develops, the second pair of ribs swings forward and grows over the shoulder blades, while the muscle plate tucks inward and forms the edge of the turtle's shell.

Serendipitously, Ngashima's work was confirmed by the discovery of *Odontochelys*. *Onontochelys* lacks an upper shell (carapace) but posesses a lower shell (plastron). It has short ribs that did not fan out as with turtles proper. This means that *Onontochelys*' second pair of ribs did not swing over its shoulder blades during its early development. A veritable chelonian *Archaeopteryx*, *Onontochelys* is the long-awaited transitional form that also confirmns the evo-devo model, and vice-versa. MAK130121

Links: Figures and Tables from the above-referenced article "An ancestral turtle from the Late Triassic of southwestern China" in the Journal *Nature*; Oldest Turtle Found; May Crack Shell-Evolution Mystery; First known turtle swam on the half shell; Hairy Museum of Natural History; Niches - Turtleology MAK100520

Image: Hairy Museum of Natural History - larger image

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Chelonii: Testudines

Proganochelys, Chinlechelys

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--o Testudinata
   |--Proganochelys
   |--Chinlechelys
   `--o Casichelydia
      `--+--Proterochersis
         |--Kayentachelys
         `--+--Meiolanoidea
            `--+--Pleurodira
               |--Paracryptodira
               `--o Eucryptodira
                  |--Protostegidae
                  `--+==Xinjiangchelyidae
                     |==Sinemydidae
                     |--Trionychoidea
                     `--+--+--Chelonioidea
                        |  |--Chelydridae
                        |  `--Kinosternoidea
                        `--Testudinoidea
```

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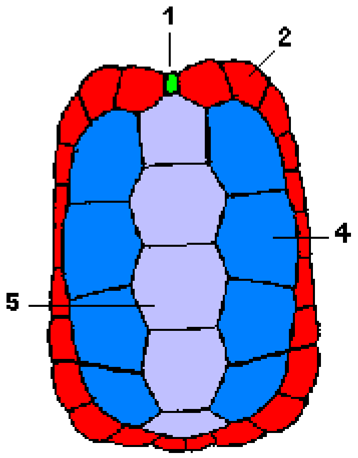
---

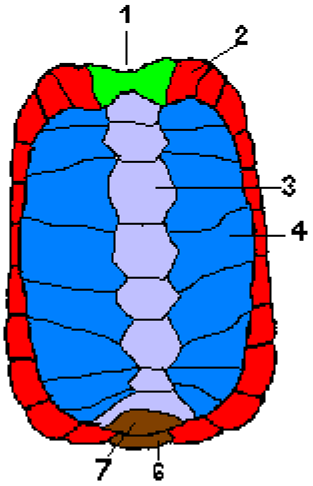
1. *Chinlechelys* X
2. *Proganochelys* X
3. Testudines / Testudinata

A Primer on the Swiss Loi de Douane and Turtle Shell Anatomy

Only the Swiss would would define turtles by law. Then again, perhaps only Americans would find this amusing. In any case, the Swiss Federal Veterinary Office of the Department of Economic Affairs has adopted very detailed regulations (in both French and German) describing the various turtle species. It is unclear just what would occur if a turtle evolved, or developed some unregistered mutation. Undoubtedly, the legal consequences would be quite severe. Let it be clearly understood that all reptiles are well-advised not to behave in such a disorganized fashion within the borders of the Swiss Republic.



Carapace: Epidermal Scutes



Carapace: Dermal Bones

1	**Cervical (1)**	1	**Nuchal (1)**
2	**Marginals (12L+12R)**	2	**Peripheral (11L+11R)**
4	**Pleurals (4L+4R)**	3	**Neural (8)**
5	**Vertebral (5)**	4	**Costal (8L+8R)**
		6	**Pygal (1)**
		7	**Suprapygal (1)**

Fortunately, this loss to Chelonian liberty is partially offset by the public availability of a certain amount of zoological information. Turtle shells are constructed with a layer of epidermal scutes overlying a layer of dermal bone. Pursuant to § 820.112.41(1), the FVO has decreed that the scutes of all turtle carapaces (dorsal shells) ***shall*** have the form shown in the figure at right.

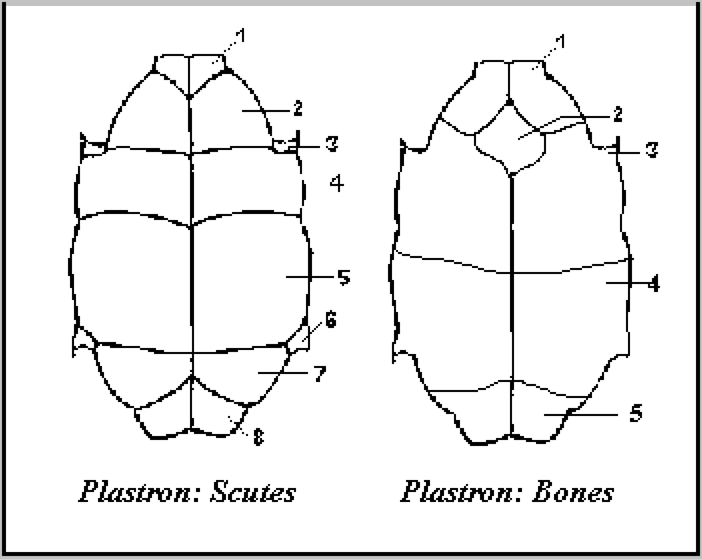
The names have been changed to protect the innocent and, more to the point, to reflect the generally accepted names of the scutes. Unfortunately, the original regulations confuse the names of the epidermal scutes (shown here) with the names of the underlying dermal bones. The bones do *not* conform to the same pattern and have rather different names. The marginal scutes are numbered from the cervical, in both directions, so that the marginal immediately to the left of the cervical, for example, is the First Left Marginal. The scute numbered "2" is thus the Second Right Marginal. Similarly, the scute labelled "4" is the Second Right Pleural and "5" points to the Third Vertebral. This pattern, like the pattern of the dermal bones and the pattern of the scutes and bones of the plastron (ventral shell) is remarkably consistent across all turtles, paticularly extant forms.

The underlying dermal bones are shown in the right half of the figure. These are numbered in the same fashion as the scutes. The first four pairs of costals each fuse with a pair of ribs.

The corresponding pattern of scutes and bone in the plastron is shown in the figure at left.

What is perhaps most extraordinary about this arrangement is that turtles have maintained this particular dual structure for well over 100 My -- even without regulatory supervision under the ever-vigilant eyes of the Federal Veterinary Office. There appears to be no satisfactory explanation for the remarkable stability of this particular arrangement. Bear in mind that turtles inhabit an extraordinary number of different environments and have developed some impressive adaptations. Thus for example, the pleurodire *Rheodytes* has evolved the ability to breath through its cloaca, a talent rarely found except among politicians. Yet, something as apparently trivial as the pattern of epidermal scutes has remained almost completely unaffected from the Triassic *Proganochelys* to the present day.

Either this arrangement has some unknown, but obviously critical, functional significance, or we are missing an important point about evolution. Of all the many fundamental unanswered questions in vertebrate paleontology, one of the most strange and difficult is the mundane constancy of turtle shells. ATW



1	**Gular**	**1**	**Epiplastron**
2	**Humeral**	**2**	**Entoplastron**
3	**Axillary**	**3**	**Hyoplastron**
4	**Pectoral**	**4**	**Hypoplastron**
5	**Abdominal**	**5**	**Xiphiplastron**
6	**Inguinal**		
7	**Femoral**		
8	**Anal**		

Descriptions

**Testudines : **turtles, tortoises, and their kin

Range: from the Triassic.

Phylogeny: Chelonii : *Odontochelys* + * : *Proganochelys* + *Chinlechelys* + Casichelydia

Characters: For testudines above the Odontochelys grade: completion of CR, Dermal carapace, Fan-shaped ribs, Encapsulation of scapula (ref fig 3); Original definition: Double shell (carapace & plastron) with dermal scutes. Beak covers maxilla, premaxilla & dentary. Retracted neck in K; otic capsule enlarged & jaw adductor passes over this or trochlear process of pterygoid, giving more vertical pull on lower jaw; carapace with 59 dermal bones, 8 fused to neural arches, 8 pairs fused to widened ribs; ribs external to girdles; plastron dermal bone plus clavicles & interclavicals; shell kinesis in some species; ATW

Notes: [1] Mesozoic forms, even in the Cretaceous, apparently had shell fontanelles, less remodeling of ribs, and underdeveloped shell elements compared to modern forms. ATW030422

[2] Many workers prefer "Chelonia" for the stem group, reserving "Testudines" for the crown group (LCA extant turtles). For various reasons, the traditional nomenclature is used here. Gaffney, 1975 coined Casichelyidia for Pleurodires and Cryptodires, but this does not seem to have caught on among more recent workers, who use

Testudinata for the stem group and Testudines for the crown group. "Pantestudines" [1] is an alternative term for the stem group (turtles > crocs, lizards, etc), equivalent to Chelonii as here defined. For the sake of convenience, Testudines or Testudinata is here informerly used for all chelonii with a developed carapace (unless secondarily reduced in aquatic or marine forms) and toothless beak ATW, MAK121222

Note: In cladistics, distinguishing between crown group taxa and the group as a whole has led to some confusion, e.g. Crown Group Tetrapods become Tetrapods, Crown Group Testudines (the group that includes the common ancestor of all extant testudines and its descendents, are just called Testudines, and so on. One way around this has been to append the prefix *Pan-* (Meaning "all") to the more inclusive non-crown clade, e.g. Pantestudines (Joyce et al 2004)
back

Image: from Herp Pictures - Turtles (former site) by permission.

Links: Higher Reptile Taxa; Turtle and Tortoise Ring (with 224 sites at last count!); Introduction to Testudines; Order Testudines (ADW); Testudines Turtle Skull Reproductions; Higher Relationships of Testudines; Order Testudines (Czech & English); Tortoise Trust Web - Start Page; Willkommen beim Reptilien Projekt (German & English); Turtles and Tortoises; The Center for North American Herpetology - Web Portal; Testudines (Tree of Life); Testudines Turtle Skull Reproductions (great collection of skull casts); Georgia Wildlife Web Site; reptiles- testudines (nice summary of diversity); Testudines (Spanish); APUS.RU | ????? ·???????? - Testudines (Russian); NatureServe Explorer Species Index- Order TESTUDINES; BiologyBrowser (links); Testudines (turtles, tortoises) (South African turtles); Link to NCBI Front Page; The EMYSSystem (**Best on the Web**); Testudines; Order Testudines. ATW030422 Testudines - Animal Diversity Web.

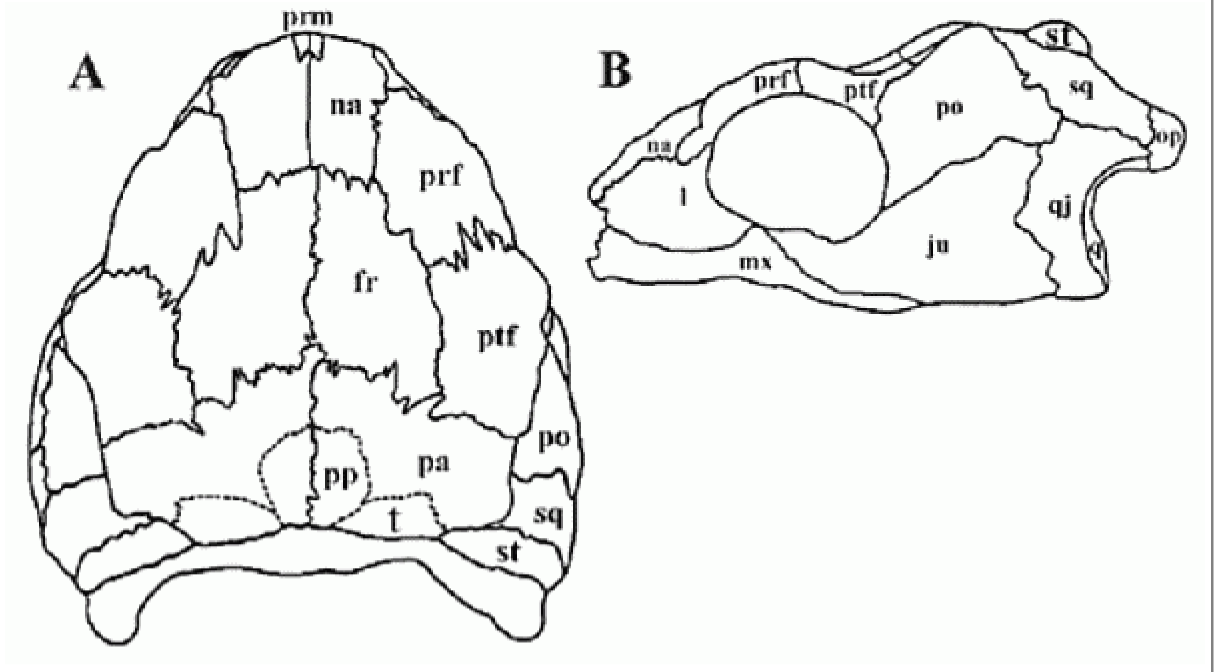
References: Gauthier *et al*. (1988); Lee (1996); Rieppel (1995); Shaffer et al. (1997). ATW030422.

The proto-chelonian *Proganochelys quenstedti* - Norian of Germany
Photo by Claire Houck - Wikipedia

Proganochelys

Range: Late Triassic of Europe (P. quenstedtii), related forms in SE Asia (Thailand) & NAm.

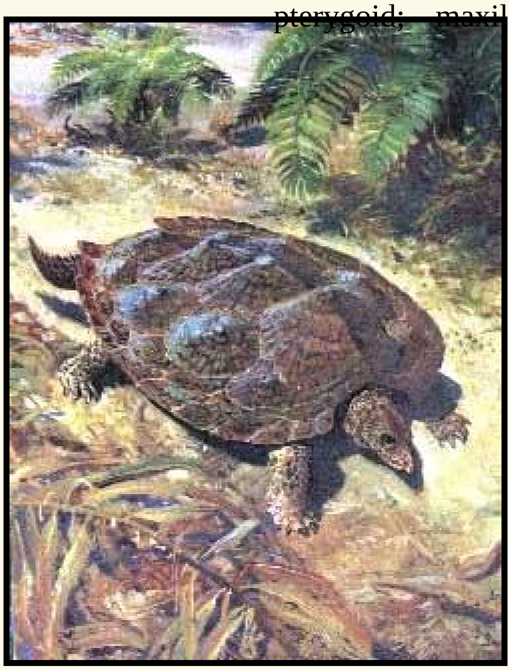
Synonyms: *Chelytherium*, *Psammochelys*, *Stegochelys*, *Triassochelys*, .



Skull of *Proganochelys quenstedti* Baur 1887. After Kordikova 2002, url). Dorsal (A) and ventral (B) views. Abbreviations: ju - jugal, l - lacrimal, mx - maxilla, na - nasal, pa – parietal, po - postorbital, prf - prefrontal, prm - premaxilla, ptf - postfrontal, pt - pterygoideum, q - quadrate, qj - quadratojugal, sq - squamosal, st - supratemporal, t - tabular.

Phylogeny: Testudinata : Casichelydia + *Chinlechelys* + *.

Characters: turtle skull and beak; but denticles on vomer, palatine and pterygoid; maxilla, premaxilla, and dentary edentulous; vomers paired (primitive); interpterygoid vacuity present; moveable basipterygoid articulation (primitive); nasals paired; lacrimal small, but present, with lacrimal duct (primitive); supratemporal present (primitive); expanded posttemporal fenestra (allows jaw muscles to become longer and stronger – muscle origin on occiput); quadrate concave posteriorly and exposed laterally on cheek; postparietals and postfrontals absent; stapes solid, rodlike, without foramen or processes; middle ear without bony lateral wall (primitive); **$** paroccipital process of opisthotic attached to braincase only at its distal end (primitive); paroccipital process only loosely attached to squamosal (**note**: this is slightly inconsistent with previous character); squamosal & postorbital tightly sutured; cervical vertebrae not specialized; 10 trunk vertebrae; 10th trunk vertebra not in sacrum; **$** tail club (? or at least osteoscutes on tail); fully developed bony shell consisting of a carapace (formed from costal bones with fused ribs, neural bones with fused thoracic vertebrae, and marginal bones), a plastron (formed from interclavicle, clavicle, and five paired bones sutured together); carapace and plastron enclosing shoulder girdle and pelvic girdle; cleithrum absent; gracile scapulocoracoids and pelvic girdle; pelvic girdle not fused to carapace; **$** phalangeal formula (manus and pes) of 2-2-2-2-2 (maybe 2 digits with 3 phalanges on manus?); fresh water habitat, but not exclusively aquatic.



Comments: A common animal from the German Keuper (mid Norian). Attained a length of 60 cm. In contrast to *Odontochelys*, the plates had already fully formed. there were also smaller marginal plates. The contemporary *Chinlechelys tenertesta* is more primitive in certain respects (and more advanced in others), with a much thinner shell. MAK100520

Links: Proganochelys (**Best on the Web**); Chelonian Ancestry; Anapsida: Life History and Ecology; Phylogeny and Classification of Amniotes (figs 1D, 2D, & 3D are *Proganochelys*); Molecular Evidence for Higher Relationships Among Turtles; Biology 356; tortugas.html (Spanish); qui (French -- with homemade Bach-omorph fugue & variations!); Turtle Origins; The Paleo Art of D.W. Miller; Turtle.htm; Proganochelys; American Museum of Natural History: Proganochelys; turtle; Paleontology and Geology Glossary: Pr; I. ¿Qué tan viejas son las tortugas? (Spanish). ATW010606. Wikipedia

Chinlechelys *C. tenertesta* Joyce, et. al. 2008

Range: Late Triassic (Revueltian: Mid Norian), Chinle Group of New Mexico

Phylogeny: Testudinata **:** Casichelydia + *Proganochelys* + *).

Characters: very thin (1 to 3mm) shell (hence the name: "delicate shelled turtle from the Chinle"), neck spines formed by multiple osteoderms, ribs only loosely fused to carapace (upper shell). Terrestrial habits.

Graphic: Life restoration by Mary Sundstrom, from HMNH

Comments: Joyce, et. al. 2008 argue (on the basis of *Chinlechelys*) that testudines evolved from terrestrial forms, and that dermal ossifications (armor plating) in the skin evolved independently from and fused and integrated with the costal bones, (ribs and vertebrae), which would seem to support the parierasaur origin hypothesis. But this is refuted by the discovery the following year of *Odontochelys*, a more primative marine form with a fully-developed plastron (lower shell) but no carpace (upper shell). Reisz & Head 2008 argue that Odontochelys descended from carpaced ancestors, but lost the dermal ossifications secondarily after moving into the sea. like leatherbacks and soft-shelled turtles. (A Carpaceless Turtle link/link(mirror postings))

After Joyce, Lucas, Scheyer, Heckert & Hunt, 2009 (from Mikko's Phylogeny Archive):

```
o Testudines
|--Chinlechelys
|--Proganochelys
`--+--Palaeochersis
   |--Australochelys
   `--+--Proterochersis
      `--+--Kayentachelys
         `--+--Mongolochelys
            `--Testudines crown group
```

References: Joyce, et. al. 2008

Links: Hairy Museum of Natural History, Chinleana, Palaeblog MAK100520

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Chelonii: Early Chelonians

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   |--Chinlechelys
   `--o Casichelydia
      |--Palaeochersis
      |--Australochelys
      `--+--Proterochersis
         `--o Cryptodira
            |--Kayentachelys
            `--+--Meiolanoidea
               `--+--Kallokibotion
                  `--+--Pleurodira
                     |--Paracryptodira
                     `--Eucryptodira
```

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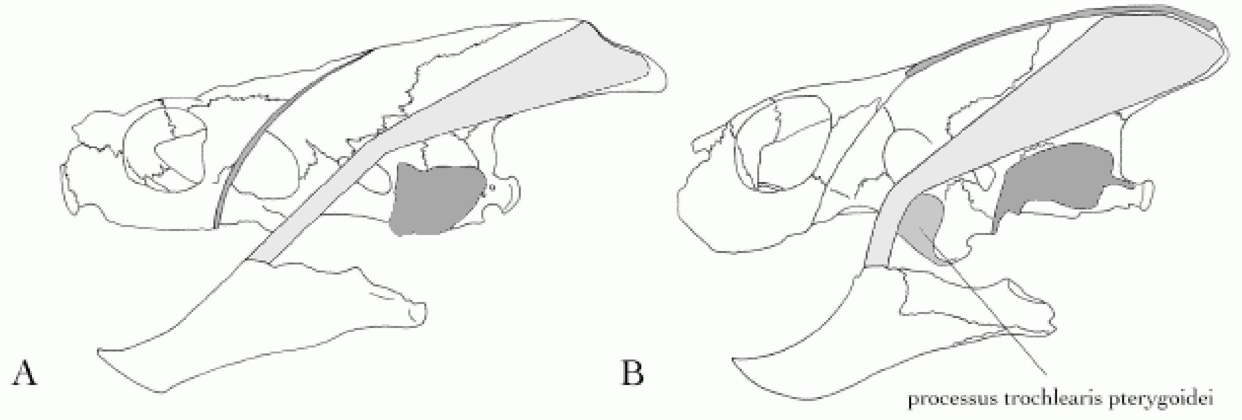
2. Casichelydia
3. *Kayentachelys* X
4. *Palaeochersis* X
5. *Proterochersis* X

Brief History of

Chelonian phylogenetics and systematics

The ancestral cryptodire *Kayentochelys aprix*, Early Jurassic of North-west Pangea, life reconstruction by Nobu Tamura, Creative Commons Attribution from via Wikipedia

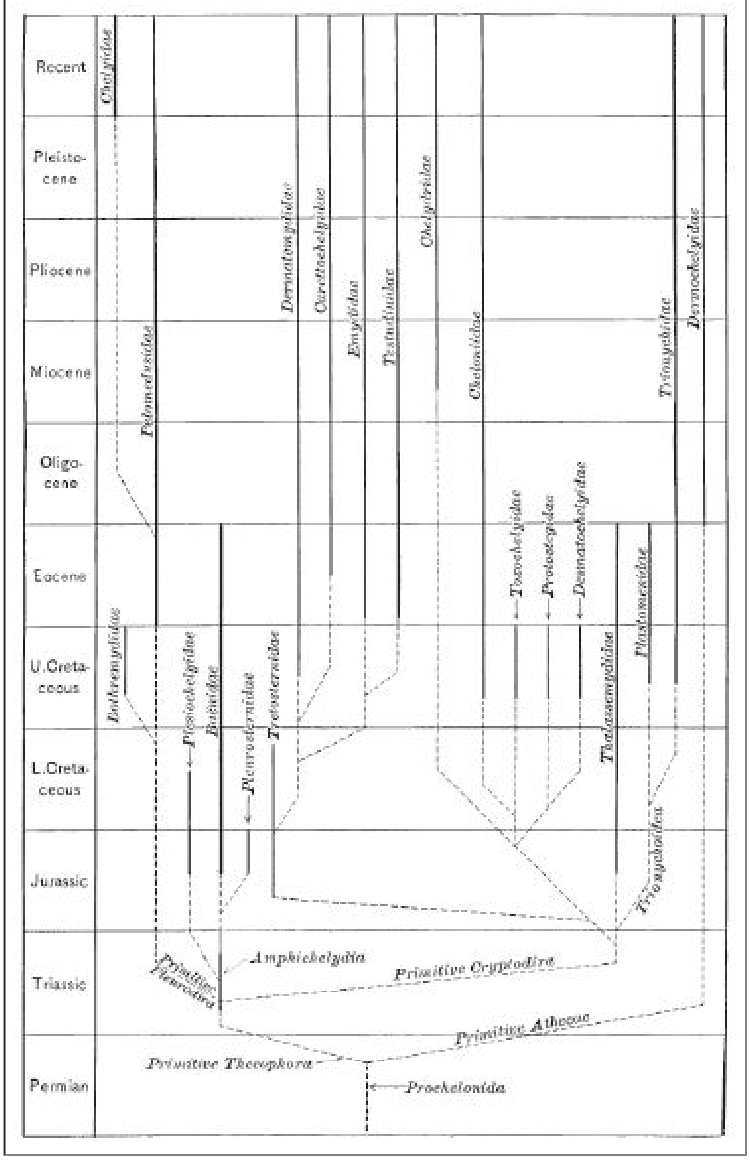
In the eighteenth century, all Chelonian species were included in Linnaeus' single genus, *Testudo*. By the early 19th century, this genus had been subdivided into further genera. Higher category classifications were at first based on habitat-related features; but as morphologic information became available new higher taxa such as the suborders pleurodires (side-neck) turtles and the cryptodires ("hidden"-neck) turtles (both named by Cope in the 1860s), were recognized. (Gaffney, 1984)



Jaw closure mechanism, traditionally used as one of the ways of classifying chelonians. A, the cryptodire *Chelydra serpentina* , showing the main adductor musculature (light grey) is redirected by the otic chamber (dark grey). B, the pleurodire *Elseya dentata*, in which the jaw muscles are redirected by the *processus trochlearis pterygoidei* (medium grey). Diagram modified from Anquetin, 2009 p.32, in turn modified from Joyce 2007 p.73

These two groups differ in a number of ways, including the manner in which the pelvis is attached to the shell, the method used for retracting the neck, and the use of different "pulley" mechanisms to give additional mechanical advantage to the muscles closing the jaws.

At the time, many Jurassic turtles were being rather arbitrarily placed in either the Cryptodira or the Pleurodira. In 1889 Lydekker erected a suborder *Amphichelydia* (Paleobiology Database), further elaborated by Baur 1891 and Hay 1905. At this time, there was the tendency to adopt something along the lines of the following classification (modified from Hay 1908 p.25) (Ironically, the distinct position of the Trionychoidea (also in Zittel, Eastman, et al. 1902) would be confirmed a century later by molecular sequencing)



Earliest phylogeny of higher taxa of living and extinct turtles, published by Hay (1908). From Iverson et al 2007 p.86. The hypothetical Permian branching of ancestral testudines (here, "Prochelonida") into Thecophora and Athecae reflects the popular at the time but now long rejected view that the Dermochelyidae or leatherback sea turtles are distinct from all other chelonii because of the absense of a bony shell. It is now known that both Dermochelyids and Cheloniids (hard shelled sea turtles) evolved from a common hard shelled ancestor sometine during the Late Cretaceous,

Order Testudines.
    Superfamily or Suborder I. Amphichelydia.
        Families. Pleurosternidae, Baenidse, Plesiochelyidae
    Superfamily or Suborder 2. Pleurodira.
        Families. Bothremyidae, Pelomedusidae, Chelyidae, Miolanidse.
    Superfamily or Suborder 3. Cryptodira.
        Families. Thalassemydidae, Toxochelyidas, Desmatochelyidas, Protostegidae, Cheloniidae, Tretosternidae, Chelydridae, Dermatemydidae, Platysternidae, Kinosternidae, Carettochelydae, Emydidae, Testudinidae. The Family Dermochelyidae was sometimes placed in its own suborder, Athecae).
    Superfamily or Suborder 4. Trionychoidea.
        Families. Plastomenidae, Trionychidae.

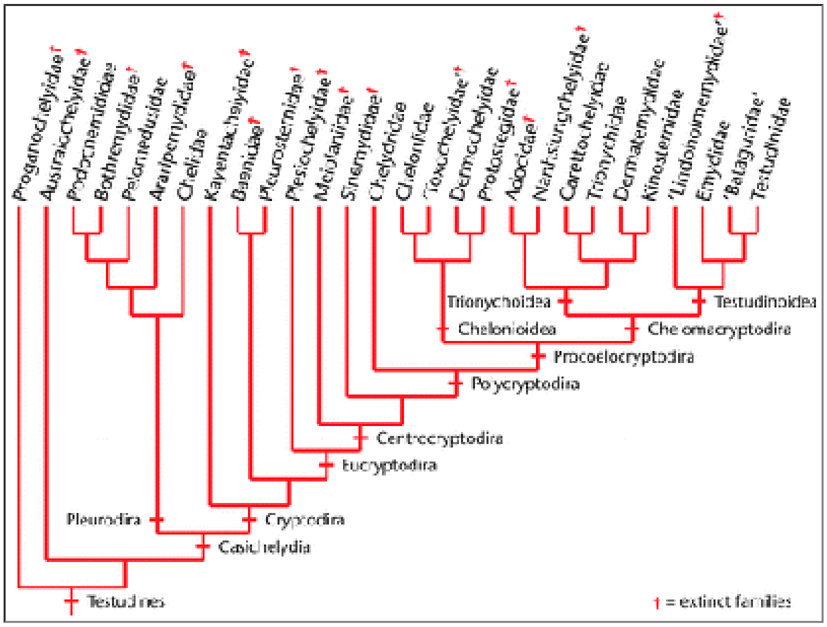
As described by these various authors, the Amphichelydia represented those testudines which had not yet developed the distinctive features of either of the two living suborders, and a taxonomical solution to the problem of many forms that were too far removed from living groups to be identified in one or the other. They were defined for example by a supposed intermediate state between the cryptodire free pelvis and pleurodire condition fused pelvis (Gaffney argues that in these and other regards the Baenidae are actually much closer to the Cryptodiran nature (Gaffney, 1975 pp.407-414)) as well as the skull showing characters that would be expected in the ancestors of Cryptodira and Pleurodira, and a non-retractable neck. Simpson 1938 pp. 251-252 and Romer 1956, pp. 497-498) considered the Amphichelydia as essentially a "horizontal" group (or grade) of intermediate mostly Mesozoic, forms, such as the Pleurosternidae and Baenidae, and including the common ancestors of the two modern groups, the Cryptodira and Pleurodira (Gaffney, 1975 pp.402-6)

An additional suborder, *Proganochelydia*, was erected by Romer (taxon list) in 1966 for specifically Triassic ancestral forms (Gaffney, 1975, p.407). Eunotosauria sometimes turned up as well, as it was thought at the time that the parareptile *Eunotosaurus* might be a possible candidate as testudine ancestor (Watson, 1914, Haughton & Brink. 1954 cited in The Paleobiology Database)

This gave the following situation by the 1960s to mid 70s (from Colbert 1969)

```
Subclass Anapsida
          Order Chelonia
                     Suborder ?Eunotosauria (doubtful ancestor)
                     Suborder Proganochelydia
                     Suborder Amphichelydia
                     Suborder Pleurodira
                     Suborder Cryptodira
```

A revolution in chelonian systematics occured with Eugene Gaffney's ground-breaking application of cladistic methodology. The aim was to find a testable methodology for determining evolutionary relationships (i.e., phylogeny), along the requirements suggested by philosopher of science Karl Popper, according to whom science should be understood as series of refutable but not confirmable hypotheses. Here Willi Hennig's phylogenetic systematics was selected as the most fruitful approach (Gaffney, 1975 pp.391-2). Hennig had developed cladistics to understand insect evolution, insects have a notoriously poor fossil record. This was one of the first instances of cladistics (phylogenetics) applied to a tetrapod taxon, well represented by fossils. As a result of detailed analysis, Gaffney rejected paraphyletic taxa like Proganochelydia and Amphichelydia, although *Proganochelys* itself was recognised as an ancestral form. The genera previously placed in the Amphichelydia were relocated among the monophyletic Pleurodira and Cryptodira (however Proganochelydia was retained in Linnean classifications (e.g. Wikispecies). This gave the established consensus from the mid 70s to the mid noughties (Gaffney, 1975, Carroll, 1988, Meylan 2001), as shown by the cladogram on the left



Testudine cladogram, based on Gaffney, 1975 and later papers, showing both extinct and living forms. From the *Encyclopedia of Life Sciences*, via biogeography of leatherback turtles.

At the base was *Proganochelys* . From this ancestral stem (to which were later added additional very basal forms like *Australochelys* and *Palaeochersis*), as early as the Late Triassic to Earliest Jurassic, chelonians had already diversified into the two established clades, the Cryptodira and Pleurodira. Neither group had any mechanism for withdrawing the neck under the shell in these basal forms. Both groups independently evolved this defense mechanism much later, during the Cretaceous.

Morphology or Molecules?

The relation between the Pleurodira, Paracryptodira, and Eucryptidira has become somewhat more complicated following molecular phylogenies. In both earlier and more recent cladistic morphological-based accounts, the Pleurodira are always distinct from the Cryptodira, the two being monophyletic taxa . This is the case regardless of whether there is an earlier Gaffney, 1975, Gaffney and Meylan, 1988) or later (Joyce 2007) divergence between the two groups. Moreover, the Trionychoidea or soft-shelled turtles are nested deep in the Cryptodiran crown group. This has been challenged by certain molecular studies (Krenz et al 2005, Barley et al. 2010) which not only are unanimous regarding the polyphyletic (artifical) status of the Trionychoidea, but also place one group, the Trionychia (= Trionychoidae), at the base of the Cryptodiran family tree (Shaffer, 2009, Barley et al. 2010, p.1190). A few results even raise the possibility that the pleurodires are a specialised branch of cryptodires, and the Trionychia being the most basal group. This would mean the cryptodire condition being the ancestral morphological states and the pleurodire the derived one. It also means that the cryptodire neck retraction mechanism evolved twice. Several cladograms also nest the pleurodire within the cryptodires (and not just within the cryptodires but the eucryptodires) (Joyce 2007 p.56 fig.15, Anquetin, 2009 pp.187f), and this counter-intuitive result may be simply due to convergent characteristics (Joyce 2007 p.53), although the general parallel with some of the molecular trees is intriguing. However whether the cryptodires are paraphyletic or monophyletic vary according to the type of analysis, as shown in the phylograms below. In any case it would seem that these various groups probably emerged through a rapid evolutionary radiation (Danilov & Parham, 2006, p.579; Krenz et al 2005, p.189, but see Shaffer, 2009 for the opposing view) the possibility that the pleurodires are a specialised branch of cryptodires, p.189;), which is why resolation of the branching order is difficult. Whatever the truth of the situation, chelonian evolution is clearly a lot stranger and more complex then was previously supposed. MAK100902

A few cladograms

After Gaffney et al 1991; Gaffney, 1996 (using Hennigian cladistics):	After Joyce 2007 (a seminal computational-cladistic morphology-

```
o (all testudines)
|--Proganochelys
`--o Casichelydia
   |---Pleurodira
   `---o Cryptodira
       |--Paracryptodira
       `---o Eucryptodira
           `--+--Plesiochelyidae
              `--+--Xinjiangchelyidae
                 `--o Centrocryptodira
                    |--Meiolanoidea
                    `--+==Sinemydidae/Macrobaenidae
                       `--o Polycryptodira
                          |--o Chelydridae
                          |  |--Chelydra
                          |  `--Platysternon
                          `--o Procoelocryptodira
                             |--Chelonioidea
                             `--+--o Trionychoidea
                                |  |--Kinosternoidea
                                |  `--Trionychoidea
                                `--Testudinoidea
```

based paper):

```
o (all testudines)
|--Proganochelys
`== Assorted stem forms
   `--+--o Pleurodira
      `--+--Paracryptodira
         `---o Eucryptodira
             `== Plesiochelyidae
(paraphyletic)  `--+-
-Xinjiangchelyidae `--
+==Sinemydidae        `---o
Cryptodira crown group    |-
-Chelonioidea             `--+-
-Chelydridae                 `--
+--Platysternon
|--o Trionychoidea
|  |--Kinosternoidea
|  `--Trionychia
`--Testudinoidea
```

After Krenz et al 2005 (option A) (and Barley et al. 2010 option B is similar):

```
o (all testudines)
`--+--Carettochelyidae
   `--+--Trionychidae
      `--+--Pleurodira
         `--+--+--+--Kinosternidae
            |   |   `--Chelydridae
            |   `--Chelonioidea
            `---Testudinoidea incl. Platysternon
```

Here both Cryptodira and Trionychia are paraphyletic

After Krenz et al 2005 (option B) and Barley et al. 2010 (option A): This would also be the consensus molecular phylogeny of later papers with a monophyletic Cryptodira and Trionychia

```
o (all testudines)
|---Pleurodira
`---o Cryptodira
    |--o Trionychia
    |  |--Carettochelyidae
    |  `--Trionychidae
    `--+--+--+--Kinosternidae
        |   |   `--Chelydridae
        |   `--Chelonioidea
        `---Testudinoidea incl.
Platysternon
```

Here is a phylogeny by Danilov & Parham, 2008, based on Chinese discoveries (including *Yehguia*, the oldest known trionychoidan) :

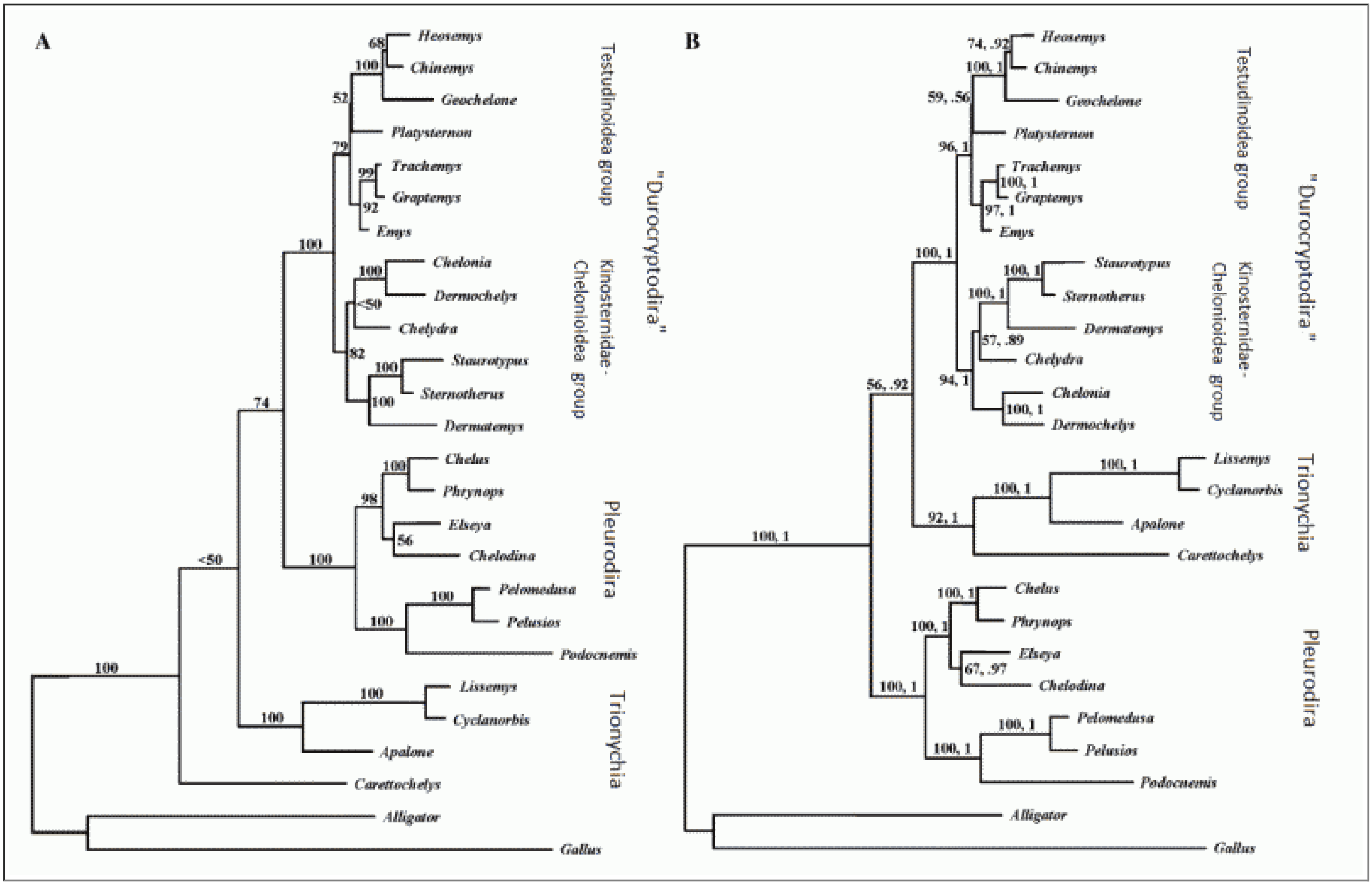
```
o Eucryptodira
`--+--Plesiochelyidae
   `==+== Sinemydidae  (paraphyletic)
        `--+--Xinjiangchelyidae
           `---o Cryptodira crown group
               |--+--Adocusia
               |  |--Peltochelys
               |  `--Trionychia
               `--o Durocryptodira
                  `--+--+--Platysternon
                     |   `--Testudinoidea
                     `--+--Kinosternidae
                        `--+--Chelydridae
                           `--+-- Some Macrobaenidae
                              `--Chelonioidea
```

Placing Sinemydidae stemward of Xinjiangchelyidae contradictrs all other cladistic analyses. The earlier paper Danilov & Parham, 2006 introduced the Durocryptodira, a name that did not catch on among later workers, probably because morphology-based hypotheses have a totally different tree topology, and molecular-based hypotheses tend only to use names based on recent taxa

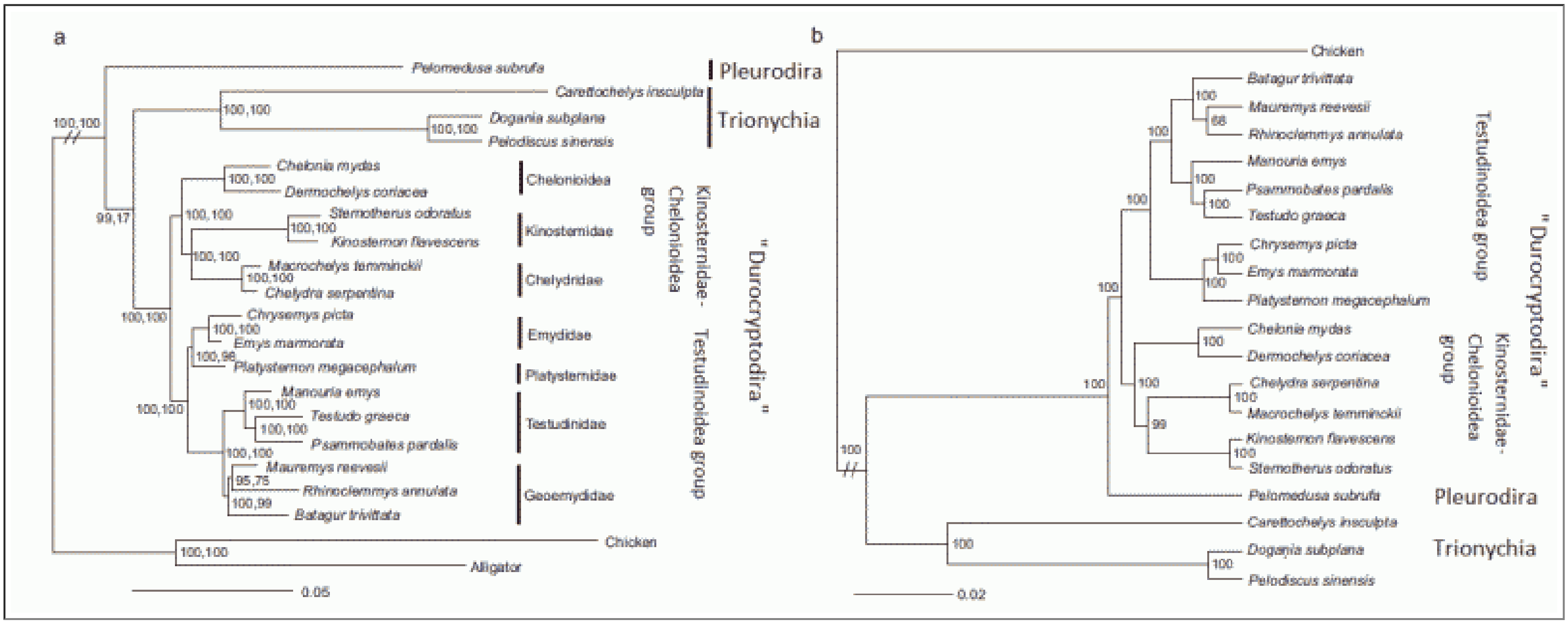
After Anquetin, 2009 (building on the work of Joyce 2007):

```
  o (all testudines)
  |--Proganochelys
  `== Assorted stem forms
    `--+--Paracryptodira
       `--+--Plesiochelyidae
          `--+-
-Xinjiangchelyidae
             `--+--o
Panpleurodira
                `---o Cryptodira
crown group
                    |==
Macrobaenidae/Sinemydidae
                    |-
-Chelonioidea
                    `--+--+-
-Kinosternoidea
                       |  `-
-Trionychia
                       |-
-Chelydridae
                       `-
-Testudinoidea
```

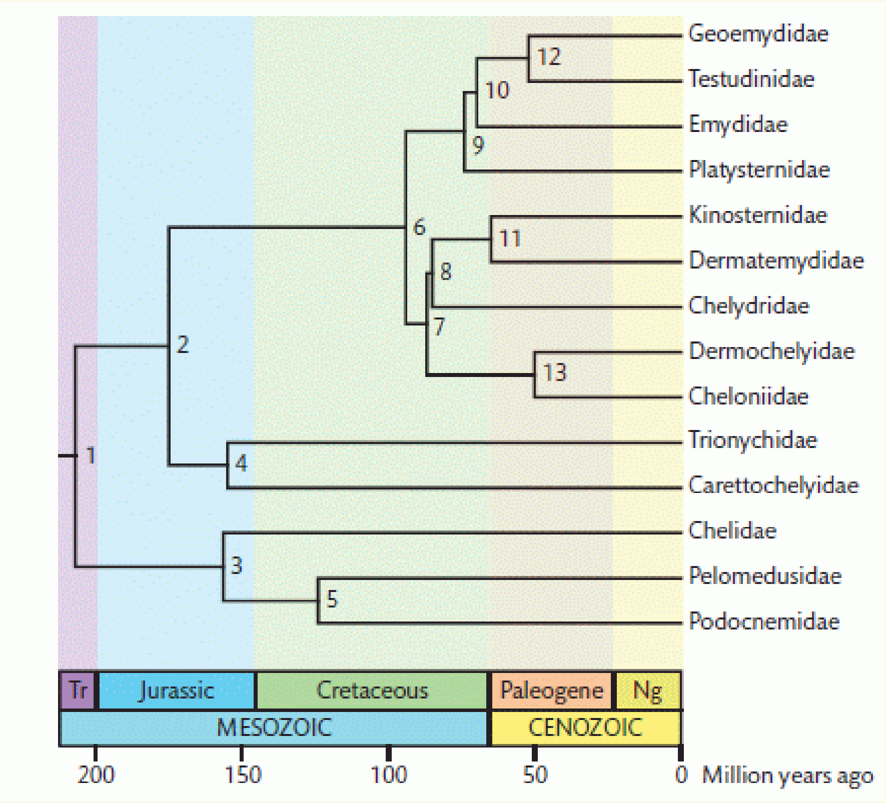
The following diagrams combine two sets of molecular analyses with the Trionychia + Durocryptodira of Danilov & Parham, 2006 and 2008:



Molecular phylogeny according to Krenz et al 2005, (A) Maximum parsimony phylogram for 2793 nucleotides of RAG-1 ((Recombination activating gene,a slowly evolving gene which has a very homogeneous base composition across the included taxa (Krenz et al 2005, p.186.)) for 24 turtle species. (B) Maximum likelihood and Bayesian analysis phylogram of RAG-1. Similar results are had using a combined analysis of RAG-1, cytochrome b, and 12S rDNA nucleotides (ibid, p.187 fig.5).



Molecular phylogeny according to Barley et al. 2010. (a) Phylogram generated from concatenated phylogenetic analysis of 14 nuclear genes.. Concatenation uses phylogenetic reconstruction is done after the gene sequences are concatenated head-to-tail to form a super-gene alignment, in contrast to the consensus approach where phylogenies are inferred separately for each gene and the resulting gene trees are used to generate a consensus phylogeny (Gadagkar et al 2005, pp.64-5). (b) Species tree generated from BEST phylogenetic analysis of 14 nuclear genes. BEST uses the joint posterior distribution of gene trees in order to estimate a species tree in a multiple locus analysis (Liu & Pearl, 2007)



Molecular phylogeny matched with molecular clock (note that molecular clocks aren't the same as molecular phylogeny, although the two are often matched), which supports an early diversion of Pleurodires and Cryptodires (Gaffney, 1975), but is incompatable with more recent analyses and discoveries (Joyce 2007 ,Sterli, 2008, Anquetin et al. 2009), from Shaffer, 2009 (url) and more recent molecular dating (Lourenço et al 2012 p.502). I tend to be sceptical of too much reliance placed on the molecular clock, because it assumes that evolution proceeds at a steady rate. In fact there many obstacles to accurate molecular dating, including not only rate heterogeneity but also use of inappropriate fossils as a source for calibration dates and the fact that fossils will almost always underestimate lineage originations (Parham & Irmis, 2008, p.132) However, the antiquity of the Trionychia (Danilov & Parham, 2006 is supported here. By this dating the Paracryptodires and Eucryptodires would be located between node 2 and node 6

Over the last several years however, this picture has been supplemented and challenged by new cladistic studies. The main thesis here is Joyce 2007 , which supports the earlier but then forgotten work of Dryden 1988. This has been supplemented by new discoveries (Anquetin, 2009, Anquetin et al. 2009, Sterli, 2008), all of which place the pleurodire-cryptodire divide much later, so that a number of basal genera previously considered pleurodires or cryptodires are now understood to be part of a diverse assemblage of transitional stem forms. These intermediate types were placed at the stem of the Chelonian tree, albeit higher up than *Proganochelys* and company, but predating the Pleurodire-Cryptodire split. *Proterochersis* and *Kayentachelys* (previously considered the earliest pleurodire and cryptodire respectively) , along with a host of Jurassic and later forms, now represent a paraphyletic assemblage of basal types. In this revised phylogeny, true pleurodires and cryptodires did not appear until the mid to late Jurassic.

Concerning this, a few more cladograms (or more technically, dendrograms), emphasising stem testudine taxa (refs Mikko's Phylogeny Archive, Joyce 2007 p.4, and Anquetin 2009 p.13), can be offered here:

After Gaffney, 1996 and Meylan 2001 (building on Gaffney, 1975, the classic morphology-based cladistic study).

```
o (all testudines)
|--Proganochelys
`--+--Australochelys
   `--+--+--Proterochersis
      |     `--o Pleurodira
      `--+--Kayentachelys
         `--+--Kallokibotion
            `--+--o Paracryptodira
               |   |--Pleurosternidae
               |   `--Baenidae
               `--o Eucryptodira
                   |--Plesiochelyidae
                   `--+--Xinjiangchelys
                      `--o Centrocryptodira
                         |--Meiolania
                         `--+==Sinemydidae/Macrobaenidae
                            `--o Polycryptodira
```

After Dryden, 1988	After Hirayama, Brinkman, & Danilov, 2000

```
  o (all testudines)
  |--Proganochelys
  `--+--Kayentachelys
     `--+--Meiolania
        `--+--Pleurosternidae
           `--+--Baenidae
              `--+--Plesiochelyidae
                 `--o Testudines crown group
                     |--Pleurodira
                     `--Cryptodira crown group
```

```
  o (all testudines)
  |--Proganochelys
  `--+--Australochelys
     `--+--+--Proterochersis
        |  `--Pleurodira
        `--+--Kayentachelys
           `--+--+--+-- Sinochelyidae
              |  |  `--Otwayemys
              |  `--+--Meiolania
              |     `--Mongolochelys
              `--+--Kallokibotion
                 `--+--Paracryptodira
                    `--+--Plesiochelyidae
                       `--+--Plesiochelyidae
                          `--+==Sinemydidae
                             `--+--Extant
Cryptodira
```

After Joyce 2007 p.62 (selected taxa) - this was the definitive paper on which most later analyses are based:

```
  o (all testudines)
  |--Proganochelys
  `--+--Palaeochersis
     |--Australochelys
     `--+--Proterochersis
        `--+--Kayentachelys
           `--+--+--Mongolochelys
              |  `--Meiolania
              `--+--Kallokibotion
                 `--o Testudines crown group
                    |--Pleurodira
                    `--+--Paracryptodira
                       `--+--Eucryptodira
                          `--Cryptodira
```

After Sterli, 2008 (*Condorchelys*):

```
  o (all testudines)
  |--Proganochelys
  `--+--+--Palaeochersis
     |  `--Australochelys
     `--+--Kayentachelys
        |--Condorchelys
        |--Indochelys
        `--+--Heckerochelys
           `--+--+--Mongolochelys
              |  `--Meiolania
              `--+--Kallokibotion
                 `--Testudines crown group
```

After Anquetin, Barrett, Jones, Moore-Fay & Evans, 2009 (*Eileanchelys*):

```
  o (all testudines)
  |--Proganochelys
  `--+--Palaeochersis
     `--+--Australochelys
        `--+--Proterochersis
           `--+--Kayentachelys
              |--+--Eileanchelys
              |  `--Heckerochelys
              `--+--+--Mongolochelys
                 |  `--Meiolania
                 `--+--Kallokibotion
                    `--Testudines crown group
```

After Danilov & Parham, 2008:

```
  o (all testudines)
  |--Proganochelys
  `--+--Palaeochersis
     |--Proterochersis
     |--Australochelys
     `--+--Kayentachelys
        `--+--+--Mongolochelys
           |   `--Meiolania
           `--+--Kallokibotion
              `--+--Paracryptodira
                  `--o Testudines crown group
                     |--Pleurodira
                     `--+--Plesiochelyidae
                        `==+==Sinemydidae
                             `--+--+-
-Xinjiangchelyidae
                                |   `-
-Chengyuchelys
                                `--o Cryptodira
crown group
                                    |-
-Trionychia
                                    `--o-
-Durocryptodira
                                       |== Some
Macrobaenidae
                                       `-- Other
Durocryptodira
```

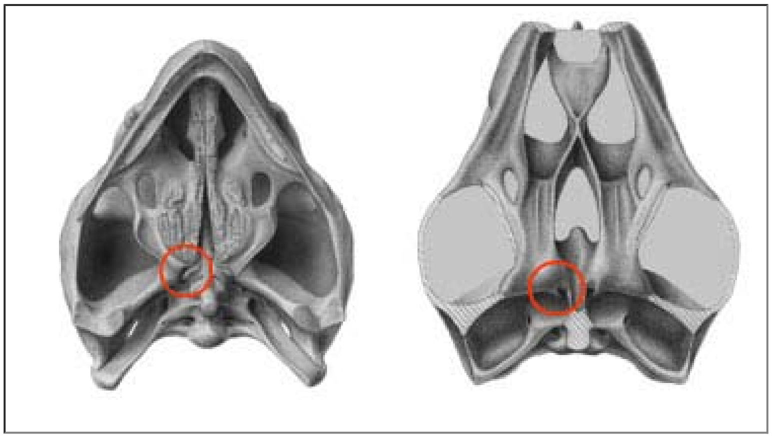
After Anquetin 2009 p.188 (selected taxa):

```
o (all testudines)
|--Odontochelys
|--Proterochersis
`--+--  Proganochelys
   `--+--Palaeochersis
      |--Australochelys
      `--+--Kayentachelys
         |--Indochelys
         `--+--Heckerochelys
            |--Chengyuchelyidae
            `--+--Eileanchelys
                `--+--o Meiolaniidae (incl.
Mongolochelys)
                   `--+--Kallokibotion
                      `--+--o Paracryptodira
                         `--+--o Plesiochelyidae
                            `--+--o
Xinjiangchelyidae
                               `--+--o Pleurodira
                                  `--o Cryptodira

|==Sinemydidae/Macrobaenidae
                                     `--o Other
Cryptodira
```

One reason for the very different phylogenies aquired through Gaffney and his coworkers on the one hand, and more recent authors, is the former consider choosing fewer, well-analysed characters is better than large numbers of poorly analysed characters (Gaffney et al 1991. The ability of more and more powerful computers to process greater amounts of quantitative data does not necessarily give more accurate trees. Another problem is homoplasy, the independent aquiring of the same characteristics by different lineages. Hence the contradiction between what might be called the Gaffney paradigm and the Joyce paradigm, and the even bigger problem of the disjunction between morphology-based and molecular analyses. MAK110922 130311

Descriptions



Palate view of skull of *Proganochelys* (left) and *Australochelys* (right) showing basicranial articulation. *Proganochelys* has an open articulation, indicating its primitive status. More advanced chelonians, such as *Australochelys*, *Palaeochersis*, and *Proterochersis*, and all more derived forms, have a fused articulation. Graphics from the Royal Tyrrell Museum - Phylogeny of Turtles - the reasearch interests of Eugene Gaffney

Casichelydia Gaffney, 1975

Range: from the Late Trassic. Cosmopolitan

Phylogeny: Testudines **:** *Proganochelys* + *Chinlechelys* + * **:** *Australochelys* + Palaeochersis + (*Proterochersis* + Cryptodira)

Characters: closed interpterygoid vacuity, middle ear with lateral wall present (Gaffney, 1975 p.430), lacrimal formane absent, vomer single,, fusion of braincase and palate (Benton, 2004 p.233)

Comments: "Casichelydia" was coined by Gaffney, 1975 for Pleurodira + Cryptodira. The discovery of a number of new primitive Middle Jurassic species, and the current statistical-computational approach in cladistic methodology, means that a number of taxa that have since been relocated outside the turtle crown group (see e.g. Joyce 2007, Anquetin et al. 2009, and Sterli, 2008 and comment here)

[2] To explain the jargon listed under "characters" above (most of the following is taken pretty much verbatum from Meylan 2001's very readable explanation): Much of early testudine evolutions involved a reduction in the number of bones that make up the skull. The lacrimal bone and lacrimal duct (which is the basic or primitive condition for amniotes) occurs in *Proganochelys* but not any other chelonians. Likewise, the presence of a pair of vomers seems to be a primitive amniote condition. Again, *Proganochelys* has two, all other chelonians one. A supratemporal bone is found in primitive tetrapods including Proganochelys, but not in higher testudines. As well as the reduction in the number of bones (which no doubt helps to strengthen the skull), there is also a closing up of the skull which again results in a more solid structure. The moveable articulation of fusion of braincase and palate (or neurocranium and palatoquadrate to use osteological jargonspeak), which is found in generalized amniotes and in *Proganochelys* is absent in *Australochelys* and other chelonians (see diagram), where these elements are tightly sutured. Generalized amniotes, such as captorhinids, and also Proganochelys, have a middle ear region that is open at least at the sides (laterally) and the bottom (ventrally). Technically speaking, Casichelydia should include the LCA of *Proterochersis* and *Kayentachelys* and all their descendents, which means that it does not include *Australochelys*. However I have followed the account given by Meylan 2001. Benton, 2004 p.233 gives a cladogram that distinguishes between the node leading to *Australochelys* and the next one up which is the Casichelydia. But the characteristics he give for each are both covered by Meylan 2001. MAK100917 130120

References: Gaffney, 1975 pp.425, 430; Meylan 2001; Benton, 2004 p.233 .

Links: Palate view of *Proganochelys* and *Australochelys*

Australochelys

Range: Early Jurassic of South Africa.; related form (*Palaeochersis*) from Late Triassic of Sth Am.

Phylogeny: Casichelydia **:** Palaeochersis + (*Proterochersis* + Cryptodira) + *

Characters: fusion of braincase and palate (see graphic, below left), partial enclosure of middle ear. Retain some palatial teeth and long tail. May or may nor form a monophyletic clade (family Australochelydidae) with *Palaeochersis* MAK100917 130120

References: Gaffney and Kitching 1994, Gaffney and Kitching 1995, Benton 2000 p.235

Palaeochersis : *Palaeochersis talampayensis*

Range: Latest Triassic of South America. (Upper Los Colorados Formation, Argentina)

Phylogeny: Casichelydia **:** *Australochelys* + (Proterochersis + Cryptodira) + *

Comments: Study of forelimb proportions shows that, like the related but more primitive *Proganochelys*, this was a terrestrial form, indicating a terrestrial origin for early testudines (Joyce & Gauthier, 2004). Included with *Australochelys* in the Australochelydidae MAK100917

Graphic: Paleoargentina

Size: Length: 70 cm

References: Rougier et al. 1995

Links: Palaeocritti - Palaeochersis talampayensis

Proterochersis

Range: Late Triassic of Europe.

Phylogeny: Casichelydia **:** *Australochelys* + Palaeochersis + (*Cryptodira* + *)

Comments: *many standard pleurodire features, e.g., pelvis fused to shell. For this reason was for a long time considered the oldest known pleurodire (e.g. Gaffney, 1975, Carroll, 1988, Gaffney & Meylan 1988, Hirayama, Brinkman, & Danilov, 2000, Meylan 2001, etc). The current consensus however is that this represents an earlier stem-testudine (Joyce 2007, Anquetin 2009, Sterli, 2010, Pérez-García & Murelaga 2012, etc etc) that predates the Pleurodires. As parallelism seems to be frequent in testudine evolution, it would not be surprising if pleurodire features arose several times independently. MAK130120*

Links: *Studium Integrale Journal 6/2 (Oktober 1999): Streiflichter (German); Untitled Document; Pleurodira. 010412.*

Graphic: *Plastron of Proterochersis robusta, photograph by Ghedoghedo, Wikipedia*

Cryptodira **:** *snapping turtles, soft-shells, tortoises & sea turtles.*

Range: *from the Early Jurassic*

Phylogeny: *Casichelyidia* **:** *Australochelys + Palaeochersis + (Proterochersis + ** **:** *Kayentachelys + Condorchelys + Eileanchelys + (Meiolanoidea + (Kallokibotion + Hispaniachelys + Testudines crown group)))*

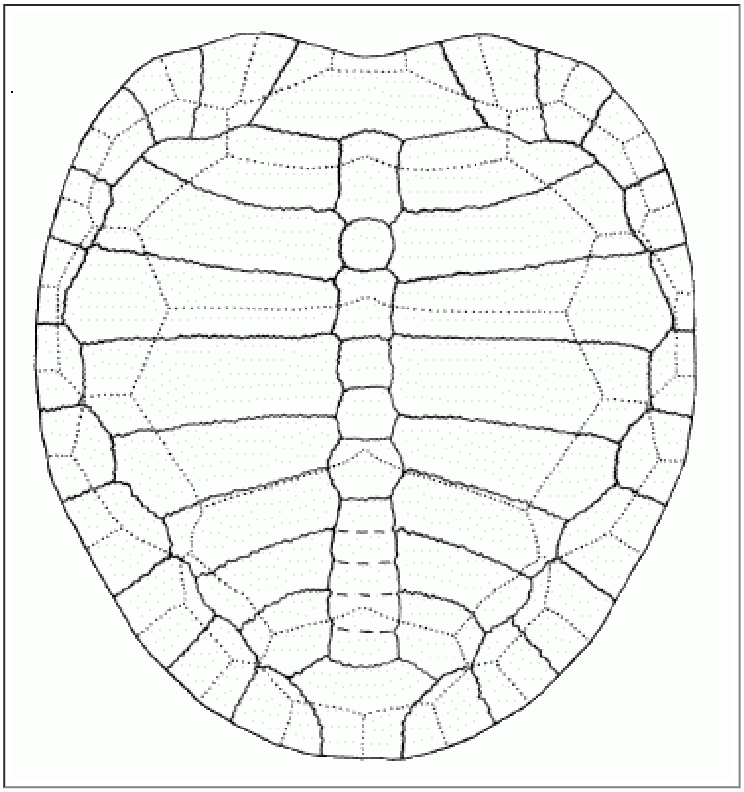
Characters: *Head (refer to BIODIDAC): pentagonal in dorsal view, with 2 large temporal emarginations dorsally; parietal covers the crown of the skull, which is markedly domed and tapers to a thin ridge between emarginations; this post parietal process overlies a long post supraoccipital process; occipital condyle below, and overhung by, supraoccipital process; ventrally, the skull has 2 large openings roughly below the emarginations, with a strong pterygoid bar passing between them; post margin of skull formed dorsally by squamosal + opisthotic & ventrally by quadrate + basisphenoid; small medial frontals ant to parietals; broad postorbitals form sides; prefrontal at apex pf rostrum; prefrontal and vomer in contact; (refer to BIODIDAC) upper jaw formed by maxilla w. small premaxilla at tip, both covered in life with keratinous beak; jugal and quadratojugal line up posterior to maxilla;* **$** *jaw adductor tendon passes over process of otic capsule formed by prootic and quadrate; adductor may pass over parietal as well in some species.;* **$** *vertical flange on external process of pterygoid; lower jaw (see BIODIDAC) formed largely by dentary and surangular; dentary has splenial and (post to splenial) a coronoid; retracted neck bent vertically; neck bend by way of specialized condyles – details vary among species. & may have evolved independently; no J forms have ability to retract neck; 2 relatively distinct sacral vertebrae; pelvic girdle sutured (not fused) to both plastron and carapace (see BIODIDAC and shellgirdle). Dominant crown group except in Aus; only Recent turtles in Northern hemisphere. ATW030531*

Comments. *Traditionally considered the sister group to Pleurodira (Gaffney, 1975, Joyce 2007) although some morphological findings nest the Pleurodires within the Cryptodires, making the latter paraphyletic group (Danilov & Parham, 2006, and Anquetin, 2009), some molecular research suggests likewise (Krenz et al 2005, Barley et al. 2010). The current nomenclatural tendency now is limit the clade to Crown Cryptodira (= Polycryptodira Gaffney), although not everyone agrees with this form of taxonomy (see notes on "tetrapoda"). To retain consensus with both Evolutionary Linnaean (e.g. Carroll 1988) and Hennigian (via Gaffney) formalism we are using a morphology- (in cladistics-speak "apomorphy") based definition here instead MAK100917 130119*

Image: *Geochelone carbonaria from* ***Merkblätter****.*

Links: *Turtle, Tuatara, Crocodile Checklist--3; Halsbergers (Cryptodira); \Snapping Turtle Page\ - information and photo gallery page; WIEM: Zólwie skrytoszyjne (Polish); Higher Relationships of Testudines; Mongoleus; Order*

Testudines (Czech & English); Higher Reptile Taxa; Testudines; Cryptodira; Basal Cryptodira (Mikko's phylogeny); CRYPTODIRA (very nice summary of paleodiversity); APUS.RU | Подотряд Скрытошейные ·черепахи - Cryptodira; Halsbergerschildkröten (Cryptodira)- Kriechtiere (a remarkable set of links); Phylogeny of Turtles/Dr. E. S. Gaffney; tierdach.de- Halsberger-Schildkröten (German: possibly ***Best on the Web****); Dr. Robert Wocheslánder (abstracts); home2; Ocean Ambassadors -- Turtle Biology (sea turtles, natural history); Testudines Turtle Skull Reproductions; Jomonjin_KameDataBase. ATW030531. Wikipedia*



Kayentochelys aprix carapace, from Anquetin, 2009

Kayentachelys

Range: *Early Jurassic of North America (Arizona).*

Phylogeny: *Cryptodira* **:** *Condorchelys + Eileanchelys + (Meiolanoidea + (Kallokibotion + Hispaniachelys + Testudines crown group))) + **

Comments: *The oldest known cryptodire, based on its trochlear system, other characters, such as palatal teeth, are plesiomorphic with respect to all extant pleurodires and cryptodires (Dryden 1988, cited in Gauthier et al, 1989). As with Proterochersis, the current consensus, based on statistical cladistics, is that it predates the Pleurodire-Extant Cryptodire split. This means that cryptodire features are primitive for stem cryptodires. MAK130119*

Links: *Kayentachelys*.

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Chelonii: Derived Stem Testudines

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   |--Chinlechelys
   `--+--Australochelys
      `--+--Proterochersis
         `--o Cryptodira
            |--Kayentachelys
            `--+--Condorchelys
               |--Eileanchelys
               `--+--Solemydidae
                  |--Meiolaniidae
                  `--+--Kallokibotion
                     |?-- Hispaniachelys
                     `--o Testudines crown
group
                        |--Pleurodira
                        |--Paracryptodira
                        `--Eucryptodira
```

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2. Crown Group Testudines
3. Cryptodira
4. *Eileanchelys* X
5. *Hispaniachelys* X
6. *Kallokibotion* X
7. Solemydidae X

Descriptions

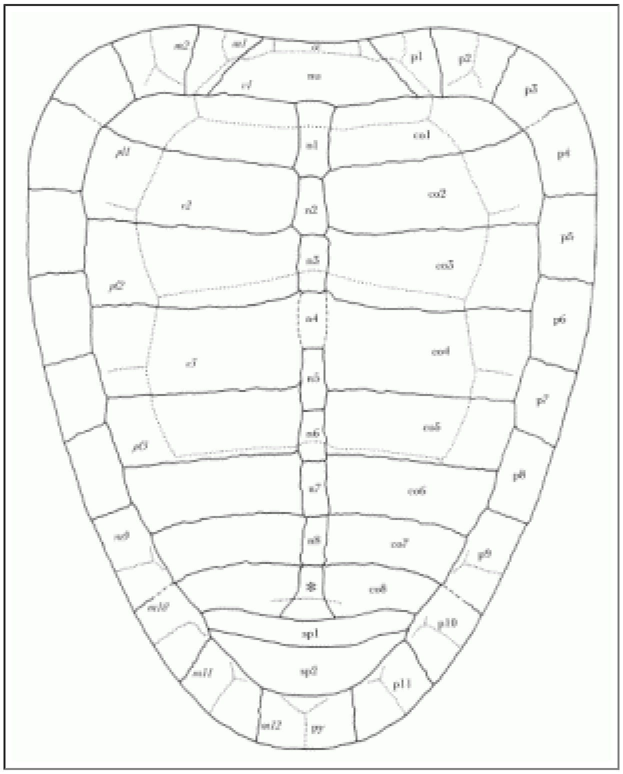
Condorchelys: *Condorchelys antiqua*.

Range: Middle to Upper Jurassic of SA (Patagonia & Argentina).

Phylogeny: Cryptodira : *Kayentachelys* + *Eileanchelys* + (Solemydidae + (Meiolanoidea + (*Kallokibotion* + *Hispaniachelys* + Testudines crown group))) + *

Comments: A late surviving, primitive chelonian, similar to early Jurassic forms like Kayentocheyls and *Indochelys*, but also possessinga number of more advanced features. Cladistic analysis shows that these are stem forms, which were more diverse than previously thought. Differ from more advanced forms in having a primitive jaw closure mechanism.

References: Sterli, 2008.



Eileanchelys waldmani carapace, from Anquetin, 2009

Eileanchelys: *Eileanchelys waldmani*.

Range: Middle Jurassic (Bathonian) of Scotland.

Phylogeny: Cryptodira : *Kayentachelys* + *Condorchelys* + (Solemydidae + (Meiolanoidea + (*Kallokibotion* + *Hispaniachelys* + Testudines crown group))) + *

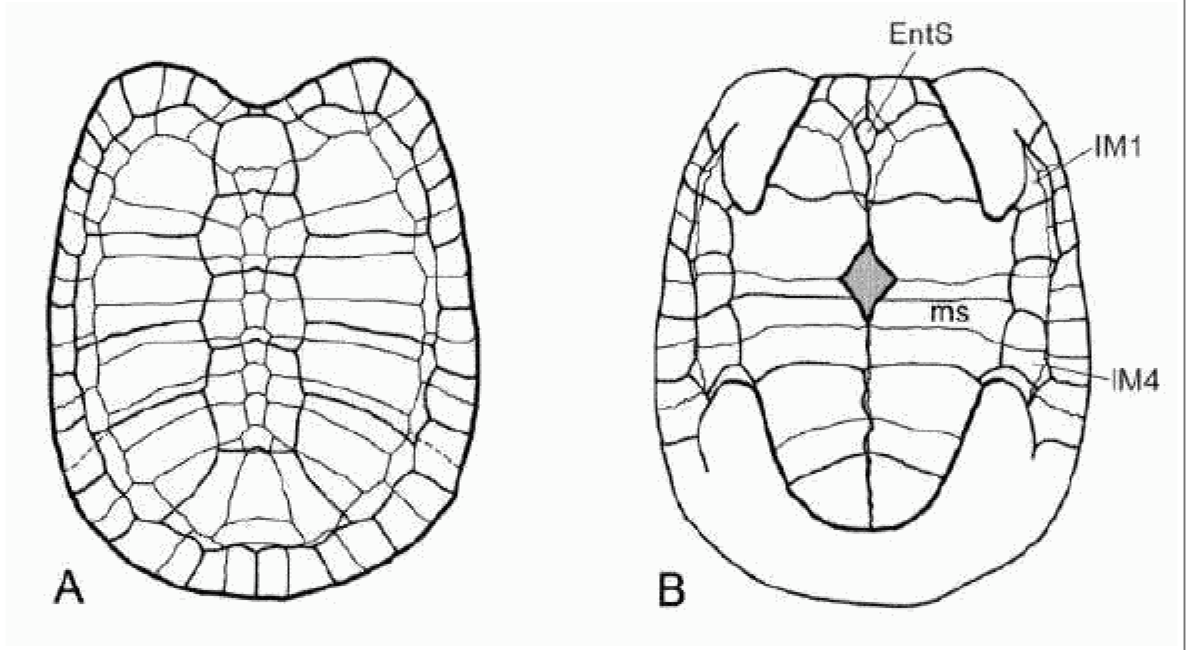
Comments: The earliest known aquatic turtle (*Odontochelys*). Known from cranial and postcranial material of several individuals, this is the most complete Middle Jurassic chelonian described to date. Like *Condorchelys*, this is a transitional form between the Late Triassic-Early Jurassic basal forms and the crown-group testudines that appear and diversify during the Late Jurassic. *Heckerochelys romani* from the Middle Jurassic of Russia is either closely related (Anquetin, 2009) or slightly closer to crown testudines (Joyce et al 2011, cladograms p.93).

Size: carapace length 25-30 cm

References: Anquetin, 2009, Anquetin et al. 2009.

Solemydidae Cope, 1868 : *Solemys*, *Helochelydra*, *Naomichelys*.

Range: Late Kimmeridgian (Late Jurassic) to Maastrichtian (Latest Cretaceous) of Europe; Aptian to Campanian (Mid to Late Cretaceous) of North America, also from Asia.



Solemys vermiculata, Late Createcous of Europe. Dorsal (A) und Ventral (B) view. Length of shell 1 meter. Drawing from Böhme, 2005, p.363.

Phylogeny: Cryptodira : *Kayentachelys* + *Condorchelys* + *Eileanchelys* + (Meiolanoidea + (*Kallokibotion* + *Hispaniachelys* + Testudines crown group) + *)

Comments: A group of poorly known, tall-shelled forms with a carapace upto a meter long. Shells distinguished by ornamentation of single raised knob- or pillar-like structures, covered by scutes The best known genus is *Solemys* of the Late Cretaceous (Campanian to Maastrichtian) of France and the Iberian Peninsula (Böhme, 2005, p.361). At least some species of genus *Solemys* had a lifestyle similar to extant fresh or brackish water turtles (terrapins) Marmi et al 2009, as the flattened solemydid palate implies an aquatic molluscivore. Both the North American *Naomichelys speciosa* and the English *Helochelydra* aff. *nopcsai* are known to have had limbs covered with osteoderms, indicating a terrestrial habitat. It may be that solemydids were opportunistic terrestrial omnivores that fed on plants, fungi, insects, and terrestrial snails, and may have searched decaying plant matter and dinosaur dung for grubs (Joyce et al 2011 pp.94-5. Along with Meiolaniidae, Chengyuchelyidae, Kallokibotionidae and Mongolochelyidae these are considered basal taxa, although affinities to Pleurosternidae have also been proposed. Hirayama et al 2000 consider *Solemys* a junior synonym of *Tretosternon* Owen, 1842 and included in the family Kallokibotionidae, and made *Naomichelys* another synonym. However Anquetin, 2009 p.195 includes *Naomichelys* in the Meiolaniid clade. Joyce et al 2011 include *Naomichelys* among the Solemydidae. Perhaps this genus represents a transitional form. Phylogenetic analysis by Joyce et al 2011, using a recently (1998) discovered nearly complete skull of *Helochelydra nopcsai* from the Barremian Wessex Formation of the Isle of Wight, places *Helochelydra* close to *Mongolochelys*, *Meiolania platyceps* and *Kallokibotion* just outside crown Testudines, but further relationships cannot be resolved with confidence. MAK100914 130120

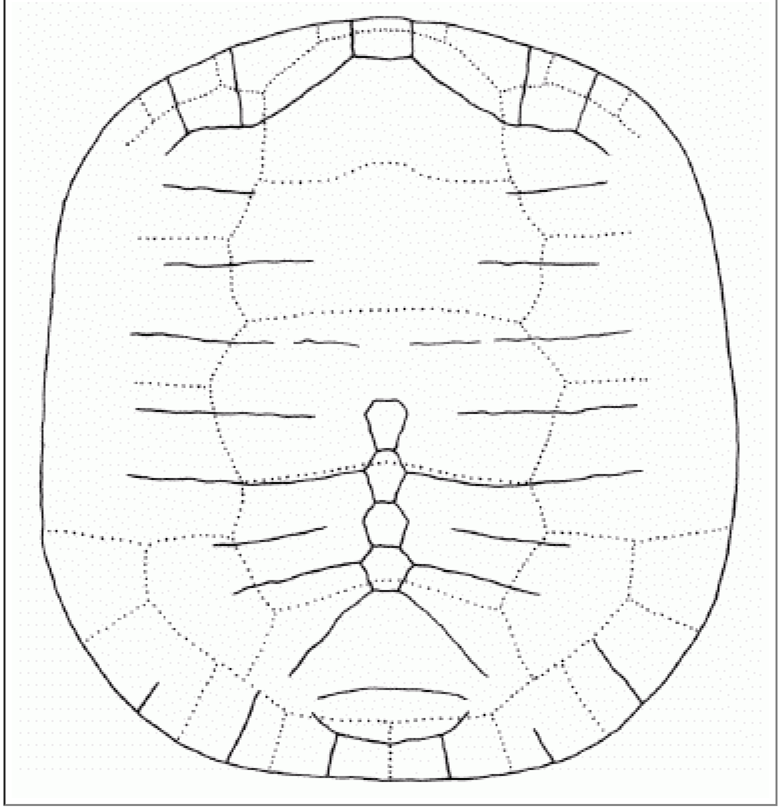
References: Hirayama et al, 2000 p.185; Scheyer 2007 pp.56-7, Joyce et al 2011

Kallokibotion *Kallokibotion bajazidi* Nopsca, 1923

Range: Late Cretaceous (Maastrichtian) of Romania

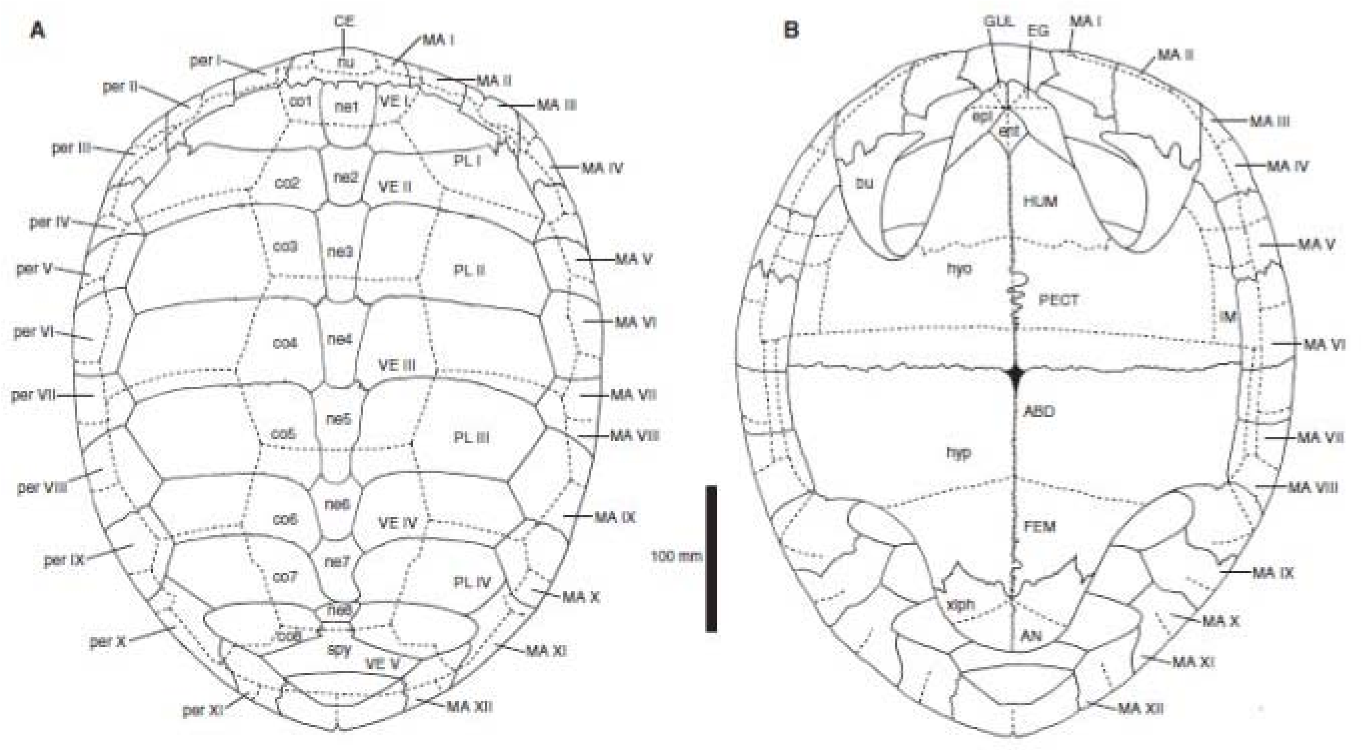
Phylogeny: Cryptodira : *Kayentachelys* + *Condorchelys* + *Eileanchelys* + (Solemydidae + (Meiolanoidea + (*Hispaniachelys* + Testudines crown group *)))

Comments: Probably aquatic. The skull of *K. bajazidi* is about 40 cm long (Zittel, Eastman,



Kallokibotion bajazidi carapace, from Anquetin, 2009

Woodward, et al(1932) p.306), making this among the larger of the chelonians. Some species attributed to "*Tretosternon*" (nomen dubum) may be related (Hirayama et al 2000 p.189), if so this clade extends from the earliest Cretaceous to the end of the period. *Kallokibotium* shows diagnostic baenoid features Gaffney, 1975 p.427, although computational-statistical cladistic analyses have been unanimous in placing this taxon as a siter species to crown testudines (e.g. Joyce 2007, Sterli 2008, Anquetin 2009, Anquetin 2012). However new phylogenetic analysis by Sterli, 2012 finds Kallokibotion to be a basal meiolaniid (or meiolanoid), which would give the latter clade a cosmopolitan distribution. The uncertain position of this genus is no doubt due to the plesiomorphic features it shares with meiolaniids and paracryptrodires. MAK100914 13021



Hispaniachelys prebetica restored carapace (A) and plastron (B). Abbreviations: ABD, abdominal scute; AN, anal scute; bu, axillary buttress; CE, cervical scute; co, costal bones; EG, extragular scute; ent, entoplastron; epi, epiplastron; FEM, femoral scute; GUL, gular scute; HUM, humeral scute; hyo, hyoplastron; hyp, hypoplastron; IG, intragular scute; IM, inframarginal scute; MA, marginal scute; ne, neural bones; nu, nuchal bone; PECT, pectoral scute; per, peripheral bones; PL, pleural scute; spy, suprapygal bone; VE, vertebral scute; xiph, xiphiplastron. From Slater et al 2011, © The Palaeontological Association

Hispaniachelys *Hispaniachelys prebetica* Slater et al 2011

Horizon: Lorente Formation; *Bimammatum* Ammonite Biozone, Late Oxfordian; Riogazas-Chorro-Sponges section, Sierra de Cazorla: Prebetic, southeast Spain

Phylogeny: Cryptodira **:** *Kayentachelys* + *Condorchelys* + *Eileanchelys* + (Solemydidae + (Meiolanoidea + (*Kallokibotion* + Testudines crown group + *)))

Characters: Basal features including dorsal epiplastral processes, reduced cleithra, no medial contact of the extragulars and a long first thoracic rib. Derived characters including an absence of mesoplastra and the vertebral 3 . 4 sulcus crossing neural 5. - Slater et al 2011

Comments: The oldest known turtle from southern Europe, features a mosaic of primitive and advanced characters. Either a basal testudine or a paracryptodire, but distinct from eucryptodires like *Plesiochelys*. MAK130121

Crown Group Testudines: Chelonia crown group (LCA extant turtles).

Range: from the Jurassic. Cosmopolitan

Phylogeny: Cryptodira **:** *Kayentachelys* + *Condorchelys* + *Eileanchelys* + (Solemydidae + (Meiolanoidea + (*Kallokibotion* + *Hispaniachelys* + * **:** Pleurodira + Paracryptodira + Eucryptodira)))

Comments: Uncertainty regarding the phylogenic placement of the Pleurodires makes this taxon quite ambiguous (see e.g. Gaffney, 1975 and Gaffhey and Meylan, 1988, Joyce 2007, Sterli, 2008, Anquetin et al. 2009, and Sterli, 2010). We are assuming here a pleurodire-paracryptodire-eucryptodire trichotomy. MAK130120

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Chelonii: Meiolaniidae and related chelonians

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--o Cryptodira
         |--Kayentachelys
         `--+--Condorchelys
            |--Eileanchelys
            `--+--Solemydidae
               |--o Meiolanoidea
               |   |--Chelycarapookus
               |   |--Chubutemys
               |   |--Naomichelys
               |   `--+--+--Mongolochelys
               |      |  `--Otwayemys
               |      `--o Meiolaniidae
               |         |--Niolamia
               |         `--+--Ninjemys
               |            `--Meiolania
               `---+--Kallokibotion
                   `--+--Pleurodira
                      |--Paracryptodira
                      `--Eucryptodira
```

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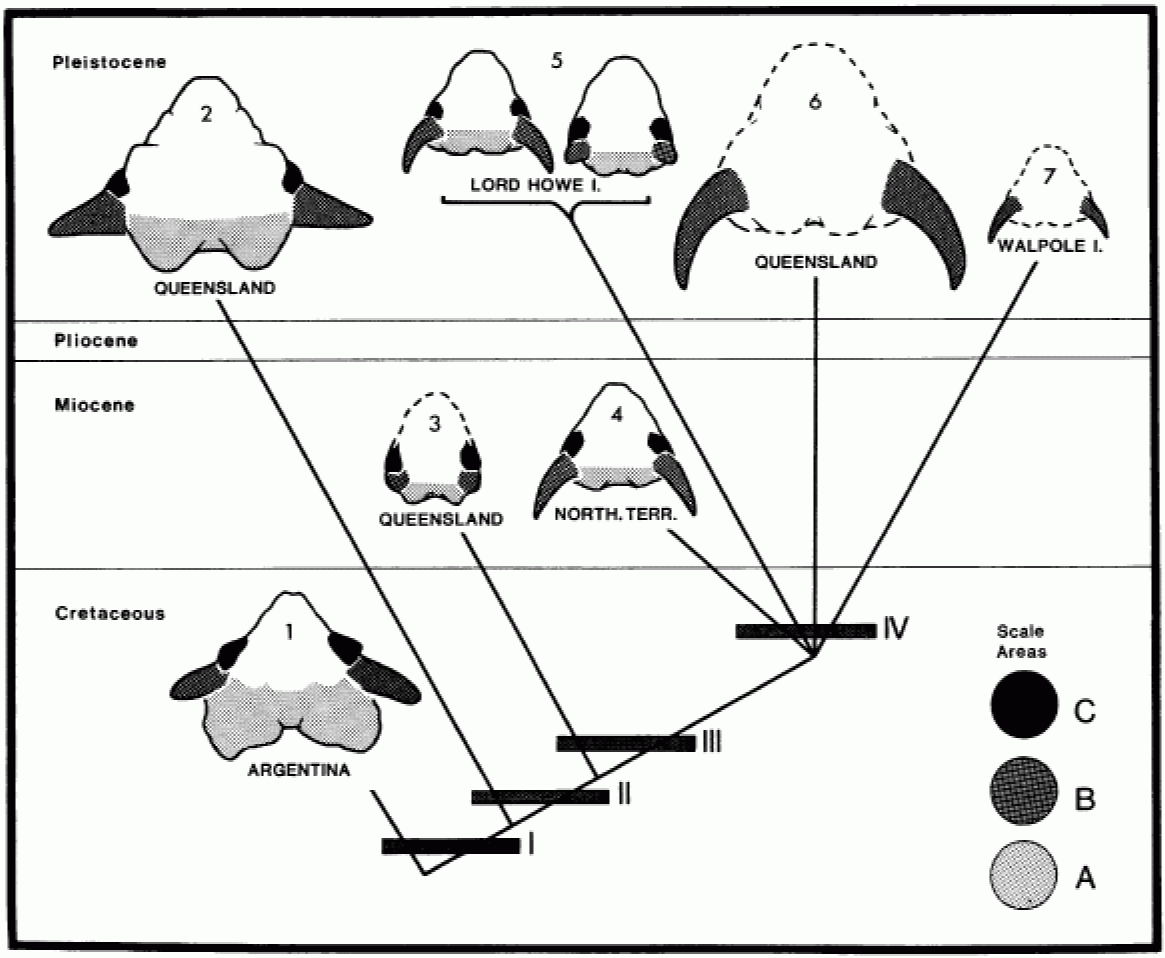
2. *Chubutemys* X
3. *Meiolania* X
4. Meiolaniidae X
5. Meiolanoidea X
6. *Mongolochelys* X
7. *Naomichelys* X
8. *Ninjemys* X
9. *Niolamia* X
10. *Otwayemys* X

The Meiolaniids

Meiolania platyceps, Pleistocene to Holocene.

The Meiolaniidae were among the most extraordinary of all the chelonia. They were an exclusively Gondwanan family, known from South America, Australia, and nearby islands, and it can therefore be is assumed that they also lived in Antarctica in the Cretaceous and early Tertiary. They were large, probably herbivorous forms, with heavily armored heads and tails. The unusually shaped skull was characterised by many knob- and horn-like protrusions. The tail was protected by armored 'rings' and sported thorn-like spikes at the end. The club-like tail evolved independently of a similar structure in *Proganochelys*, and even the ankylosaurids and glyptodonts, the latter also distinguished by armoured rings around the tail. The animal survived on south pacific Islands until very recently where, like other endemic Island populations, it had few or no natural enemies and was was particularily vulnerable to human predation.



Dendrogram of meiolaniids, showing three scale areas (A, B, C) for comparison. (1) *Niolamia argentina*, (2) *Ninjemys oweni*, (3) *Warkalania carinaminor*, (4) *Meiolania brevicollis*, (5) *Meiolania platyceps* (showing two extremes of horn variation), (6) *Meiolania* sp., Wyandotte, (7) *Meiolania mackayi*. Gaffney 1996 p.120

Gaffney 1996 devoted much study to these creatures, and noted that on the one hand they had features similar to modern cryptodires, but on the other were much more primitive in many ways. He therefore classified them as stem centrocryptodires, intermediate between the Xinjiangchelyidae and the Sinemydidae, Others such as Joyce 2007, Anquetin, 2009, etc, who used a computational-statistical approach to cladistics rather than Gaffney's recognisable synapomorphy-based hennigian method, unanimously give it a much more basal stem position, in this case its many eucryptodire features would be examples of convergence. If this hypothesis is correct, the Meiolaniids were the chelonian equivalent of monotremes, living fossils, a relict group surviving alongside their more successful pleurodire and cryptodire (or marsupial and placental, to continue the analogy) contemporaies. If this hypothesis is correct it makes their recent extermination at the hands of man even more tragic. [1]

The Gondwanan Meiolaniids have also been grouped with Asiamerican forms in a larger clade. According to Anquetin, 2009, the North American species *Naomichelys speciosa*, traditionally classified in the family Solemydidae, another very primitive group, is closely related to the Meiolaniids as well as to *Mongolochelys efremovi*. This would make either the Solemydids as a whole related, or exclude *Naomichelys* from the Solemydids. According to Sterli (ref), the latest Cretaceous European *Kallokibotion*, traditionally considered the sister taxon to higher testadines (pleurodira + paracryptodira + eucrypotodira, or equivalent), may also be related, which gives the Meiolanoidea a cosmopolitan distribution, as well as making it one of the more important of the early testudine clades. MAK110922, 130130

Notes:

[1] This also raises a question about the stability of phylogenetic nomenclature. If crown taxa are defined by their existence in the modern world, and the last representatives of an imnportant sub-clade are wiped out in historical (or even recent) time, do all the previously crown taxa that had been included suddenly become stem taxa? Is an arbitrary historical cut off point decided? And if it is, what are the defining factors. And for that matter, if a long-extinct animal, say a woolly mammoth, had to becloned and brought back to lifde (something conceivably possible within the next few decades given current advances in genetic engineering), would a previous stem group then become a crown clade?

Descriptions

Meiolanoidea.

Range: Cretaceous to Holocene, probably cosmopolitan during the Late Cretaceous.

Phylogeny: : : *Chubutemys* + (*Naomichelys* + ?Solemydidae) + (*Otwayemys* + *Mongolochelys*) + Meiolanoidea

Comments: the greatest surprise of recent cladistic analyses is the emergence of an important and previously unrecognised clade of stem testudines, of which the Meiolaniids are only the most specialised, and only Cenozoic, forms (Hirayama, Brinkman, & Danilov, 2000, Anquetin 2009, Sterli, 2010, Pérez-García & Murelaga (2012). The group seems to have originated in Western Gondwana sometime between the Middle Jurassic and the Early Cretaceous and if *Kallokibotion* is included it had a cosmopolitan distribution duyring the late Cretaceous (Sterli, 2012). The term Meiolanoidea is not usually used in the literature, but was suggested by Gaffney. An equally appropriate and complementary name is Ceratocryptodira (Bour & Dubois 1986).

Chubutemys copelloi

Range: Middle Cretaceous of Patagonia

Phylogeny:

Comments:

Chelycarapookus:

Range: Early Cretaceous

Phylogeny:

Comments: .

Naomichelys:

Range: Late Cretaceous of N Am

Phylogeny:

Comments:

Otwayemys :

Range: Early Cretaceous Eumeralla Formation, Victoria, Australia

Phylogeny: Casichelydia **:::** (Meiolaniidae + *Mongolochelys*) + *

Comments: The shell of *Otwayemys* is similar to *Xinjiangchelys* from the Jurassic of China; although it might be a member of the Centrocryptodira, possibly closely related to the Sinemydidae of Asia on the basis of the opisthocoelous cervicals Gaffney et al 1998. Both anterior and posterior caudals of this turtle, however, are opisthocoelous as in *Meiolania*, *Mongolochelys*, and baenids, and along with other factors (Hirayama et al 2000 p.189). A lot depends also on whether Meiolaniids are centrocryptodires or stem turtles; If the latter it would mean that formed central articulation on the cervical and caudal vertebrae (and therefore greater flexibility of the neck and tail, and the loss of mesoplastron (retained only in primitive forms) were acquired independently of the centrocryptodires.

References: Gaffney et al 1998

Mongolochelys: *Mongolochelys efremovi*,

Range: (Late Cretaceous (Maastrichtian) of Mongolia

Phylogeny: Casichelydia **:::** (Meiolaniidae + *) + (*Kallokibotion* + (Pleurodira + Cryptodira)) (Joyce 2007)

Comments: Large turtles, probably aquatic. Contain a unique combination of primitive and advanced features, the only Central Asian chelonian apart from the much earlier *Chengyuchelys*, to retain mesoplastra, a very primitive feature. Perhaps on this this basis, both these forms are generally considered stem Testudines. However there are no indications that these two general are otherwise related. In other features, variously resembles the early Jurassic *Kayentachelys*, the latest Cretacous (contemporary) Kallokibotion, and most of all the late Jurassic and Early Cretaceous Pleurosternidae (Sukhanov, 2003, p.349) whilst some unite it with the Meiolaniidae (Hirayama, Brinkman, & Danilov, 2000, Joyce 2007,Joyce 2007, Anquetin 2009, p.196, etc).

Links: *Albanerpeton* and *Mongolochelys* (life reconstruction), A catalog of Mongolochelys collected by the HMNS-MPC Joint Paleontological Expedition (PDF)

Carapace of *Mongolochelys* (Mongolochelyidae) from the Nemegt Formation, Late Cretaceous of Gurilin Tsav, Western Gobi.(from Suzuki & Narmandakh 2004)

Meiolaniidae Lydekker 1889 **:** huge, "horned" turtles.

Range: Eocene (or possibly Cretaceous) of Argentina, Miocene to the Pleistocene of Australia, Pleistocene to Holocene of nearby islands.

Phylogeny: Parent clades: Either Centrocryptodira **:** (Sinemydidae + Polycryptodira) + *
or Casichelydia **:::** Otwayemys + (*Mongolochelys* + *) (Hirayama, et al, 2000, Anquetin 2009, p.196)

Daughter clades: * **:** *Niolamia* (*Ninjemys* + *Meiolania*)

Characters: "horned" head; tail spiked, with club. The nasomaxillary sinuses are unique to meiolaniids, but their presence/absence can only be determined in *Ninjemys* and *Meiolania*. Their function is not known (Gaffney 1996 p.119; Anquetin 2009, p.196).

Comments: An isolated group that although similar to extant cryptodires cannot be matched with any specific groups (Carroll 1988 p.212). Studies by Gaffney put them in the Centrocryptodira Gaffney, 1996. More recent cladistic studies (Joyce 2007, Anquetin 2009) place them outside the Testudine crown group. These animals reached upto 2.5 meters in length (unlike recent chelonians, the tail is very long), with the horned skulls upto 30 to 50 cm wide. Like modern giant tortoises, which they resemble in size and perhaps lifestyle, they were most likely herbivores.

Links: Wikipedia

References: Shaffer et al. (1997). ATW020214.

Illustration: *Meiolania platyceps*, photograph by Claire Houck, Wikipedia/creative commons

***Niolamia*:**

Synonym: *Crossochelys*

Range: Cretaceous or Eocene of Argentina

Phylogeny: Meiolaniidae **:** (*Ninjemys* + *Meiolania*) + *

Comments:. The earliest known and least specialsed member of the family, known only from the skull and tail ring,

References: Gaffney 1996

***Meiolania*:** *M. platyceps*, *M. brevicollis*, *M. mackayi* and "Wyandotte species". However only *platyceps* and *brevicollis* can be diagnosed adequately (Gaffney 1996 p.92)-

Synonyms: *Miolania*, *Ceratochelys*

Front view of *Meiolania platyceps*. Specimen in Lord Howe Island museum. Wikipedia, photo by David Morgan-Mar

Tail view of *Meiolania platyceps*. Lord Howe Island Maritime Museum. Wikimedia - photo Fanny Schertzer

Range: Oligocene to Late Pleistocene of Australia, Pleistocene to Holocene of Lord Howe Island, New Caledonia, Vanuata, etc

Phylogeny: Meiolaniidae **:** *Niolamia* (*Ninjemys* + *)

Characters: snout broad, horns point to the rear

Comments:. The type genus and best known member of the family, common in the Pleistocene of Australia and nearby Lord Howe Island. Mainland forms has a shell length of about a meter, and an overall length of 2.5 meters. This makes it the second-largest known tortoise, surpassed only by the Pleistocene *Colossochelys atlas* of Asia. Specimens from New Caledonia and Lord Howe Island however were rather smaller, as a result of island dwarfism. Relic populations survived until only 2000 years ago, but were wiped out after only two hundred years (link), although it is even possible some may have survived until the 18th century (Gaffney et al 1984). The Pleistocene fossils from Lord Howe Island are particularly well-known.

Links: Meiolania the Horned Turtle; Meiolaniidae; Meiolania; PANGEA; qui (French); Fassaden (German); Wikipedia, photo - Australian Museum

References: Gaffney 1996

***Ninjemys*:** *Ninjemys oweni*

Range: Late Pleistocene of Queensland, Australia

Skull of *Ninjemys oweni*. Wikipedia - photo by Ghedo

Phylogeny: Meiolaniidae **:** *Niolamia* (*Meiolania* + *)

Characters: laterally projecting (side-pointing) B horns (the largest pair of horns); anterior extension of the nasals beyond rest of skull (Gaffney 1996 p.78); snout narrow (a primitive feature)

Comments: a large meiolaniid, immediately distinguished from *Meiolania* by the side-pointing horns. Known only from skull and tail. The generic name honours the Teenage Mutant Ninja Turtles. Its weight is estimated at 200 kg.

Links: Wikipedia

References: Gaffney 1996

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Chelonii: Pleurodira

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Meiolanoidea
         `--+--o Pleurodira
            |  |--Platychelys
            |  |--Dortokidae
            |  `--+--Chelidae
            |     `--Pelomedusoidea
            |        |--Podocnemoidae
            |        |  |--Bothremyidae
            |        |  `--Podocnemidae
            |        `--Pelomedusidae
            |--Paracryptodira
            `--o Eucryptodira
               |--Protostegidae
               `--+==Xinjiangchelyidae
                  `--+==Sinemydidae
                     |--Trionychoidea
                     `--+--+--Chelonioidea
                         |  |--Chelydridae
                         |  `--Kinosternoidea
                         `--Testudinoidea
```

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2. Chelidae
3. Dortokidae X
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5. Pelomedusoidea
6. *Platychelys* X
7. Pleurodira
8. Podocnemoidae
9. Podocnemidae

Pleurodires are now the less common of the two groups, restricted to the continents of the southern hemisphere, but they were once very widespread, both on land and in the estuaries and shallow seas round the coasts.

Descriptions

Pleurodira (= Panpleurodira of Joyce et al 2004)

Range: from Late Triassic (Gaffney, 1975, Shaffer, 2009) or Late Jurassic (Joyce 2007, Anquetin, 2009)

Phylogeny: *Parent clades:* a choice of options:
Pantestudines **:** Casichelyidia **:** Cryptodira + * **:** *Proterochersis* + (Eupleurodira **:** Daughter clades) (Gaffney, 1975)
Pantestudines **:** (assorted stem forms) **:** Cryptodira + * **:** Daughter clades (Joyce 2007, Sterli, 2008, Anquetin et al. 2009)
Pantestudines **:** (assorted stem forms) **:** Paracryptodira + (Eucryptodira **:** Xinjiangchelyidae + (Cryptodira + * **:** Daughter clades). (Anquetin, 2009) (inspired by Krenz et al 2005, Danilov & Parham, 2006, and Anquetin, 2009),
Daughter clades: *Platychelys* **:::** Chelidae + Pelomedusoidea.

Characters: Skull roof not complete; **$** no epipterygoid (not even cartilage); **$** major jaw adductor passes over enlarged lateral trochlear process of pterygoid; retracted neck is S-shaped horizontally; neck retraction by ball-and-socket joints; cervical postzygapophyses closed or fused; **$** fusion of all pelvic elements to shells (ilium fused to carapace; pubis & ischium to plastron); sacrum may involve up to 4 vertebrae (2 in cryptodires). Now S hemisphere only; dominant in Aus; formerly world-wide (until Cz). Almost all fresh water species.

Links: Anapsida -- The Dinosauricon (cladogram); Animal Fact Sheets; Pleurodira; PLEURODIRA; Order Testudines; Higher Reptile Taxa; Yahoo! Groups : Pleurodira; Dr. Christian Beisser; ETI - Turtles of the World: Classification; histo (Spanish); DigiMorph - Elseya dentata (and related pages); Phylogeny of Turtles/Dr. E. S. Gaffney (**Best on the Web**); I. ¿qué tan viejas son las tortugas? (Spanish).

Discussion: One startlingly odd thing about turtle phylogeny is the ability of all turtles, except clearly derived specialists, to withdraw the head inside the carapace. This appears to be a unique ability, but not a synapomorphy, i.e. not a shared derived character. Pleurodires diverged from cryptodires perhaps as early as the late Triassic (perhaps 220 My), and certainly by the late Jurassic (150 My). However, *no* turtle is known to have possessed the specializations needed to withdraw the head into the carapace until the Cretaceous (roughly 100My), at which point both major turtle lineages developed the same ability using quite different biomechanical strategies. In fact, there is enough variation among the methods used by Cryptodires that the ability may have developed more than twice, entirely independently.

On its face, this is a bizarre set of facts. Why would two separate lineages develop the same strategy at roughly the same time, long after the two had diverged? It is not particularly strange that both groups would develop the ability to withdraw the head. Turtle morphology is quite conservative and, even after 50-100 My, all turtles had a great deal in common. But what conceivable selective pressure would emerge for the first time in the Cretaceous to force both lineages to develop the same strategy and eliminate virtually all turtles which could not adapt in this unique fashion?

There are a number of possible speculative answers – bird predation comes to mind, for example. However, turtles cover a good many ecological roles in a wide variety of environments, both terrestrial and marine. Any explanation must apply to all of these cases.

References: ES Gaffney (1975), **Bull. Am. Mus. Nat. Hist.** 155:387-436. Basic changes in skull morphology may have occurred prior to pleurodire- cryptodire split. ES Gaffney & JW Kitching (1994) **Nature** 369:55. ATW 020225.

Note: The above comments are based on the phylogeny of Gaffney, 1975, according to whom *Proterochersis* was the first pleurodire. If the latter is not included, then Eupleurodira ((**Characters:** cervical centra not amphiplatyan. Link: Pleurodira 020202.) is synonymised with Pleurodira

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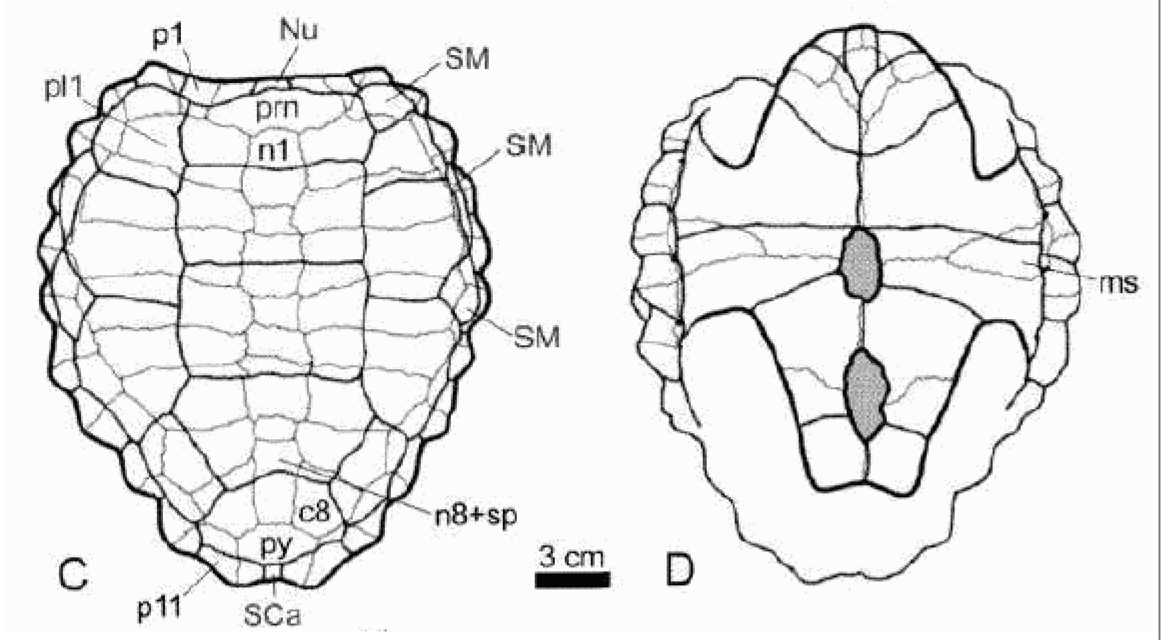
***Platychelys*:** *Platychelys oberndorferi* Wagner, 1853



Platychelys oberndorferi, Late Jurassic of Germany. Shell in Dorsal (left) and Ventral (right) view. Drawing from Böhme, 2005, p.352.

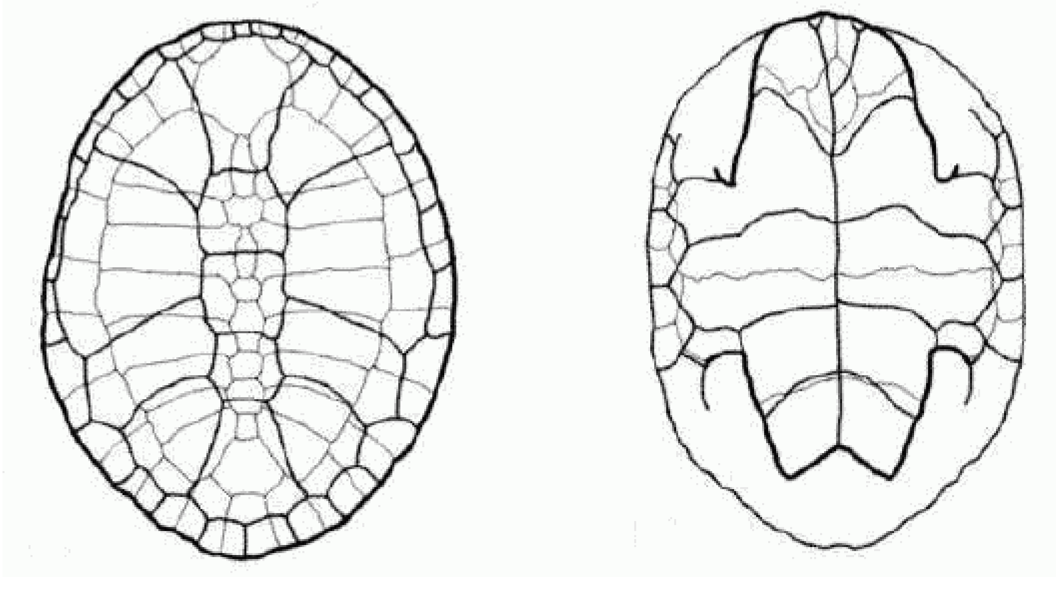
Phylogeny: Pleurodira **:** * + Dortokidae + (Chelidae + Pelomedusoidea)

Range: Late Jurassic of Bavaria, France, and England. (Zittel, Eastman, et al (1902), p.207

Characters: "Carapace somewhat depressed, with a number of more or less distinct ridges or prominences on the neurals and costals. Neurals short and of irregular contour, the width usually much exceeding the length. Bridge short. Mesoplastrals not meeting in the middle line. Vertebral shields much wider than long ; nuchal shield present; intergular undivided. No articulation between pelvis and plastron (Lydekker)".(Zittel, Eastman, et al (1902), p.207)

Comments: *Platychelys oberndorferi* is the only species in Family Platychelyidae Bräm, 1965. Possibly the basalmost (Joyce 2007, p.62) (most primitive or least specialised) of three fossil taxa currently situated along the pleurodire phylogenetic stem, hence "panpleurodira" sensu Joyce et al 2004, the other two being *Caribemys oxfordiensis* from the Late Jurassic of Cuba, and *Notoemys laticentralis* from the Late Jurassic of Argentina. *Platychelys* was first described from lithographic shales near Kehlheim, southern Germany, but is better known from the shallow marine limestones quarried near Solothurn, Switzerland (also known as the Solothurn 'turtle-limestone' or 'Schildkrötenkalk'). A comparitively rare fossil, it is thought to have been a freshwater turtle that inhabited fluvial systems, swamps and lakes of near-shore environments, whereas other taxa from the Solothurn limestone more likely lived in the near-shore marine environments. (Scheyer 2007, p.46)

Dortokidae:



Dortoka vasconica, Late Cretaceous of Europe. Shell in Dorsal (left) and Ventral (right) view, length about 18 cm. Drawing from Böhme, 2005, p.352.

Phylogeny: Pleurodira **:** *Platychelys* + (Chelidae + Pelomedusoidea) + *

Range: Late Cretaceous to Early Eocene of Europe

Comments: includes two genera: *Dortoka* Lapparent de Broin and Murelaga, 1996 from the Late Cretaceous of Spain and France (shell upto 18 cm) and *Ronella* Lapparent de Broin et al from the late Paleocene or early Eocene of Romania (shell greater than 25 cm). Less complete finds also known from the Early Cretaceous of Spain. Probably lived a lifestyle similar to taht of the extant African genus *Pelomedusa*. Feature a combination of primitive and derived characters. Variously considered ancestral to the Pelomedusoides or more closely related to Platychelys, outside the Eupleurodira. (Böhme, 2005 p.354.)

Pelomedusoidea:

Phylogeny: Pleurodira **:** *Platychelys* **:::** Chelidae + *: Pelomedusidae + Podocnemoidae.

Characters: See Pelomedusidae. ATW030416.

Chelidae Gray, 1831 **:** *Chelodina*, *Emydura*, *Elseya* (all Aus), *Platemys*, *Hydromedusa*, *Phrynops* (all S.Am.). Small to medium-sized "snake-neck" aquatic turtles of Aus & S. Am.

Range: from the Late Cretaceous of Australia, New Guinea, & South America.

Phylogeny: Pleurodira **:** *Platychelys* **:::** Pelomedusoidea + *.

Characters: Quadratojugal absent; cheek emargination from ventral margin of skull, extending more posteromedially than in any other turtle group; unique arrangement of the articulations among the neck vertebrae, cervical centra five and eight are convex, mesoplastron absent; intergular (extra scute on plastron) present; extremely long necked ambush predators of fish, or shorter-necked molluscovores with typical durophagous dental specializations.

Comments: 52 living species grouped into 15 genera, of Australasian and South American Side-Necked or Snake-Necked Turtles (so called because of the very long neck, e.g. the Australian *Chelodina longicollis* (Wikipedia page)). Aquatic or semiaquatic prefer slow-moving streams and swamps. They are carnivores that take a broad range of aquatic prey. *Chelus fimbriatus* the South American mata mata (*Chelus fimbriatus*; Wikipedia page) has flaps of skin which, along with the strikingly *Proganochelys*-like shell shell which resembles a piece of bark, and the head which resembles fallen leaves, and the growth of algae, help conceal the animal.

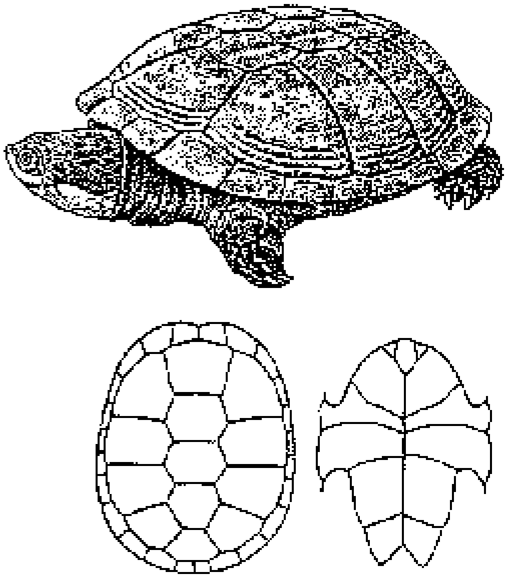
Until recently, the fossil record was very poor and restricted to the Tertiary, but recent South American finds, similar to the recent *Chelus fimbriatus*, *Hydromedusa*, and *Phrynops*, extend the range back to the Late Cretaceous. Older specimens probably represent basal panchelids (stem taxa) (Joyce et al 2004 p.999).

Links: infoplease; Turtle, Tuatara, Crocodile Checklist--13; Chelidae; THE TURTLE GALLERY; Turtle, Tuatara, Crocodile Checklist--Literature Cited; CTTC - Matamata, Chelus fimbriatus by William H. Espenshade; Testudo hermanni site. Chelidae; chelidae (Japanese); ETI Turtles Info - Temperature-dependent sex determination; Molecular Evidence for Higher Relationships Among Turtles; DGHT-AG Schildkröten: Arbeitskreise (Deutsch); Mag. Christian Beisser (surprisingly cool research!); pintroduction (Français); side-necked turtle. The Columbia Encyclopedia; ????? ???? (Chinese); WWW.chelidae.COM / home; ??????? chelidae (Japanese, I think); Chelidae, Schlangenhalsschildkröten (German); Familie Chelidae, Schlangenhalsschildkröten: Bilder (German); familia Chelidae; Testudo hermanni site; Digimorph - Elseya dentata (northern snapping turtle); tierdach.de: Halswender-Schildkröten (German); Digimorph - Chelus fimbriatus (mata mata); pintroduction (French); Turtles and Tortoises; CTTC - Matamata, Chelus fimbriatus by William H. Espenshade; ??? - ??????? Chelodina longicollis (Chinese).

Image: *Chelodina novaguinea*, courtesy Darrell Senneke of the Tortoise Trust, USA. ATW020910.

Pelomedusidae Cope, 1868 **:** *Pelomedusa*, *Pelusios*, *Platycheloides*, *Teneremys*. Medium to large FW aquatic turtles from Africa and South America. Defined polyphyletically as all living pelomedusoids.

Range: from the Early Cretaceous.



Pelomedusa subrufa

Phylogeny: Pelomedusoidea: Podocnemoidae + *.

Characters: **$** frontals have transverse anterior margin rather than projecting anteriorly between the prefrontals; **$** quadrate completely surrounds stapes; quadrate does not contact basioccipital; carotid enters the skull through the prootic; **$** posterior pleurals meet on midline between neurals & suprapygal.

Comments: The African and South American sideneck turtles; 2 genera and eighteen extant species. Most fossils currently attributed to this clade exhibit few diagnostic characters. The fossil record of crown Pelomedusidae extends at least to the Miocene. the most basal form is *Teneremys lapparenti* from the Aptian of Niger (Joyce et al 2004, p.999)

Links: Pelomedusidae; Turtle, Tuatara, Crocodile Checklist--15; Summary sequence view; Zardoya, R & A Meyer (1998); UTDMG - Pelusios sinuatus; Pelomedusidae; CTTC - Matamata, Chelus fimbriatus by William H. Espenshade; Pelomedusidae (Spanish); pelomedusidae (Japanese); ETI Turtles Info - Pelomedusa subrufa example; side-necked turtle. The Columbia Encyclopedia, Sixth Edition. 2001; Schildkröten (German); pelomedusidae, pelomedusenschildkröten, reptilien, reptilia (German); ??????? pelomedusidae (Japanese); Digimorph - Pelusios sinuatus (East African serrated mud turtle); Testudo hermanni site (Italian); pintroduction (French).

Image: *Pelomedusa*: Swiss Federal Veterinary Office regulations § 820.112.46(1). ATW020802.

Podocnemoidae:

Range: fr up(?)K.

Phylogeny: Pelomedusoidea: Pelomedusidae + *: Bothremydidae + Podocnemidae.

Characters: Splenial absent(?); nasals absent; **$** quadrate contacts basioccipital; parietal & jugal in contact; post-otic antrum small or moderate; cervical centra generally biconvex; cervical scute absent; mesoplastra reduced and lateral; neural series on carapace not complete, interrupted by costals; pectoral scutes usually contact entoplastron.

Comments: African and South American Side-Necked Turtles. Generally oomnivores. Current forms limited to Africa , Madagascar , and South America , but were more widespread .

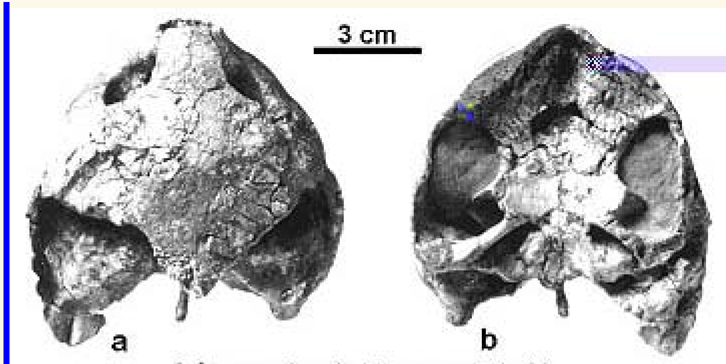
Links: Pleurodira; Araripemys barretoi. photo - Araripemys - wiki commens

References: Gaffney & Meylan (1988); Meylan (1996).

Note: This is the clade that unites the extant podocnemids with the Cretaceous bothremyids. The original cladogram of Gaffney & Meylan (1988) described the bothremyds as the sister group of living pelomedusids, and united the two based on the occipital condyle being formed only by the exoccipitals (that is, the basioccipitals were excluded from the condyle). Meylan (1996) reanalyzed the data with the inclusion of new material from very basal pelomedusoids and determined that the bothremyds were, instead, intermediate between the pelomedusids and podocnemids. Given the extensive re-engineering of neck joints in *all* turtles in the late Cretaceous, it makes good sense to suspect that podocnemids secondarily re-integrated the basioccipitals with the occipital condyle at about that time, when they diverged from the bothremyd stock. 011109.

Bothremyidae: ***Bothremys***, ***Foxemys***,

Polysternon, Rosasia, Taphrosphys



Crâne, vue dorsale (a), vue ventrale (b)
Skull, dorsal vue (a), ventral vue (b)

Range: Late Cretaceous to Miocene. Cosmopolitan.

Phylogeny: Podocnemoidae: Podocnemidae + *.

Characters: $ stapedial canal open anteriorly; $ eustachian tube separated from columellar notch; $ quadrato-basisphenoid covers prootic in ventral view; marine & fresh water.

Comments: a group of widely distributed fossil chelonian taxa that frequented near-shore environments, while some taxa like "*Foxemys* cf. *F. mechinorum*" inhabited fluvial or lacustrine environments (Scheyer 2007, p.46)

Links: Museé.Dinosaures - les Collections (in French. English at MuséeDinosaures - Types; Chéloniens (in French); Pleurodires- research in progress (Best on the Web).

Image: *Foxemys* Late Cretaceous of France, from Museé. Dinosaures - les Collections.

Notes: There are a completely unreasonable number of excellent web resources for such an obscure taxon. 011001.

Podocnemidae: Gray, 1869 (=Podcnemidae): ***Erymnochelys, Neochelys, Peltocephalus, Podocnemis.***

Range: Fresh water turtles from South America. Probably originated in the Late Cretaceous.

Phylogeny: Podocnemoidae: Bothremyidae + *.

Characters: Carotid canal greatly enlarged, forming large channel; large pterygoid flange extends posteromedially covering prootic.

Comments: Eight living species grouped into three genera currently recognized, includes a number of South American and African taxa such as the Madagascan Big-headed, Big-headed Amazon River Turtle and South American sideneck river turtles. The gigantic Late Miocene/Early Pliocene *Stupendemys geographicus*, the largest chelonian known, is included in Podocnemidae based on morphological characters of the postcranium, especially on the saddle-shaped central articulations of the cervicals. (Scheyer 2007, p.48). The group goes back to the Middle Cretaceous, if the basal forms ("Panpodocnemidae") *Brasilemys josai* (Lapparent de Broin, 2000b) and *Cearachelys placidoi* (Gaffney et al., 2001) from the Albian of Brazil, are included (Joyce et al 2004 p.999).

Links: Pleurodira; Podocnemidae; Untitled Document. ATW010518.

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Chelonii: Cryptodira: Paracryptodira

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Kayentachelys
         `--+--Meiolanoidea
            `--+--Kallokibotion
               `--+--Pleurodira
                  |--o Paracryptodira
                  |  |--Compsemys
                  |  |--+-Dorsetochelys
                  |  |  `--o Pleurosternidae
                  |  |     |--Pleurosternon
                  |  |     `--Glyptops
                  |  `--+--Arundelemys
                  |     `--o Baenidae
                  |        |--Trinitichelys
                  |        `--+--Neurankylus
                  |           `--o Baenodda
                  |              |--o
Plesiobaena-Palatobaena lineage
                  |              |  |-
-Plesiobaena
                  |              |  `--+-
-Peckemys
                  |              |     `--+-
-Cedrobaena
                  |              |        `-
-Palatobaena
                  |              `--o Eubaena-
Stygiochelys lineage
                  |                 |--Boremys
                  |                 `--+-
-Stygiochelys
                  |                    `--o
Baenini
                  |                       |-
-Baena
                  |                       `-
-Chisternon
                  `--Eucryptodira
```

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2. *Baena*
3. Baenidae
4. Baenini
5. Baenodda

6. *Boremys*
7. *Cedrobaena*
8. *Chisternon*
9. *Compsemys*
10. *Dorsetochelys*
11. Eubaena-Stygiochelys lineage
12. *Glyptops*
13. *Palatobaena*
14. Paracryptodira
15. *Peckemys*
16. *Plesiobaena*
17. Plesiobaena-Palatobaena lineage
18. Pleurosternidae
19. *Pleurosternon*
20. *Stygiochelys*
21. *Trinitichelys*

Descriptions

Paracryptodira

Range: Jurassic to Eocene, Laurasia

Phylogeny: Testudines crown group **:** Pleurodira + Eucryptodira + * **:** *Compsemys* + ((*Dorsetochelys* + Pleurosternidae) + (*Arundelemys* + Baenidae))

Characters: reduced prefrontal exposure on the dorsal surface of the skull, reduced fenestra perilymphatica, secondary reduced supraoccipital crest. posterior foramen for the internal carotid canal located midway along the basisphenoid-pterygoid suture. (Gaffney, 1975 via Wikipedia)

Comments [1] Compared to more basal turtles, these forms have a more advanced system of blood flow to the head and a simplified plastron (Meylan 2001), although they are still more primitive than living cryptodires in the arrangement of the carotid arteries (Carroll 1988) and were unable to withdraw their head into their shell. MAK121118

[2] The discovery of the clade Paracryptodira is thanks to the early cladistic analyses of Eugene Gaffney (Gaffney, 1975 and later papers); prior to that time paracryptodires were included in the generic stem-group Amphichelydia, a testudine equivalent of cotylodsaurs, thecodonts, and condylarths. Gaffney's research, using Hennigian methodology that emphasised a small number of well understood synapomorphies, showed that the Paracryptodires were the sister group to the Eucryptodires (all recent cryptodiran turtles and their fossil relatives). The later change of methodology to statistical-computational trees unsettled this finding somewhat. A phenomenon first noted by (Lipka et al 2006 p.305, is the tendency of statistical trees to resolve Paracryptodira as stem pleurodires (see also for example fig and fig). This may be explained in terms of shared primitive characteristics, which wouyld be the reason why some paracryptodires such as *Pleurosternon* were previously classified as pleurodires (e.g. Zittel, Eastman, et al (1902)). Molecular phylogeny and stratigraphy both indicate that pleurodires, paracryptodires, and eucryptodires all emerged at around the same time from mid Jurassic stem testudines (Danilov & Parham, 2006). Since pleurodfires are a specialised offshoot of the primitive "cryptodire" condition (see Joyce 2007 and subsequent cladistic analyses; note that these authors limit the term "cryptodire" to the crown group only, contra Gahhney and co-workers) it is difficult to determine the exact branching point, and we have shown these groups as an unresolved trichotomy (the situation is further complicated by some cladistic analyses (e.g. Sterli 2008 and 2010, Pérez-García & Murelaga (2012)) not recognising Eucrptodira) MAK130311

Links: Wikipedia.

Compsemys Leidy.

Range: Late Cretaceous (Campanian) and Paleocene of N Am

Phylogeny: Paracryptodira **:** ((*Dorsetochelys* + Pleurosternidae) + (*Arundelemys* + Baenidae)) + *

Description: "Nasals free; a squamoso-parietal arch; descending processes of prefrontals joining vomer; stapes in an open groove of the quadrate; pterygoids narrow in the middle, without ring-like lateral expansions, separating quadrate and basisphenoid ; epipterygoid well developed and free; dentary bones distinct. Cervical vertebrae with well - developed transverse processes, with single articular faces, biconcave; dorsal and surra! vertebrae with well -developed ribs. Pelvis not anchylosed to the carapace and plastron. Epiplastra in contact with hyoplastra, entoplastron oval or rhomboidal; a complete series of marginals connected with the ribs." (Zittel, Eastman, et al (1902), p.206)

Comments: A common but poorly known genus, the basis for the paraphyletic suborder Amphichelydia Lydekker. Cladistic analysis places it as a basal paracryptodire (Lyson & Joyce 2011). The basal placement of *Compsemys* in the Paracryptodira implies a minimum ghost range of 70 Ma, from the Tithonian to the Campanian. But as the shell sculpturing of the most common Morrison turtle, *Glyptops plicatulus*, is almost identical, it is quite possible that many shell fragments attributed to *G. plicatulus* in particular, or *Glyptops* in general, may actually belong to *Compsemys*. Ironically, *G. plicatulus* was originally named *Compsemys plicatulus* by Cope, 1877. This would make *Glyptops* a junior synonym of *Compsemys*, and that either the species currently included in *Glyptops* consist of several distinct and even unrelated lineages (some of which would require new generic names), or that *Compsemys victa* is actually a highly derived pleurosternid. This latter, non-parsimonious (according to the cladograms by Lyson and co-workers) hypothesis is in keeping with the general tendency of molecular phylogeny to reveal morphological evolution to be endemically homoplastic and characteristred by frequent reversals (or, alternatively, for morphology to reveal the same about macromolecular evolution; the current consensus in phylogenetics however is to for the former). *Compsemys*' lack of specialised paracryptodire synapomorphies may also be compared with the similar situation in the Chelydridea, resulting in its basal placement in Hennigian cladistics, in contrast to the highly derived position given by molecular phylogeny.

There are a number of striking similarities between *C. victa* and the equally enigmatic extant big-headed turtle *Platysternon megacephalum* (either a chgelydrid or a testudinoid, depending on your choicxe of phylogenetic methodology), which would be the result of convergences due due to similar environments and carnivorous diet, hence the large head and well-developed premaxillary beak.

Based on the fine grained lithology in which it is most commonly preserved, *Compsemys victa* has been interpreted as inhabiting slow moving or ponded water environments. Taphonomic evidence reveals that other basal paracryptodires had similar environmental preferences. The quarries from which much of the Morrison (Kimmeridgian-Tithonian) possible pleurosternids *Dinochelys whitei* Gaffney, 1979, *Uluops uluops* Bakker, 1990, and *G. plicatulus* material was recovered (Dry Mesa Quarry, Breakfast Bench Quarry, and Quarry Nine, respectively) are thought to represent low energy pond or swamp environments, indicating that this is the original paleoecology for North American paracryptodires. (Lyson & Joyce 2011), in contrats to the lagoonal-coastal *Pleurosternon*, clearly a specialised ecomorph

Lyson & Joyce place all Campanian to Paleocene specimens in the single species *Compsemys victa*, which indicates either a very long-lived species or the possibility of this being divided into chrono-species. MAK130407

Dorsetochelys

Phylogeny: Paracryptodira **:** *Compsemys* + ((*Arundelemys* + Baenidae) + (Pleurosternidae + *))

Range: Late Jurassic (Morrison Formation) of N Am

Characters:

Comments: A very primitive paracryptodire. Joyce 2007's computational-cladistic study was the first to assess the placement of Dorsetochelys delairi within a global testuidine analysis, revealing its placement as the sister taxon to Paracryptodira, although likely ancestral to the condition seen in more derived pancryptodires. It's basal position is also recovered by Sterli 2010, although the more detailed paracryptodire cladograms presented in Lyson & Joyce 2011 and Lyson et al 2011 presented *Dorsetochelys* as a basal Pleurosternid. This shows that advanced paracryptodire features evolved phyloparallelistically

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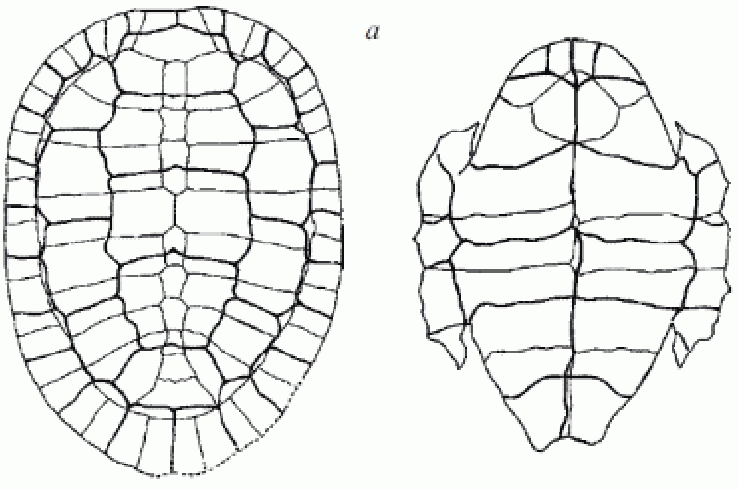
Pleurosternidae Cope, 1868 : *Compsemys*, *Glyptops*, *Pleurosternon*



Pleurosternon bullocki (Owen, 1842) (= *Pleurosternum ovatum* Owen, 1853) from the Purbeck Limestone Formation (Berriasian, Early Cretaceous) of Durlstone Bay, Dorset County, UK. Carapace 50 cm, plastron 44 cm long as preserved) (Hirayama et al, 2000, p.185)

Range: Jurassic (Kimmeridgian) to Paleocene (Danian), Laurasia

Phylogeny: Paracryptodira : *Compsemys* + ((*Arundelemys* + Baenidae) + (*Dorsetochelys* + * : *Pleurosternon* + *Glyptops*))

Characters: $ Long basisphenoid reaching palatines (Gaffney, 1979a).

Comments: a possibly paraphyletic assemblage of Marine and Freshwater forms. Best known by *Pleurosternon* from the Early Cretaceous of England and *Glyptops* from the Late Jurassic of North America. *Compsemys* from the Late Cretaceous and Paleocene of North America might also be a member of this assemblage. *Glyptops* is sometimes placed in a separate family. The skull of *Pleurosternon* associated with postcranial fragments was originally referred to as *Mesochelys*.

Links: *Glyptops* - Wikipedia.

References: Gaffney, 1975. Hirayama et al, 2000 p.185

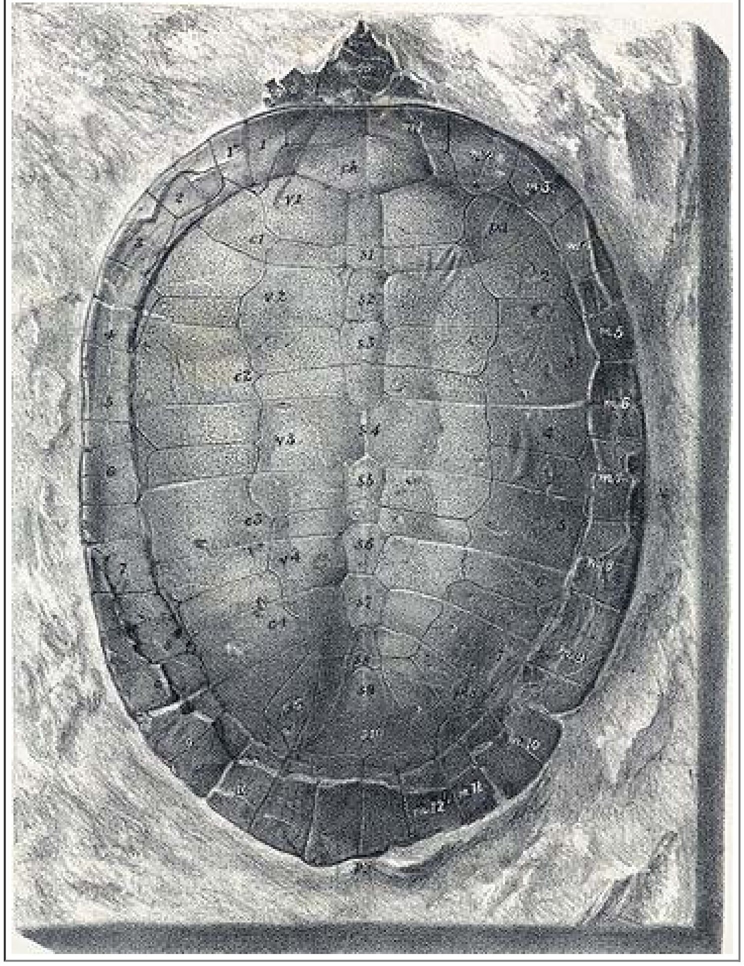
Pleurosternon Owen 1853

Synonyms: Pleruosternum, Megasternum

Range: Late Jurassic (Tithonian) of England

Phylogeny: Pleurosternidae **:** *Glyptops* + *

Description: "Carapace much depressed, rounded posteriorly, without vacuities, and firmly united by a long bridge on each side with the plastron, which is also continuous. Surface of shell very finely pitted and deeply impressed with the suture-lines of the epidermal shields. Neural bones moderately elongated, hexagonal, with their anterolateral surfaces short. Mesoplastrals well developed, meeting in the middle line ; entoplastral relatively large ; xiphiplastrals deeply notched. No nuchal shield ; intergular shield not divided ; inframarginals present. Pectoral arch resembling that of the existing Chelys." (Zittel, Eastman, et al (1902), p.207)



Carapace of *Pleurosternon ovatum* (syn of *Pleurosternon bullocki*) from the Purbeck Limestone, Swanage, Dorset. Original url, Joseph Dinkel, public domain, via Wikipedia

Comments: From Wikipedia: - Pleurosternon fossils were first described by Richard Owen in 1841 under the living genus *Platemys* (Owen 1841). It was not until 1853 however, that it was published under the name Pleurosternon in a paper Owen presented to the Palaeontographical Society (Owen 1853)

Pleurosternon has a very depressed carapace, much flatter than similar genera, such as the North American Late Jurassic and Early Cretaceous Glyptops. Adults show little or none of the nuchal emargination that is more visible in juveniles. The Xiphiplastras also have a large, V-shaped notch near the back of the bone (Milner 2004). Together with *Platychelys*, it is one of the few turtle genera to exhibit the characteristics of both modern turtle suborders, the Cryptodira and the Pleurodira. (Hay 1908 p.45, Neaverson, 1955 p.114)

In Europe, most species of Pleurosternon are best known from southeast England's Purbeck Group and Portland stone, some specimens were even recovered in the Purbeck's type locality. (Neaverson, 1955 p.446) Several areas within the formation became noted by some for producing pleurosternon fossils. Among them were Swanage, Durlston Bay, Langton Matravers, and Herston. (Milner 2004 p.1448).

The genus has also been found in several rock formations from the upper Jurassic in both France and Spain (Pérez García et al 2009), and from the Cretaceous Wealden group of both England and northern Germany (Abel 1919 p.412). The Purbeck formation, at the time was a coastal region with a complex system of shallow lagoons that slowly lost their salinity over time (Radley date p 48). Similarly, the younger Wealden group was also coastal plain dominated by lagoons but with the addition of braided streams (Jackson 2008). The Portland stone, however is a maritime deposit of similar age near the Purbeck, most bones found there are interpreted as having washed out to sea from the Wealden or the Purbeck. Because of this, Pleurosternon has been described as a "shore-turtle". (Boule & Priviteau 1935)

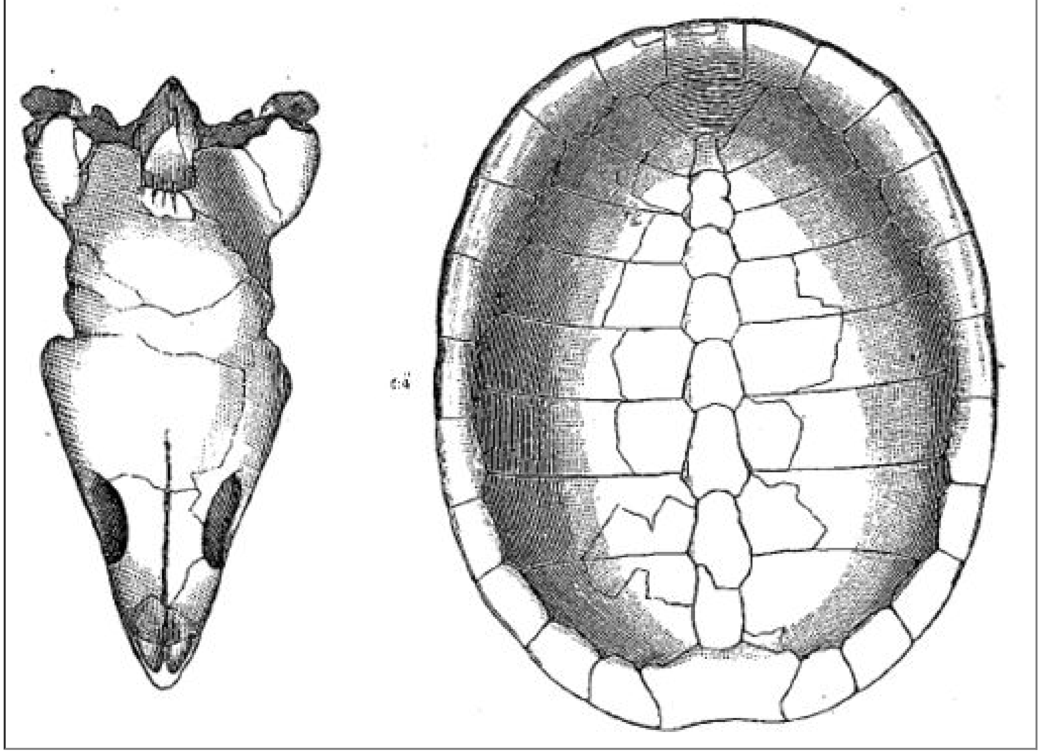
Three species: *Pleurosternon bullocki* (Owen, 1853) (Type species), *P. portlandicum* (Lydekker, 1889), P. *provinciale* (Matheron, 1869)

Glyptops Marsh, 1890

Phylogeny: Pleurosternidae : *Pleurosternon* + *

Range: Late Jurassic to Early

Cretaceous of North America



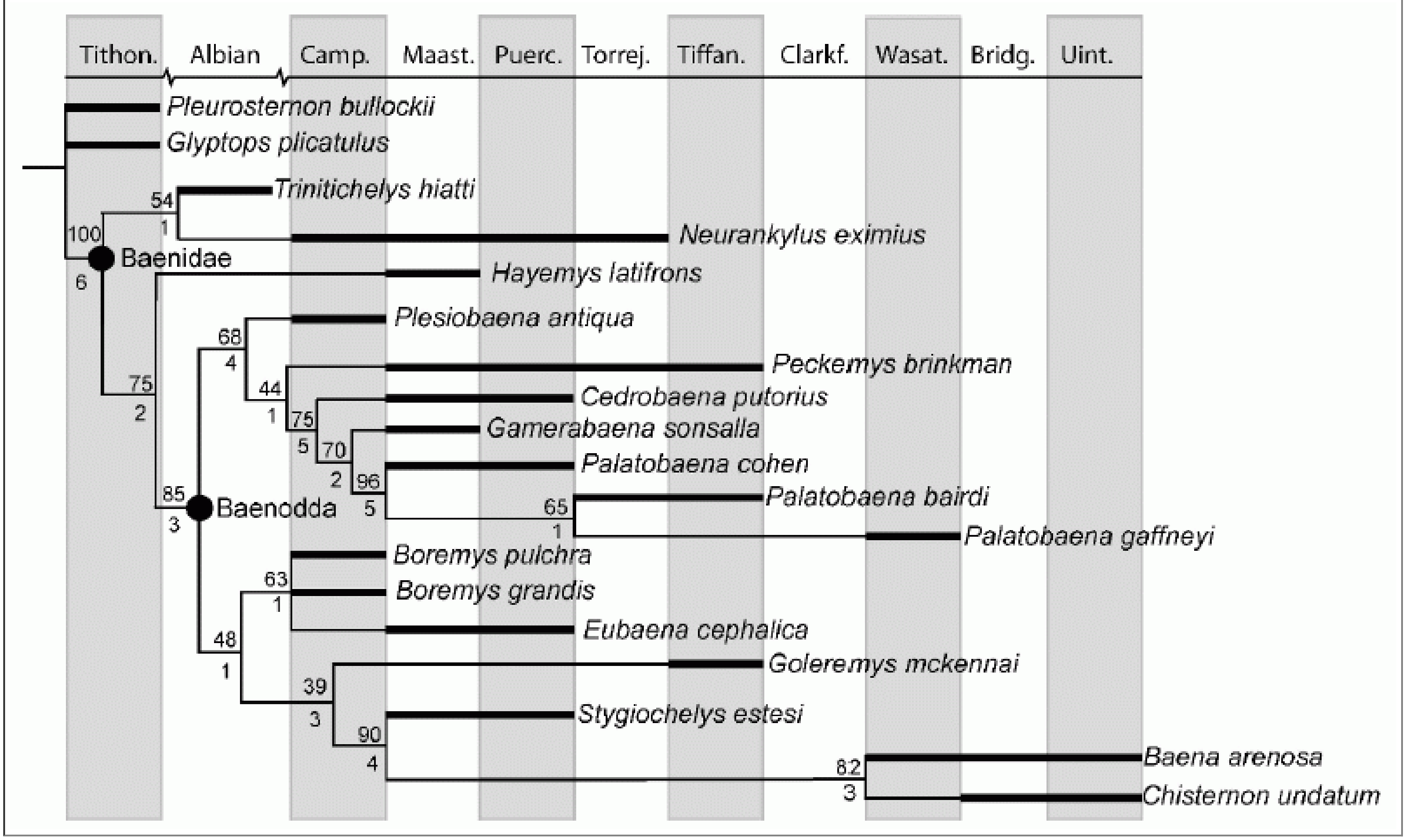
Skull and shell of *Glyptops ornatus*, image by Othniel C. Marsh, 1890, public domain. Via Wikipedia

Comments: Adapted from Wikipedia: The generic name *Glyptops* (Greek for "grooved face") has been used to include a variety of fossil cryptodires from the Late Jurassic and Early Cretaceous of North America. Fossils have been found in South Dakota, Wyoming, Colorado, Utah, New Mexico, Oklahoma, and Texas from both the Morrison and Cedar Mountain formations. The type species is *G. plicatulus*, which was previously named *Compsemys plicatulus* by Edward Drinker Cope. Additional species have also been assigned to this genus: *G. caelatus* Hay, 1908, *G. ornatus* Marsh et al., 1988 (illustrated right), *G. pervicax* Hay, 1908, and *G. utahensis* Gilmore, 1916, although apart from *G. plicatulus*, no cladistic analysis has been done so it is not known how closely they are related or if some of them are synonyms. Marsh assigned this genus a new family Glyptopsidae but this ranking is unnecessary as it is unanimously placed in cladistic analyses with *Pleurosternon* (Joyce 2007, Lyson & Joyce 2009, Sterli 2010, etc) (although a mongeneric subfamily Glyptopsinae Marsh, 1890 would be fine). MAK130311

Arundelemys

Range: Mid Cretaceous (Albanian) to Late Eocene (Bartonian) of North America

Phylogeny: Paracryptodira **:** *Compsemys* + ((*Dorsetochelys* + Pleurosternidae) + (Baenidae + *)



Baenid cladogram mapped against the stratigraphic range from which each taxon has been reported. Support for each node is measured using bootstrap frequency (top) and Bremer support for each clade (bottom). - Diagram and caption from Lyson & Joyce 2009 fig 12. Recent discovereies show that *Boremys* continued into the late Maastrichtian and Early Puercian (Lyson et al 2011)

Baenidae Cope, 1882

Range: Mid Cretaceous (Albanian) to late-Mid Eocene (Uintian/Bartonian) of North America

Phylogeny: Paracryptodira **:** *Compsemys* + ((*Dorsetochelys* + Pleurosternidae) + (*Arundelemys* + * **:** *Trinitichelys* + (*Neurankylus* + Baenodda)))

Characters: absence of epipterygoids; acquisition of a contact between the first thoracic rib and the axillary buttresses; reduction on in width of the vertebrals, with vertebral scales 2 to 4 as narrow as, or narrower than, pleurals (Joyce 2007 p.65, Anquetin 2009, p.196)

Comments: A relatively conservative group of freshwater turtles common in Western Laurasia (North America) (Carroll 1988 p.212). Thanks to its prominant American fossil record, this is a cladistically well-studied group (e.g. Gaffney, 1972, Gaffney and Meylan 1988, Brinkman and Nicholls 1993, Lyson & Joyce 2009). As the chrono-cladogram above shows, most taxa ranged happily across the K-T boundary, unaffected by the end Cretaceous mass-extinction (Lyson & Joyce 2009, Lyson et al 2011). "Mainly found in deposits formed by river channels. They had slightly domed and spindle shaped shells, a very long tail and recurved claws at their feet, all suggesting that these were strong, bottom-walking turtles. Baenid turtles were characterized by a curious growth pattern: When adult size was reached, the individual bony plates forming the shell fused and the shell stopped expanding. After this, growth was invested in the thickening of the shell, especially of the lower plastron, resulting in an exceptional thickness of the lower shell in some specimens. Most baenids had massive jaws, and they probably fed on mollusks." (Jehle, 2006). The neck may have been slightly retractile.

Trinitichelys hiatti

Range: Albian of NA

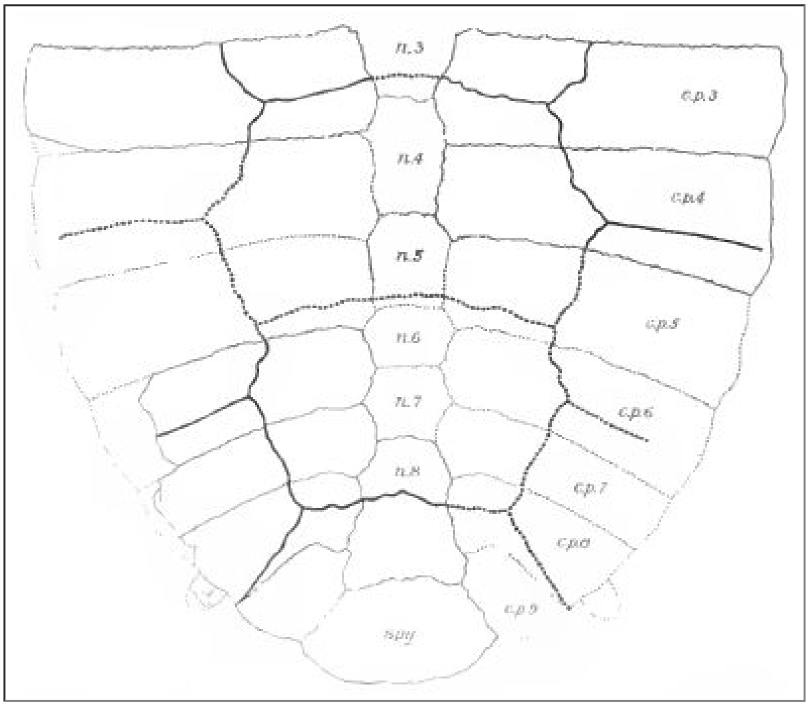
Phylogeny: Baenidae **:** (*Neurankylus* + Baenodda) + *

Comments: The earliest and most basal Baenid(Lyson et al 2011), similar to *Neurankylus* .

Neurankylus eximius Lambe, 1902

Range: Late Cretaceous (Middle Campanian) to Mid Paleocene of North America

Phylogeny: Baenidae **:** *Trinitichelys* (Baenodda+ *)



Neurankylus eximius Hinder portion of carapace of type. From Lambe's figure. c.p.3, c.p.4, etc, costal plates; n.3, n.4, etc, neural plates; spy, suprapygal. From Hay 1908 p.94

Comments: Type specimen a partial carapace collected by Lawrence M. Lambe in 1901, from Judith River deposits (Middle Campanian) of the Red Deer River, Alberta. These seem to have come from an animal wioth a total carapce length of about 30 cm (Hay 1908 p.94). Lyson & Joyce (2009)'s cladogram has this species continuing to the mid Paleocene As species tend to average only several million years in range, it is not clear whether such a long-lived taxon belongs to a single species; perhaps there were distinctions that did not fossilise, e.g. in the genome or soft tissues. Or this may simply have bene a very succesful "living fossil". regardless, Together with *Trinitichelys*, *Neurankylus* represents the "Neurankylus lineage", one of the three primary Baenid evolutionary lineages, the other two being the Plesiobaena+Palatobaena and the Eubaena+Stygiochelys lineages (or subfamilies?). Shells of the Neurankylus lineage are large, with a finely crinkled sculpture pattern, and a complete ring of marginals, these being the basal condition for crown Testudines (Lyson & Joyce 2009). Later cladistic analyses shows this to be a paraphyletic, or in other words ancestral group, with the earlier (Albian, mid Cretaceous) *Trinitichelys* being more basal (Lyson et al 2011), a nice example of stratigraphic congruency; although earlier analyses such as Joyce 2007 and Sterli 2010 recover *Neurankylus* as more basal, indicating the usual mosaic evolution and parallophyly. MAK130406

Baenodda Gaffney & Meylan, 1988

Range: Late Cretaceous (Campanian) to late-Mid Eocene (Bartonian) of North America

Phylogeny: Baenidae **:** *Trinitichelys* + (*Neurankylus* + * **:**Plesiobaena-Palatobaena lineage + Eubaena-Stygiochelys lineage)

Characters: absence or near absence of exposure of the prefrontal on the skull roof (Anquetin 2009, p.196)

Comments: The "higher" baenids. They marked an important ecological transition. Whereas basal forms like *Arundelemys* and *Trinitichelys*, each only known from a single specimen, were both found in claystone, indicative of a slow moving water environment. Neurankylus eximius appears in both claystones and mudstones, while baenodds are almost exclusively found in sandstones, indicating riverine environments. The paleoecological transition within Paracryptodira from low energy ponded environments of the earlier and more primitive forms to higher energy stream environments therefore took place near the Baenodda node (Lyson & Joyce 2011 p.798). During the latest Cretaceous this adaptive shift represented a classic evolutionary radiation attained a high level of diversity in the Maastrichtian, with nine taxa currently recognized (Lyson et al 2011). There are two main clades. A few stragglers continued through to the end of middle Eocene.

Plesiobaena-Palatobaena lineage

Range: Late Cretaceous (Campanian) to Early Eocene of North America

Phylogeny: Baenodda **:** Eubaena-Stygiochelys lineage + * **:** *Plesiobaena* + (*Peckemys* + (*Cedrobaena* + *Palatobaena*))

Characters: lack of supramarginal scutes, lack of a nuchal scute (scute located between the cervical scute and first vertebral scute), weak scalloping, anal scute located entirely on the xiphiplastron and reduced or absent gular scutes. - Lyson & Joyce 2009

Comments: of Maastrichtian and Paleocene taxa only *Peckemys brinkman* and *Palatobaena cohen* are known from shells. These are nearly identical except for the strong nuchal projection in the latter. It is assumed the other four taxa had similar shells, so identification of solitary shells beyond the lineage level is problematic. - Lyson & Joyce 2009

Plesiobaena antiqua (Lambe, 1902)

Range: Campanian to Paleocene of North America

Phylogeny: Plesiobaena-Palatobaena lineage **:** (*Peckemys* + (*Cedrobaena* + *Palatobaena*)) + *

Comments: Earliest and most primitive representative of the Plesiobaena-Palatobaena lineage. The type species, *P. antiqua* Lambe, 1902 is recorded from the Belly River Formation, Alberta (Lambe 1902), this being of Campanian age. An undescribed Maastrichtian, and a named Paleocene species (*P. putorius*), extending the genus across the K-T boundary. A cladistic redescription by Lyson & Joyce 2009 reassigned these species to the new genera *Peckemys* and *Cedrobaena* respectively. This is in keeping with cladistic systematics which tends to appoint monospecific genera, as there is probably little doubt that were these extant taxa they would all be placed in the same genus. Obviously all such categorisation is arbitrary.

Plesiobaena antiqua - from Hay 1908

Plesiobaena antiqua Fig. 37. Carapace of holotype, 1/3 life size, n.1, etc., neural bones; nu.p. nuchal bone. Fig. 38. Anterior lobe of plastron. 1/2 life size, Both from drawings by Lambe.From Hay 1908 p.62

Peckemys brinkman Lyson & Joyce 2009

Range: Latest Maastrichtian to Late Paleocene of North America; distribution Hell Creek Formation (latest Maastrichtian) of North Dakota and Montana, Lance Formation (latest Maastrichtian) of Wyoming, Hannah Formation (Tiffanian - Late Paleocene) of Wyoming, and Laramie Formation (latest Maastrichtian) of Colorado. - Lyson & Joyce 2009

Phylogeny: Plesiobaena-Palatobaena lineage **:** *Plesiobaena* + (*Cedrobaena* + *Palatobaena*) + *)

Comments: identified as Plesiobaena-Palatobaena lineage based on features of the skull

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Cedorbaena putorius

Range: Latest Maastrichtian to Late Paleocene of North America; distribution Hell Creek Formation (latest Maastrichtian) of South Dakota and North Dakota and Fort Union Formation (Torrejonian and Tiffanian) of Wyoming

Phylogeny: Plesiobaena-Palatobaena lineage **:** *Plesiobaena* + (*Peckemys* + (*Palatobaena* + *))

Comments: Skull wedge shaped, larger than either *Pl. antiqua* or *Pe. brinkman*; similar in size to Palatobaena, Chisternon, and Stygiochelys.

Palatobaena

Range: Maastrichtian to Early Eocene of North America

Phylogeny: Plesiobaena-Palatobaena lineage **:** *Plesiobaena* + (*Peckemys* + (*Cedrobaena* + *))

Comments: the most derived species of the lineage, represented by three presumably anagenetic species in stratigraphic and morphological sequence: *P. cohen*, *P. bairdi*, and *P. gaffneyi*. Co-existence with more primitivce species implies a number of co-existing lineages from a rapid mid/late maastrichtian evolutionary radiation. MAK130406

Eubaena-Stygiochelys lineage

Range: Late Cretaceous (Campanian) to late-Mid Eocene (Bartonian) of North America

Characters: (*Boremys pulchra* + *Baena arenosa* + *Chisternon undatum*) acquisition of supernumerary cervical scutes, an opisthocoelous caudal column, and the complete loss of cleithra, although the last characteristic is probably diagnostic for a more inclusive clade of baenids. - Joyce 2007 p.65; for *Eubaena cephalica* and *Stygiochelys estesi*) anterior supramarginal scales present, broken cervical scute, nuchal scute present, strongly scalloped posterior edge of shell, anal scute laps onto the hypoplastron, and well developed gular scutes - Lyson & Joyce 2009

Phylogeny: Baenodda **:** Plesiobaena-Palatobaena lineage + * **:** *Boremys* + (*Stygiochelys* + (*Baena* + *Chisternon*))

Boremys

Range: Late Campanian to Earliest Paleocene (Dinosaur Park, Judith River, Kirtland, Hell Creek and Fort Union formations) of N Am

Phylogeny: Eubaena-Stygiochelys lineage **:** *Boremys* + (*Stygiochelys* + (*Baena* + *Chisternon*)) + *

Comments: Includes the earliest representatives of the Eubaena-Stygiochelys lineage. The Maastrichtian *Stygiochelys* is a related form. Although *B. pulchra* and *B. grandis* have long been known from the Late Campanian. But recent discoveries show that *Boremys* continued into the late Maastrichtian and Early Puercian. The surprising failure to previously recognise this distinctive riverine genus in the Hell Creek Formation, which thanks to over a century of collecting provides one of the best understood terrestrial fossil vertebrate faunas, may be due to *Boremys* having a relatively thin shell in relation to other baenids, which in post-Campanian forms probably disarticulated more easily than those of other contemporaneous baenids. (Lyson et al 2011). The Maastrichtian *Eubaena cephalica* is a closely related species (Lyson & Joyce 2009)

Stygiochelys Gaffney & Hiatt, 1971

Range: Late Maastrichtian of Montana

Phylogeny: Eubaena-Stygiochelys lineage **:** *Boremys* + (*Stygiochelys* + (*Baena* + *Chisternon*)) + *

Comments: Presumably, the name "Turtle of the River Styx" refers to this riverine turtle being found in the Hell Creek formation, This animal had a shell about 30 cm in length.

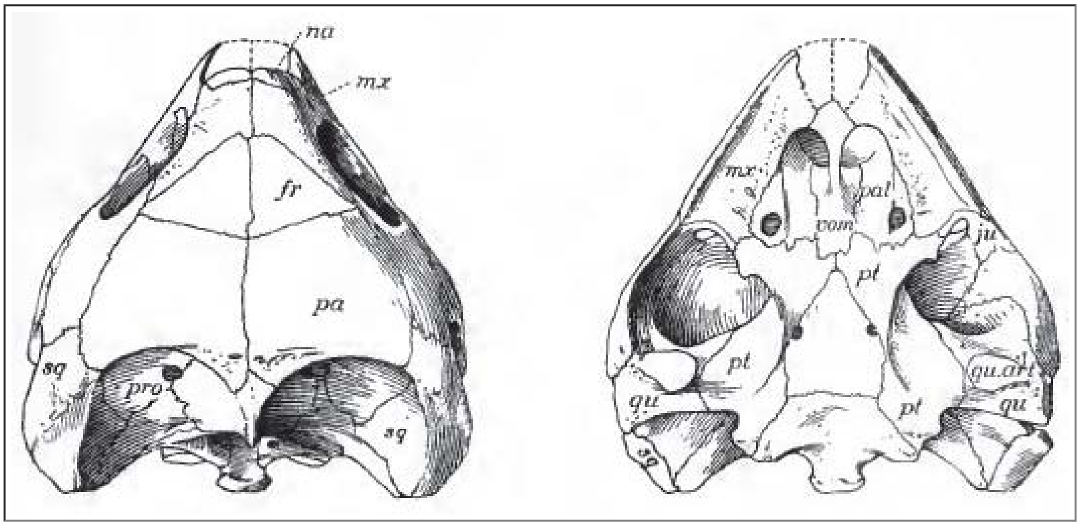
"Baenini"

Range: Eocene of N Am

Phylogeny: Eubaena-Stygiochelys lineage **:** *Boremys* + (*Stygiochelys* + * **:** *Baena* + *Chisternon*)

Characters: reacquisition of a parietal squamosal contact; loss of splenials - Joyce 2007 p.65

Comments: This clade of Eocene paracryptodires (here informally given the rank of tribe) constitute the last representatives of the group. Like the contemporary Champsosaurs, they were Mesozoic survivors in a mid Paleogene world. MAK130407



Chisternon undatum, skull, 3/4 natural size, Bridger badlands (middle Eocene) of Wyoming. Left, top view, fr, frontal; mx maxilla; na, nasal; pa parietal; pro, prootic; sq, squamosal. Right, bottom view ju, jugal ; mx, maxilla ; pal, palatine; pt, pterygoid; qu, quadrate; qu. art, articulation of lower jaw; sq, squamosal; vom, vomer. From Hay 1908 p.89 (as *Chisternon hehraicum* - junior synonym) No. 5961 of the AMNH.

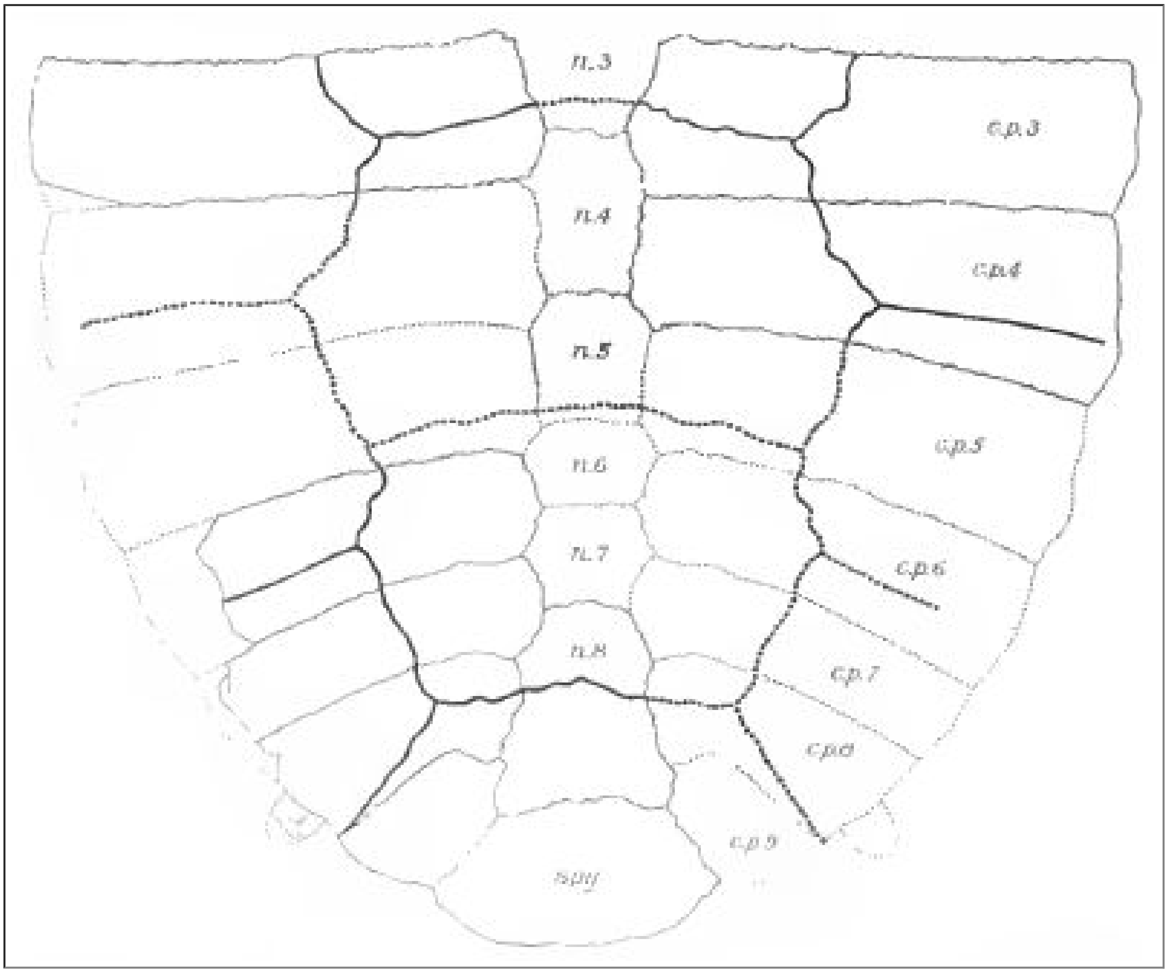
Baena arenosa Leidy

Range: Early to Middle Eocene of N Am

Phylogeny: Eubaena-Stygiochelys lineage **:** *Boremys* + (*Stygiochelys* + (*Baena* + *Chisternon*)) + *

Description: "Intergular shield divided, and xiphiplastral with depressions which appear to have received the pubis and ischium. Mesoplastrals meeting at the middle line, but with the median ends much narrower than the outer ends." (Zittel, Eastman, et al (1902), p.207)

Comments: Originally included Cretaceous specuies, these have since been assigned to new genera.



Baena arenosa left, Carapace, showing bones and scute areas. Right, Plastron, abj abdominal scute; an, anal scute; ent. entroplastroa; epi, epiplastron; fm, femoral scute; g, gular scute; hum^ humeral scute; hyo, hyoplastron; hypo, hypoplastron; infm, inframarginal scutes; mes, mesoplastron; pec, pectoral scute; xiph, xiphiplastron. Length 26 cm From Hay 1908 p.77 (as *Baena riparia* - junior synonym)

Chisternon undatum Leidy

Chisternon undatum, American Museum of Natural History, photo by Claire Houck, Creative Commons Attribution license, via Wikipedia

Range: Middle Eocene of North America

Phylogeny: Eubaena-Stygiochelys lineage : *Boremys* + (*Stygiochelys* + (*Baena* + *Chisternon*)) + *

Comments: Best known from the Middle Eocene Bridger Beds of Wyoming

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checked ATW030512, last modified MAK100917

Chelonii: Eucryptodira

Abbreviated Dendrogram

```
ANAPSIDA ?
 `--o CHELONII
    |--Odontochelys
    `--o Testudinata
       |--Proganochelys
       `--+--Kayentachelys
          `--+--Meiolanoidea
             `--+--Kallokibotion
                `--+--Paracryptodira
                   |--Pleurodira
                   `--o Eucryptodira
                      |--Thalassemyidae
                      |--Protostegidae
                      `--+--Plesiochelyidae
                         `--+--o Angolachelonia
                            |  |--Solnhofia
                            |  `--+--Sandownia
                            |     `-
-Angolachelys
                            `--
+==Xinjiangchelyidae
                               `--o
Centrocryptodira
|==Sinemydidae
                                  |-
-Trionychoidea
                                  `--+--+-
-Chelonioidea
                                     |  `--+-
-Chelydridae
                                     |     `-
-Kinosternoidea
                                     `-
-Testudinoidea
```

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1. Angolachelonia X
2. *Angolachelys* X
3. Centrocryptodira
4. Eucryptodira
5. Plesiochelyidae X
6. *Sandownia* X
7. *Solnhofia* X
8. Thalassemyidae X

Beginning in the later Middle Jurassic, the testudines underwent an evolutionary radiation and became a very successful lineage. The basal Paracryptodires were supplemented by a variety of Eucryptodires, including a number of early marine types that were quite unrelated to the Chelonoidian marine turtles of the Cretaceous to Recent. More advanced were the Sinemydidae seem to be ancestral to extant hard-shelled turtles, although they are so far known only from theCretaceous and early Cenozoic. Two groups with ambiguous positions on the Chelonian tree, the Pleurodires (side-necked turtles) and the Meiolaniids (horned tortoises) developed probably as offshoots from the early cryptodire or proto-cryptodire stem. MAK130112

Descriptions

Eucryptodira Gaffney, 1975

Range: Late Jurassic to Recent, Cosmopolitan

Phylogeny: Testudinata **:** (assorted stem forms) **:** Paracryptodira + * **:** (Thalassemyidae + Protostegidae) + (*Portlandemys* + (Plesiochelyidae + (Angolachelonia + Xinjiangchelyid - Crown Cryptodire clade))).

Characters: Mesoplastra absent, Canalis caroticus is formed by the pterygoid.

Comments: Eucryptodira was coined by Gaffney, 1975 for all crown-group cryptodires together with a number of basal fossil forms, although its status is ambiguous. The absence of mesoplastra is also a characteristic of Chelidae. Mesoplastra a primitive condition present in *Proganochelys* and most Pleurodires. Basal forms are characterised by amphicoelous cervical (neck) vertebrae with poorly developed articulation, whereas the more specialised Centrocryptodira (and also the Pleurodires) have more efficient articulation (Meylan 2001). Joyce (2007) and Anquetin (2009) recovered this clade using a different metholodology and matrix to Gaffney, but Sterli 2008 and 2010 and Pérez-García & Murelaga (2012) did not. The taxon is best defined as an assemblage of early cryptodire-like forms combining characteristics or paracryptrodires, pleurodires, and crown cryptodires, but more primitive than the latter two groups. MAK121126 130117

Thalassemyidae

Range: Late Jurassic (Late Kimmeridgian to Early Tithonian) of Bavaria and Switzerland

Phylogeny: Eucryptodira **:** (*Portlandemys* + (Plesiochelyidae + (Angolachelonia + Xinjiangchelyid - Crown Cryptodire clade))) + (Protostegidae + *)

Comments: *Thalassemys* and the contemporary *Eurysternum* are similar and may or may not be closely related. About half a dozen species are known from the late Jurassic of Switzerland and Germany, the largest, *T. hugii*, has a shell 1.2 meters long, although others are much smaller (*E. wagleri* being only 18 cm). According to both Anquetin (2009) and Mateus et al (2009), *Thalassemys moseri* is the sister taxon of the basal protostegid *Santanachelys gaffneyi* (Anquetin, following Joyce (2007), places "*Thalassemys moseri*" in inverted commas implying this species probably belongs in a separate genus); Mateus et al (2009) to the medium-sized (shell 40 cm long) *Thalassemys marina* of Wurttemberg). This is not to deny the possibility of convergence; indeed we can expect a lot of parallelism among seperate and unrelated lineages of marine cryptodires. Hence protostegids are traditionally placed as the sister group of Dermochelyidae, although recent cladistic analyses, beginning with Joyce (2007) show that the protostegids are actually a much more primitive group. Clearly the late Jurassic and Early Cretaceous saw a number of distinct but parallel explorations in aquatic and marine lifestyle among chelonians. It can be assumed that forms like *Thalassemys*, *Eurysternum*, *Plesiochelys* and *Portlandemys* they belong to a general grouping of European (central Laurasian) marginal marine (and semiaquatic) primitive Eucryptodires, but the precise relationship of these early marine turtles will probably always remain rather ambiguous. MAK130112

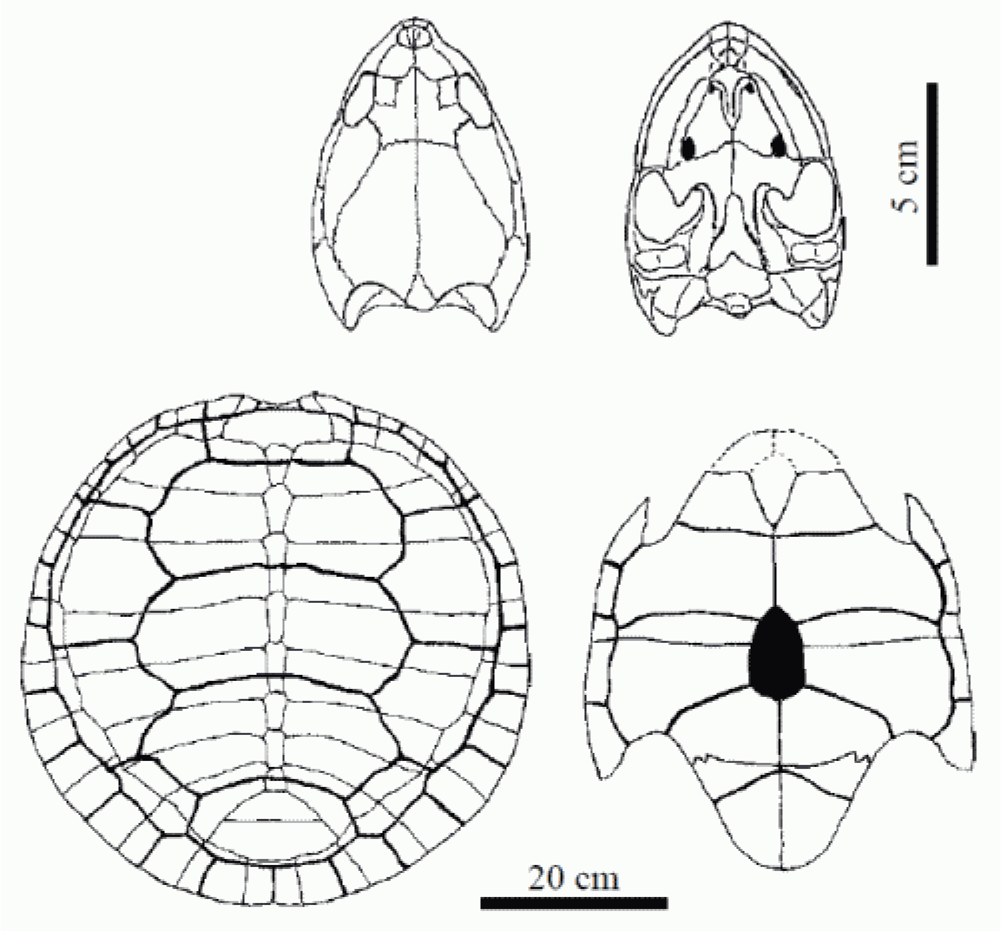
Portlandemys

Range: Latest Jurassic (Late Tithonian) to England

Phylogeny: Eucryptodira : ("Thalassemyidae + Protostegidae) + (Plesiochelyidae + (Angolachelonia + Xinjiangchelyid - Crown Cryptodire clade)) + *)

Comments: This phylogenetic placement follows Mateus et al (2009). MAK130111

Plesiochelyidae: Rütimeyer, 1873 : *Plesiochelys, Hylaeochelys*



Skull and shell of *Hylaeochelys belli* (Mantell, 1844). Purbeck Limestone Formation, Early Cretaceous (Berriasian), Durlstone Bay near Swanage, Dorset County, UK. Skull based on holotype of Dorsetochelys delairi Evans and Kemp. Carapace largely based on holotype of "Pleurosternum latiscutatum" Owen, 1853 with additions from holotype of "Pleurosternum emarginatum" Owen, 1853 [Hirayama et al, 2000, p.186]

Range: Late Jurassic (Kimmeridgian) to Early Cretaceous, Europe and Asia

Phylogeny: Eucryptodira : ("Thalassemyidae + Protostegidae) + (***Portlandemys*** + ((Angolachelonia + Xinjiangchelyid - Crown Cryptodire clade) + *))

Characters: shell thick, mesoplastra absent (Zittel 1932 p.307), broad vertebral scutes and strong plastral buttresses reaching costals (Hirayama et al, 2000 p.185), amphicoelus articulations between succeeding cervical vertebrae, which is a more primitive condition of the cervical vertebrae (also found in Pleurodira and Baenidae). Thin floor where pterygoid forms the canalis caroticus internus, which seems to be a primitive condition. In some specimens of *Plesiochelys* the seam or suture closing the canalis is still present. The thick, seamless condition is seen in all other eucryptodires, and is considered more advanced because during development the canalis floor is thin at first and shows the enclosing of the carotid. (Meylan

Hylaeochelys menkei, Early Cretaceous: Berriasian, Bückeburg, Lower Saxony, Germany. Photo from Fossil turtles

2001.)

Comments: medium-sized marine turtles. Once considered ancestral chelonioids, they are now interpreted as basal Cryptodires. *Plesiochelys* has a shell upto 50cm long, considerably vaulted in the adult (Zittel 1932 p.307). Pending phylogenetic analyses of Plesiochelys and Hylaeochelys in relation to other taxa or even each other, these are both incxluded under the family Plesiochelyidae. Eurysternidae and Thalassemyidae include similar, poorly known contemporary aquatic forms. MAK130112

References: Hirayama et al, 2000 p.185, Meylan 2001, Zittel 1932.

Angolachelonia:

Range: Late Jurassic (Kimmeridgian) to Early Late Cretaceous (Turonian) of Europe, Africa, and North America

Phylogeny: Eucryptodira : ("Thalassemyidae + Protostegidae) + (*Portlandemys* + (Plesiochelyidae + (Crown Group Cryptodira + * : *Solnhofia* + (*Sandownia* + *Angolachelys*))))

Characters: mandibular articulation of quadrate aligned with or posterior to the occiput, and basisphenoid not visible or visibility greatly reduced in ventral view. (Mateus et al 2009).

Comments: New clade of Mesozoic turtles recovered by Mateus et al (2009), based on the newly discovered eucryptodire *Angolachelys mbaxi* using the data set of Joyce (2007). As can be seen from the adjacent map (right), these animals were part of the evoplutionary and ecological radiation that resulted from the opening of the South Atlantic ocean (although at this time it was still a narrow sea). The protostegids, beginning with *Santanachelys*, represnet a distinct, and ultimately more succesful, evolutionary lineage. Unlike the angolachelonians, the protostegids did not represent the first taxon to pass through the Atlantic gateway , because early Cretaceous forms from Australia (Kear 2003) pre-date the opening of the Atlantic Ocean (Mateus et al (2009) p.588). MAK130112

Chronopaleogeography of basal eucryptodires. The paleogeographic maps are from www.odsn.de and Hay et al. (1999). The grey bar represents the time for the opening of South Atlantic. Diagram and caption by Mateus et al (2009) p.587, fig.5

Solnhofia parsonsi

Range: Late Kimmeridgian - Early Tithonian of Bavaria

Phylogeny: Angolachelonia : (*Sandownia* + *Angolachelys*) + *

Sandownia harrisi

Range: Aptian of the Isle of Wight

Phylogeny: Angolachelonia : *Solnhofia* + (*Angolachelys* + *)

Comments: The skull of *Sandownia harrisi* has one of the most extensive secondary palates among turtles, perhaps associated with the development of a broad crushing surface (Meylan et al., 2000, cited in Pérez-García & Murelaga (2012)). Variously considered an ancestral trionychoidan (Meylan et al., 2000) or an abarrent early eucryptodire (Joyce (2007), Anquetin (2009)). We have used the phylogenetic placement of Mateus et al (2009), who note that the apparent lack an epipterygoid makes *Sandownia* even more derived than *Angolachelys* (*ibid*, p.587). MAK130112

Angolachelys mbaxi Mateus et al 2009

Range: Tadi Beds, Itombe Formation, of Angola, Late Turonian, Late Cretaceous

Phylogeny: Angolachelonia : *Solnhofia* + (*Sandownia* + *)

Characters: "divided external nares separated by an internarial process of the premaxilla; sub-circular rugosity on the dorsal surface of the squamosal; squamosal wings projected posteriorly, representing about 1/4 of the total length of the skull posterior to the quadrate, and frames the temporal fenestra both dorsally and laterally."

Comments: The oldest known African Eucryptodire, and represents the first marine turtle lineage to cross from the North to South Atlantic during the Mid Cretaceous opening of the South Atlantic seaway (Mateus et al (2009) p.588). Shares a number of characteristics with *Sandownia* (the expansion of the jugal onto the secondary palate, trilobate outline and pre-maxillary prominence of the rostrum) which seem to be unique features among turtles (Mateus et al (2009) p.587). This supports the status of *Sandownia* as a stem eucryptodire rather than a basal trionychoidan, An unnamed taxon from the Albian of Glen Rose, Texas would seem to be slightly moree distrantly related to both. Mateus et al (2009) MAK130112

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Chelonii: Eucryptodira: Xinjiangchelyidae and related forms

Abbreviated Dendrogram

```
ANAPSIDA ?
 `--o CHELONII
    |--Odontochelys
    `--o Testudinata
       |--Proganochelys
       `--+--Kayentachelys
          `--+--Meiolanoidea
             `--+--Kallokibotion
                `--+--Paracryptodira
                   |--Pleurodira
                   `--o Eucryptodira
                      |--Protostegidae
                      `--+--Angolachelonia
                         `--o Xinjiangchelyid - 
Crown Cryptodire clade
                            |--Chengyuchelys
                            |--Larachelus
                            |==Xinjiangchelyidae
                            `--o 
Centrocryptodira
                               |==Sinemydidae
                               |--Trionychoidea
                               `--
+==Macrobaenidae
                                  |-
-Chelonioidea-Chelydridae-Kinosternoidea clade
                                  `-
-Testudinoidea
```

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1. Chengyuchelyidae X
2. *Chengyuchelys* X
3. *Larachelus* X
4. Xinjiangchelyid - Crown Cryptodire clade
5. Xinjiangchelyidae X

Descriptions

Xinjiangchelyid - Crown Cryptodire clade common ancestor of *Xinjiangchelys latimarginalis* and extant Cryptodira, and all its descendants

Range: Middle Jurassic to Recent

Phylogeny: Eucryptodira **:** Thalassemyidae + Protostegidae + *Portlandemys* + (Plesiochelyidae + (Angolachelonia + * **:** *Chengyuchelys* + Xinjiangchelyidae + *Larachelus* + Centrocryptodira))

Characters: anal scutes anteromedially overlapping the hypoplastra. - Pérez-García & Murelaga (2012)

Comments: node D in Fig. 5A-B of Pérez-García & Murelaga (2012). This clade includes several Mid Jurassic to Early Cretaceous Asian and Early Cretaceous European taxa along with crown group Cryptodira. It represents a more advanced grade of organisation than the late Jurassic plesiochelyids and their relatives. As the Xinjiangchelyidae are almost certainly paraphyletic (Rabi et al 2010), this clade represents the Xinjiangchelyid grade of organisation and later forms. MAK130403

Chengyuchelys Ye 1990 **:** *Chengyuchelys baenoides C. zigongensis*

Range: Bathonian (Middle Jurassic) of China

Phylogeny: Xinjiangchelyid - Crown Cryptodire clade **:** Xinjiangchelyidae + *Larachelus* + Centrocryptodira + *

Characters: Chengyuchelyidae Ye 1990 - oval carapaces lacking ornamentation, eight hexagonal neural plates, round posterior margin, mesoplastron, intergulars, and inframarginals (Lucas, 2001 p.138). Considered a definite clade by Anquetin, 2009 pp.193-4 on the basis of the following esoteria: vertebrals 2 to 4 as narrow as, or narrower than, pleurals; medial embayment of vertebral 3-4 sulcus present; dagger-shaped entoplastron present; and anal scales overlap anteromedially onto hypoplastra. Elsewhere synonymised with Xinjiangchelyidae (see notes)

Comments: *Chengyuchelys* retains mesoplastra, a very primitive feature. According to Anquetin, 2009 this is a stem clade, although the included taxa are rather unstable, jumping around a lot in the various cladograms (Anquetin, 2009 p.193). The Dashanpu locality is unusual in having at least four species of turtles, as all other turtle localities from this time have only one species each. With the earliest stratigraphic record from the Shaximiao formation of Sichuan, China (Bathonian or perhaps Bathonian-Callovian age), these are among the earliest of intermediate stem testudines, contemporary with *Condorchelys* and *Eileanchelys*. They represent either a very primitive group convergent with eucryptodires, or one of a number of diverse Jurassic eucryptodirian turtles. The phylogenetic placement of *Chengyuchelys* is very difficult to resolve (Anquetin, 2009). Anquetin, 2009 decided on a very basal placement, distinct from *Xinjiangchelys*. If so this would be an example of the co-existence of two highly endemic and similar clades of Jurassic Chinese tetrapods, one very primitive and the other more advanced, similar to that of the sauropod dinosaurs, of which two exceptionally long-necked Jurassic Chinese types are known, the primitive but successful mamenchisaurs and the more advanced euhelopines, although unlike the Jurassic turtles these two groups were not contemporary. However, Danilov & Parham, 2008, in a study of two poorly known specimens of *Chengyuchelys baenoides* from the Middle Jurassic of Dashanpu, Sichuan Province, China, found that this species came out as the sister taxon to *Xinjiangchelys*, which implies that the two families should be synonymised. Pérez-García et al (2013) include both *Chengyuchelys* and *Xinjiangchelys* in a monophyletic Xinjiangchelyidae, whilst Pérez-García & Murelaga (2012) recover both *Chengyuchelys* and *Xinjiangchelys* in an unresolved polytomy of advanced stem eucryptodires, the other taxa included there being Late Jurassic to Early Cretaceous. MAK130119.

Xinjiangchelyidae **:** *Annemys, Brodiechelys, Siamochelys, Tienfuchelys, Yanduchelys, Xinjiangchelys*.

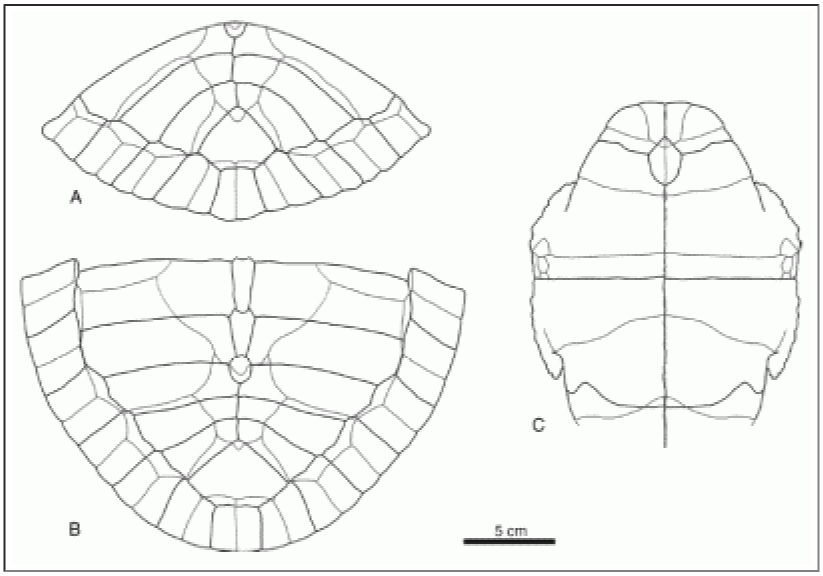
Range: Middle and Late Jurassic of Asia, early Cretaceous of Asia and Europe

Phylogeny: Xinjiangchelyid - Crown Cryptodire clade **:** *Chengyuchelys* + *Larachelus* + Centrocryptodira + *

Characters: Dorsal carapace and the ventral plastron with a ligamentous connection rather than the usual solid bridge of bone (Danilov, 2005). distinctly sinuous midline sulcus of plastral scales and gular scales restricted to epiplastra (Anquetin, 2009 p.197)

Comments: Xinjiangchelyidae are medium-sized (carapace length up to 375 mm) aquatic turtles best known from the Middle and Upper Jurassic of Asia. These are the earliest known eucryptodires (predating the more primitive Plesiochelyid grade). *Xinjiangchelys* seems more advanced than the Late Jurassic plesiochelyids and *Hylaeochelys* in the possession of the extensive posterior temporal emargination, the procoelous and opisthocoelous caudals, and narrower vertebral scutes. (Hirayama et al 2000 p.189). If *Brodiechelys brodiei* (Lydekker, 1889) from the Early Cretaceous of England and Spain is closely related (Hirayama et al 2000, Pérez-García et al (2013)), it would indicate a wider geographic and stratigraphic distribution for the group. They are generally seen as the sister group to the Centrocryptodira of Gaffney, 1975 (Scheyer 2007 p.68) although this classification is not used in more recent cladograms (Joyce 2007, Anquetin, 2009). The contemporary *Chengyuchelys* is considered much more basal, as it retains mesoplastra, a primitive feature (Anquetin, 2009) although one study places it as the sister taxon to *Xinjiangchelys* (Danilov & Parham, 2008). Most workers consider Xinjiangchelyids to be more closely related to modern cryptodires than Paracryptodira or Plesiochelyidae (Gaffney 1996; Hirayama et al. 2000; Joyce 2007; Parham and Hutchison 2003) and (with the exception of Danilov and Parham (2008)), basal to the Sinemydidae-Macrobaenidae assemblage (Rabi et al 2010) However their monophyly has not been demonstrated, with the vast majority of characters that are used to diagnose this group being symplesiomorphies for eucryptodira when mapped onto global trees (Rabi et al 2010). "Xinjiangchelyidae" is therefore likely paraphyletic grade of early eucryptodires, similar to, but less advanced than, the "Sinemydidae" and "Macrobaenidae." MAK121126 130403

Links: Annemys sp., Fossil Cryptodire and Xinjiangchelys radiplicatoides, Fossil Cryptodire from Digimorph; Mikko's Phylogeny Archive (dendrogram)



Reconstruction of the shell of *Larachelus morla*, from Pérez-García & Murelaga (2012). A, posterodorsal, B, dorsal, and C, ventral views. Scale bar is 5 cm. The high domed shell may indicate a terrestrial liufestyle

Larachelus morla Pérez-García & Murelaga 2012

Horizon: Pinilla de los Moros Formation, late Hauterivian-early Barremian, Salas de los Infantes, Burgos, western Cameros Basin, Spain.

Phylogeny: Xinjiangchelyid - Crown Cryptodire clade **:** *Chengyuchelys* + Xinjiangchelyidae + Centrocryptodira + *

Characters: "partially ligamentous epiplastrahyoplastra and hypoplastra-xiphiplastra contacts, with a linear ridge in the anterior margin of the hyoplastra and posterior margin of the hypoplastra that slots into a furrow in the posterior margin of the epiplastra and anterior margin of the xiphiplastra, respectively. Differs from other pan-cryptodires by the following: high shell; broad plastral lobes; smooth outer surface; absence of fontanelles" -Pérez-García & Murelaga (2012)

Comments: One of a number of recently discovered or redescribed European Early Cretaceous pan-cryptodiran turtles, with similarities to Asian taxa like the Xinjiangchelyidae. It is clear that these animals were widespread and diverse, with several clades of turtles, including paracryptodires, stem cryptodires, and several lineages of the crown group Cryptodira. This wide range of morphological diversity can be related to adaptation to different ecological niches. Pérez-García & Murelaga (2012) MAK130403

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Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Meiolanoidea
         `--+--Pleurodira
            |--Paracryptodira
            `--o Eucryptodira
               |--o Protostegidae
               |  |--Santanachelys
               |  `--+--Bouliachelys
               |     `--o "Euprotostegidae"
               |        |--Notochelone
               |        `--o "Protosteginea"
               |           |--Desmatochelys
               |           |--Rhinochelys
               |           `--o Protosteginae
               |              |--Chelosphargis
               |              `--+-
-Calcarichelys
               |                 `--o
Protostegini
               |                    |--
Microstega
               |                    `--o
Protostegina
               |                       |-
-Protostega
               |                       `-
-Archelon
               |--Plesiochelyidae
               `--+--Angolachelonia
                  `--+==Xinjiangchelyidae
                      |==Sinemydidae
                      |--Trionychoidea
                      `--+--+--Chelonioidea
                         |  |--Chelydridae
                         |  `--Kinosternoidea
                         `--Testudinoidea
```

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3. *Calcarichelys* X
4. *Chelosphargis* X
5. *Desmochelys* X
6. "Euprotostegidae" X
7. *Microstega* X
8. *Notochelone* X
9. *Protostega* X

10. Protostegina X
11. Protostegidae X
12. Protosteginae X
13. "Protosteginea" X
14. Protostegina X
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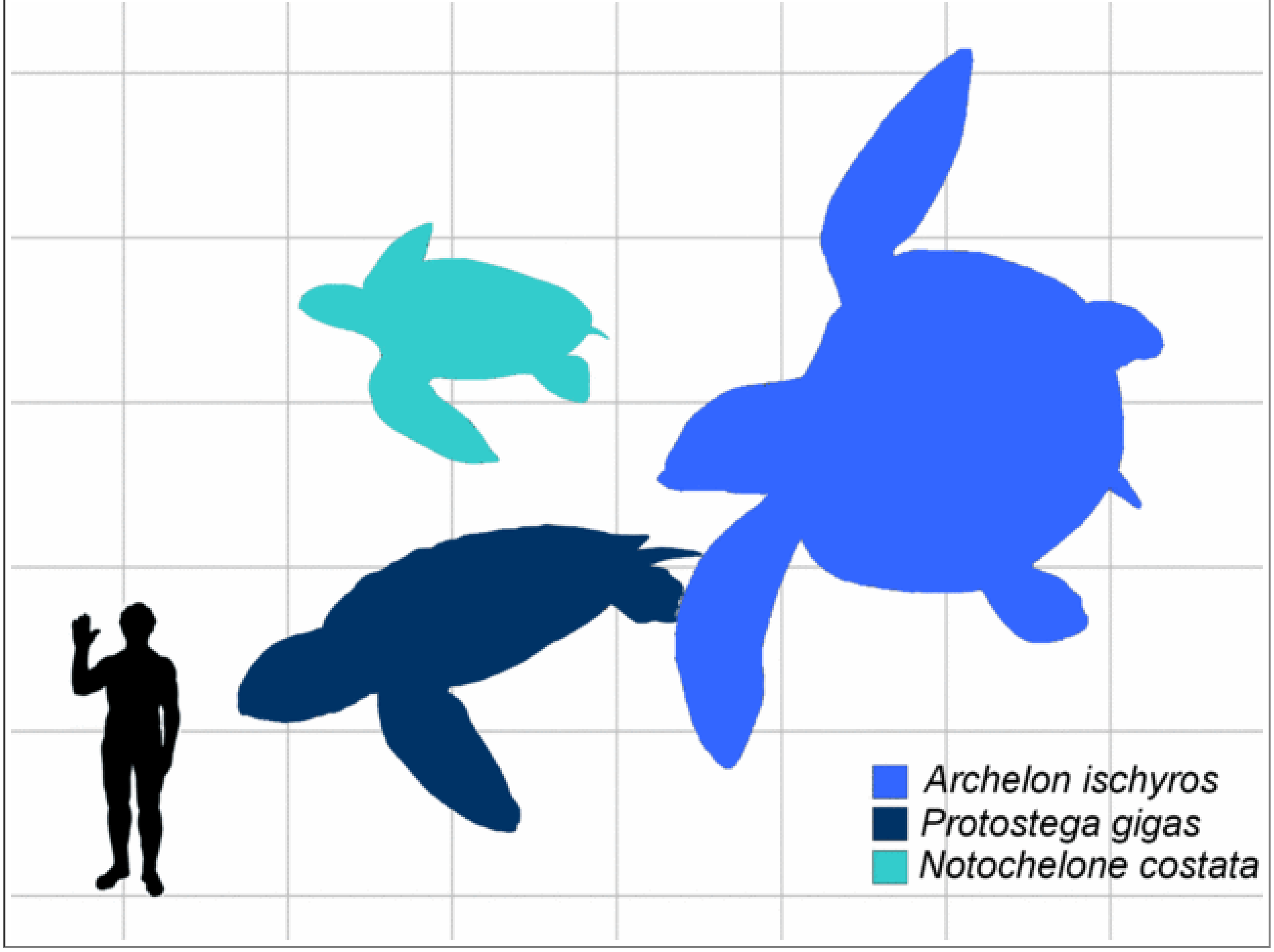
16. *Santanachelys* X

Archelon ischyros, Early Campanian of the Cretaceous Inland Sea, life reconstruction by , GNU Free Documentation/Creative Commons Attribution license, via Wikipedia

The Protostegids were the first ocean going testudines, and also included some of the largest. They were highly convergent with leatherback turtles (Dermochelyidae), and original morphological cladistic studies grouped them together in the superfamily Dermochelyoidea (Gaffney & Meylan 1988) or clade Pandermochelys (Joyce et al 2004). Subsequent computational-cladistic analysis including the ancestral protostegid *Santanachelys gaffneyi* shows that the Protostegids are not Chelonioidea at all, but belong to more ancient and primitive lineage of stem-cryptodires or even stem testudines dating back to the late Jurassic, and that the similarities to Dermochelyids are the result of convergence. As Joyce notes:

> " representatives of the Protostegidae are markedly primitive in many of their characteristics, including the absence of formed cervical articulations and the presence of elongate first thoracic ribs. A placement of Protostegidae within Chelonioidea thus either requires the systematic reacquisition of these primitive traits within Chelonioidea, or the independent loss of these traits in numerous cryptodiran lineages." - Joyce (2007) p.66

As with other marine tetrapods the tendency towards large size was prominant (*right*). Some such as *Bouliachelys*,



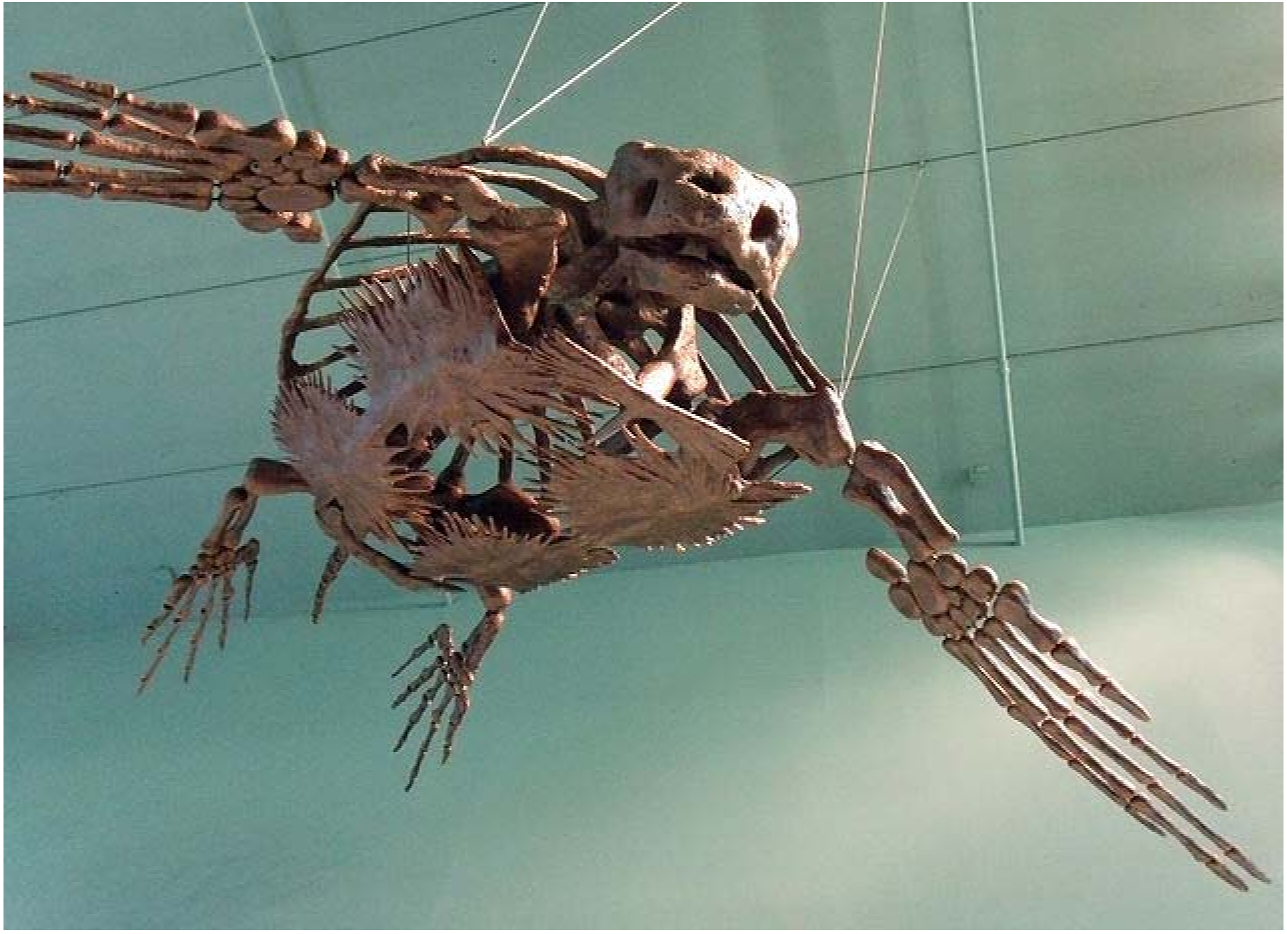
Size comparison of three members of the Protostegidae family : *Protostega gigas*, *Archelon ischyros*, and *Notochelone costata*, with a human for scale. By TheF, silouettes from artwork by by Dmitry Bogdanov. GNU Free Documentation/Creative Commons Attribution license, via Wikimedia

Desmatochelys, and

- Protostega equalled or exceeded the extant leatherback in size, while *Cratochelone* and *Archelon* would have had shells upto 3 meters in length and flipper spans of upto 5 meters. These animals would have made an impressive sight, swimming among the other equally huge reptiles of the Cretaceous seas.

Like many latest Cretaceous animals, protostegids did not make it to the end of the Mesozoic (ref Parham & Pyenson 2010)). After flourishing for some fifty million years they disappeared during the mid-Campanian, some ten million years before the asteroid strike and K-T extinction. During the very latest Cretaceous (Late Campanian and Maastrichtian) they were replaced by new dynasties of sea turtles, some of which equalled them in size. By the early Cenozoic the two lineages of modern sea turtles (Cheloniidae and Dermacheylidae) were ecologically diverse and well established (Mlynarski 1976, Parham & Pyenson 2010) MAK130313

Descriptions



Replica of a 75 million year old *Archelon ischyros* from South Dakota, now hanging out in the Wallace Building on the University of Manitoba campus, Winnipeg, Manitoba Canada. Posted to Flickr as Super Arky, photo Mike Beauregard. Creative Commons Attribution 2.0 Generic license, via Wikipedia

Protostegidae

Range: late Aptian-early Albian to early-mid Campanian, worldwide

Phylogeny: Eucryptodira **:** Plesiochelyidae + Thalassemyidae + (Angolachelonia + Xinjiangchelyid - Crown Cryptodire clade) + * **:** *Santanachelys* + (*Bouliachelys* + "Euprotostegidae")

Characters: "Nasal present; jugal–quadrate contact, excluding quatrado–jugal from lower cheek margin; lower cheek emargination absent; vomer–palatine contact lost, palatines medially meeting; foramen palatinum posterius open postero–laterally; pterygoid extending onto mandibular articular surface of quadrate; foramen posterius canalis carotici interni between pterygoid and basisphenoid; rodlike rostrum basisphenoidale; third (or second) cervical centrum biconvex; lateral process of pubis extending anteriorly beyond mideal portion of pubis; lateral process of humerus enlarged within the anterior portion of shaft, not easily visible from ventral view; radius with middle portion bent toward anterior; cervical scute overlying more than half the width of nuchal; thick neurals with median keel." - Hirayama 1998 p.707.

Further description: Carapace represented merely by a row of marginals, but the plastron very strongly developed and composed of thick ossifications. Skull with descending parietal plates. Humerus with the radial process short, blunt, and approximated to the head.Zittel, Eastman, et al (1902) pp.197

Comments: Edited from Wikipedia: As the earliest marine turtles, the protostegids set the general body plan for future lineages. They had a generally flattened body, with long oar-like front appendages specially evolved for swimming in the open ocean. Convergent with the Dermochelyidae, with which they probably shared a very similar ligfestyle. protostegids possessed extremely reduced carapaces. Some specimens had skeletal protrusions from their ribs almost wrapping around the turtles' bodies in place of a complete shell. They also had somewhat reduced plastrons, although not to the extent of dermochelyids. As with modern sea turtles, protostegids had sharp beaks. One of the defining characteristics of the members of the family was their almost-disproportionately large heads. Specifically, some specimens of *Archelon* have been found with heads a meter long.

Analysis of fossil organs has revealed entire stomachs containing fossilized shellfish (Hirayama 1998). In turn, they were preyed upon by the apex marine predators of the time. Fossil protostegids have been found with tooth impressions from the large lamnid sharks (Shimada et al 2002). Two specimens of *Protostega gigas* have been discovered to have tooth marks from large sharks. In addition, teeth of the extinct shark *Cretoxyrhina mantelli* (a Cretaceous equivalent of the Great White) have been found embedded in at least one *Protostega* skeleton.(Shimada & Hooks 2004) - Wikipedia

Classification and phylogeny:

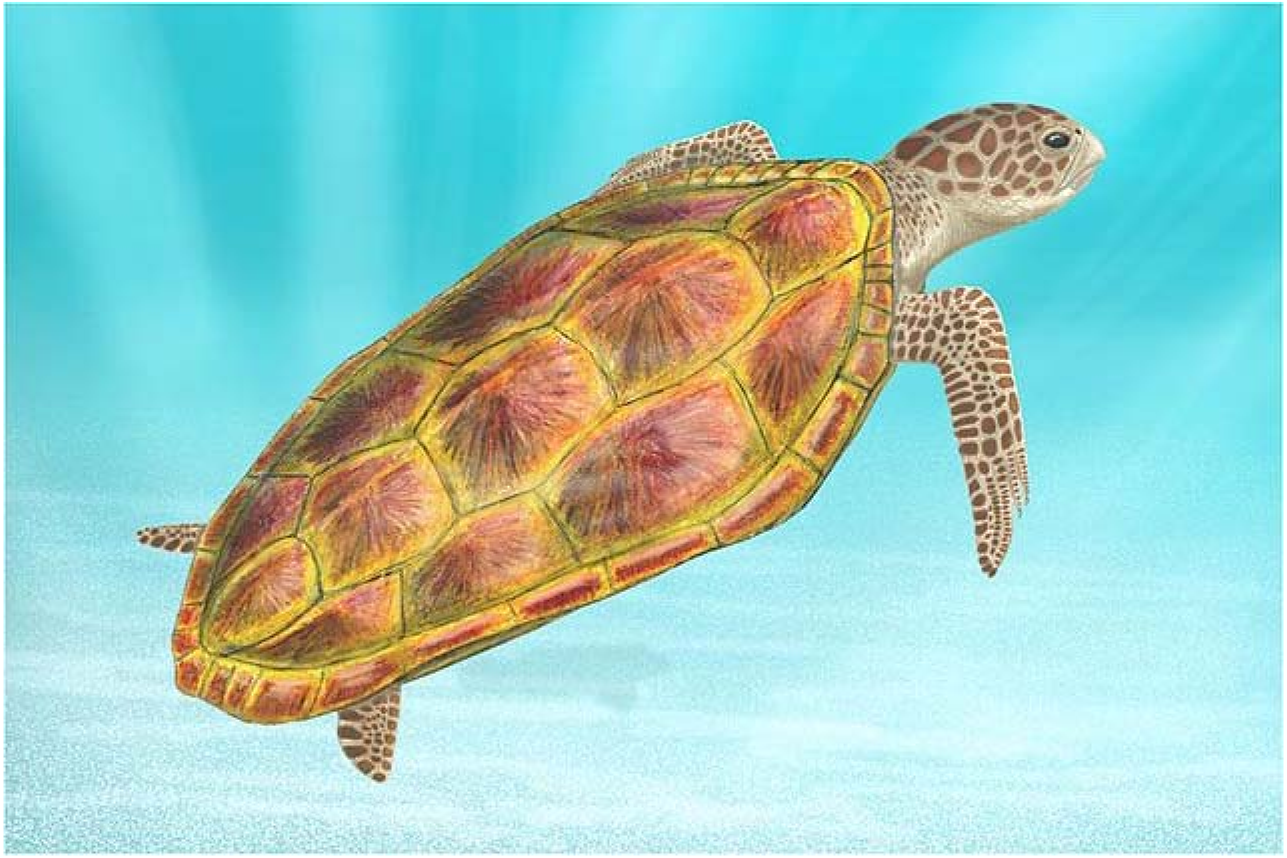
In 1888, the Belgian zoologist George Albert Boulenger published his classification of the Testudinata within the 9th edition of the Encyclopaedia Britannica. The genus *Protostega* was placed within the family Sphargidae (= Dermochelyidae) under the suborder Athecae. A year or so later, the entire suborder was downgraded by Karl Alfred von Zittel into a family within the Cryptodira. (Baur 1890)

Original cladistic studies supported the relationship of Protostegidae and Dermochelyidae, the two being considered monophyletic families and sister taxa (Gaffney & Meylan 1988, Hirayama 1998, Gaffney & Meylan 1988, Meylan & Hirayama 2000), the two teogether being included in the clade Dermochelyoide

In 1994, Hirayama proposed a three-family subdivision of the sea turtle superfamily based on cladistic analysis; Protostegidae was given full, formal family status in the system, containing most of the extinct genera, including *Archelon*, and a previously undescribed protostegid. (Hirayama 1994] The unidentified specimen was fully described in 1998, as *Santanachelys gaffneyi*. It was appended to the family after the new species was described. This specimen was later to be analyzed to be the family's oldest member.[Hirayama 1998]

But computational phylogenetic analyses conducted by Joyce (2007) and later workers, which included the most primitive protostegid species, *Santanachelys gaffneyi*, recovered the family as unrelated primitive turtles that only resemble leatherback turtles by convergence, although precise details differ. Joyce (2007) recovered Protostegidae as stem eucryptodires outside the Cryptodira crown group. *Solnhofia parsonsi* was found to be closely related. Anquetin, 2009 and 2012 arrived at a similar result, although he emphasised that future studies should include more protostegids to confirm this phylogenetic placement. Using a more restrictive dataset and a newly discovered African species, Mateus et al (2009) found *Thalassemys marina* to be the sister taxon of *Santanachelys*. Sterli, (2010), Sterli & de la Fuente (2011), Pérez-García 2012, recovered *Santanachelys* (and by implication the rest of the Protostegidae) as stem testudines outside the crown group of turtles (the least inclusive clade containing cryptodirans and pleurodirans). These results confirm that protostegids represent an independent lineage of marine turtles originating from primitive Late Jurassic forms, but astonishingly convergent with latest Cretaceous and Cenozoic Chelonoidea (Wikipedia modified by MAK130307)

Links: Oceans of Kansas, Wikipedia, Geologic History of Sea Turtles (short notes), Mikko's phylogeny (dendrogram only) MAK130313



Life restoration of *Santanachelys gaffneyi*. by Smokeybjb, GNU Free Documentation/Creative Commons Attribution license, via via Wikipedia

Santanachelys gaffney

Horizon: Santana Formation (late Aptian - early Albian) of North-East Brazil

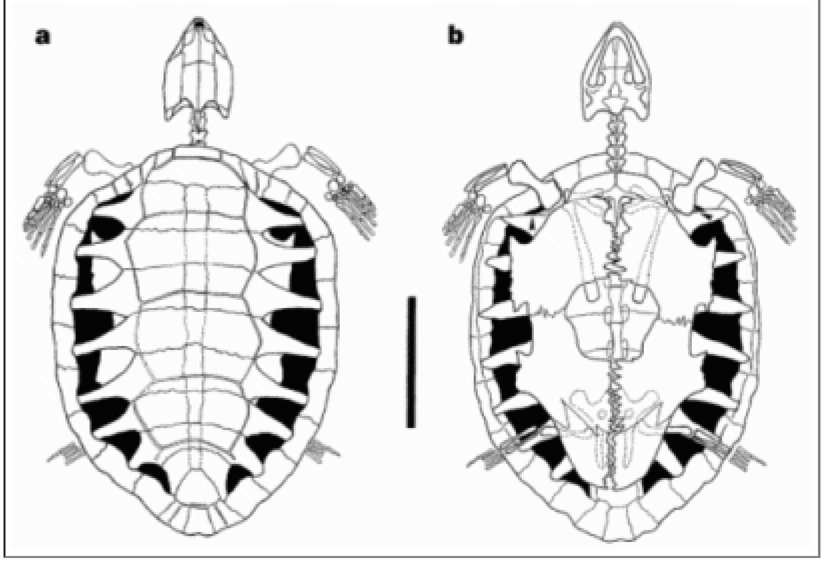
Phylogeny: Protostegidae **:** (*Bouliachelys* + "Euprotostegidae") + *

Comments: *Santanachelys gaffneyi* is the earliest known sea turtle. This 20-centimeter long animal resembled a terrapin in many respects, its marine lifestyle is indicated by the enormous salt glands around the eyes. This is confirmed by the fossil remains being found in marine sediments.

The kidneys of modern marine turtles are unable to deal with the excess salt which would result in dehydration from eating salty food or drinking seawater. To solve this problem they have enormous tear (lachrymal) glands, each bigger than their brain, adapted to excrete a salt solution more concentrated than seawater. Their presence is evident in fossil forms as well by of the large foramen in the skull where salt glands would be. From this we know that *Santanachelys* had the same type of huge salt glands situated near its eyes which allowed it to drink saltwater without dehydration.

Yet despite this advanced feature, and other characteristics shared with of modern sea turtles, it retained a number of primitive characteristics. For example, the metacarpals and short digits of the feet were still were distinct and movable, as in non-marine turtles, unlike the fully fused and rigid, hydrodynamic paddles that advanced sea turtles possess. This shows that the evolutionary return to oceanic waters of the sea turtle line evolved before the finalization and streamlining of the paddles. (Hirayama 1998)

For several years *Santanachelys gaffneyi* was considered the earliest known Pandermochelyian as well as the oldest panchelonioid (Joyce et al 2004 p.1000). More recent cladistic analysis showed it to be a much more primitive form, totally unrelated to conventional sea turtles. This means that



Santanachelys gaffneyi from Hirayama 1998

the many apomorphies and similarities between protostegids and dermochelyid chelonoidians (including - Hirayama 1998) are the result of convergence (homoplasy) rather than shared ancestry (homology). Hence identical solutions, such as for example giant tear glands for processing salt and preventing dehydration - evolved completely independently from only very distrantly related ancestors as a way of coping with a particular environmental problem. This sort of astonishing convergence means that one of the central pillars of cladistics -parsimony - is an unreliable assumption. One may even wonder to what extent such parallelism would feature in extraterrestrial life; would alien biota, rather than resembling the buf eyed mosnters of B-grade movies, actually be strongly convergent with terran life-forms? (as argued by paleontologist Simon Conway Morris (Conway Morris (year))) MAK130313

Links: Wikipedia, Studio d'Arte Corvo

Bouliachelys

Range: Early Cretaceous (Late Albian) of Australia

Phylogeny: Protostegidae **:** *Santanachelys* + ("Euprotostegidae" + *)

Comments: this primitive protostegid is similar to *Santanachelys* in having a poorly developed secondary palate, which shows that this feature evolved convergently in advanced protostegids and cheloniids. The hooked beak (an adaptation for feeding on pelagic ammonites; Hirayama 1994, 1997) of Bouliachelys is ismilar to that of more derived giant forms like Protostega, and is another convergent adaptation. *Bouliachelys* is the largest known before the Late Cretaceous - shows that early sea turtles were both larger and more diverse than was previously thought, The skull of *Bouliachelys* suggests an animal some 50% larger than *Notochelone* (maximum body length less than 1 m; Molnar 1991); an even bigger but very poorly known sympatric taxon, *Cratochelone* may have had a body length approaching 4 m, which puts it in the *Archelon* range. (Kear & Lee 2006)

"Euprotostegidae"

Range: Late Albian to Mid Campanian

Phylogeny: Protostegidae **:** *Santanachelys* + (*Bouliachelys* + * **:** *Notochelone* + "Protosteginea")

Characters: (Hirayama 1998)

Comments: "Euprotostegidae" is here used as in informal name for the group containing Notochelone and higher protostegids

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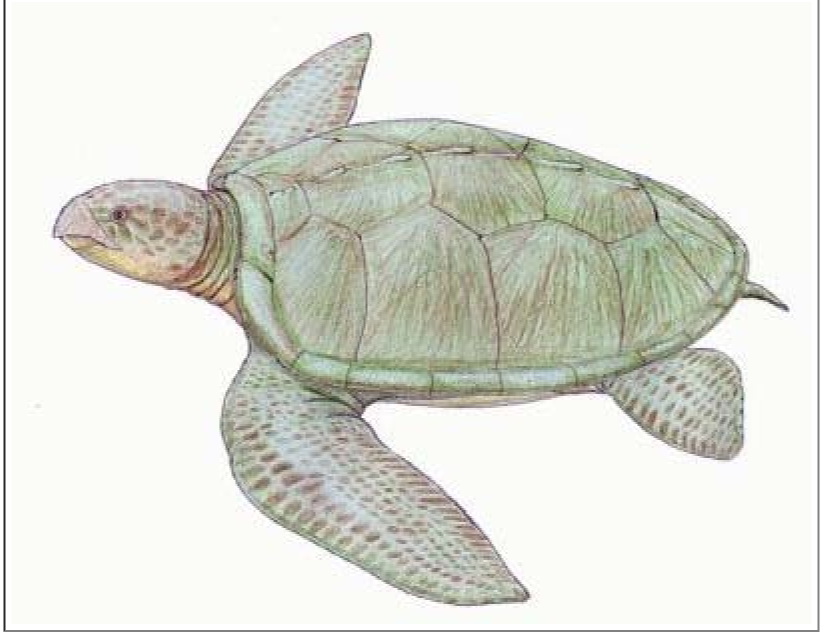
Notochelone Lydekker 1889

Range: Late Albian of Australia

Phylogeny: "Euprotostegidae" : "Protosteginea" + *

Comments: A medium-sized sea turtle, about the same size as the modern green turtle. It is thought that these animals fed on benthic molluscs. (durophagous) (Wikipedia)



Notochelone costata, an early protostegid turtle from Early Cretaceous (Albian) of Australia. Artwork by Dmitry Bogdanov, GNU Free Documentation/Creative Commons Attribution license, via Wikipedia

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"Protosteginea"

Range: Turonian to Mid Campanian

Phylogeny: "Euprotostegidae" **:** *Notochelone* + * **:** *Desmochelys* + *Rhinochelys* + Protosteginae

Characters: Foramen palatinum posterius absent; pterygoid narrow, C-shaped; large processus trochlearis oticum involving deep notch of quadrate; first suprapygal absent. (Hirayama 1998) medial contact between palatines; foramen posterius canalis carotici interni located between the basisphenoid and pterygoid; coracoid longer than scapula; and radius bends posteriorly Hooks 1998

Comments: "Protosteginea" is here used as in informal name for the group containing Desmatochelys, Rhinochelys, Cimochelys, "Protostega" eaglefordensis and the protostegids (= protosteginae)

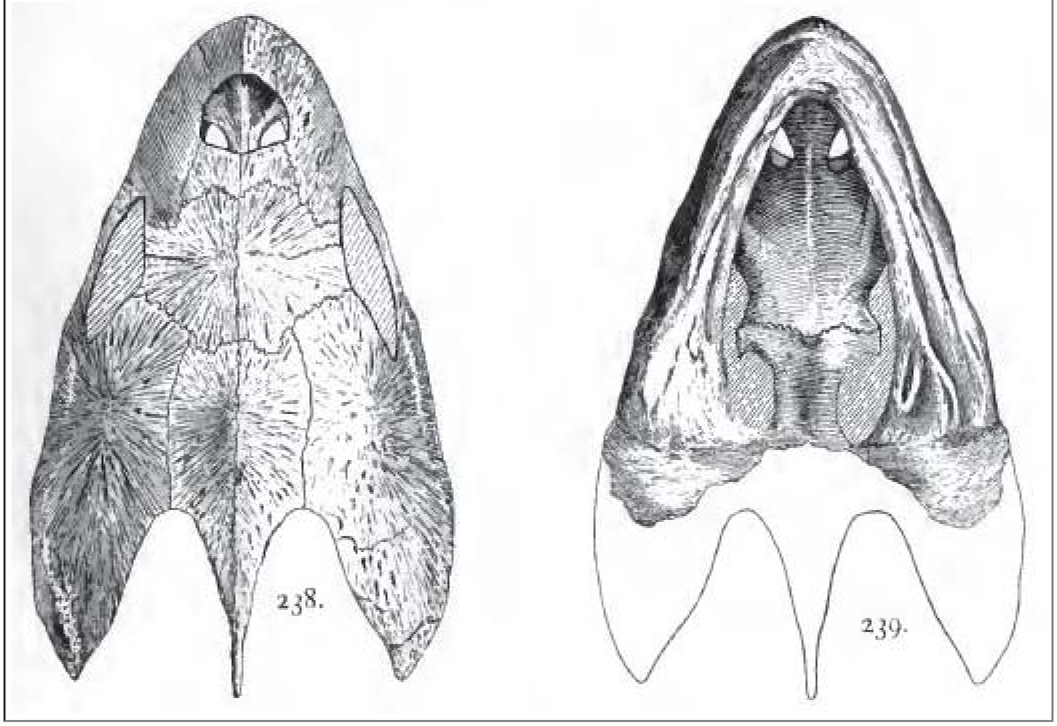
Desmatochelys

Williston.1894

Range: Turonian to Santonian-Campanian of North America

Phylogeny: "Protosteginea" : *Rhinochelys* + Protosteginae + *

Descriptions: Skull with temporal region roofed over as far backward as the occipital condyle. Large nasal bones present. Choanae placed well forward, not underfloored by the vomer, maxillae, and palatines. Small posterior palatine foramina present. Humerus indicating a paddle-like fore limb. Plastron loosely joined to the carapace.- Hay (1908) p 184



Desmatochelys lowi. Skull of type, length 20.5 cm, width 14.5 cm. Niobrara formation (Santonian), Kansas. From Hay (1908) p.185, figs 238 and 239; public domain (copyright expired).

Comments: Not to be confused with *Dermochelys* (although the two are similar in size and probably habits), this was a large intermediate grade protostegid, with a plastron length of about 1.5 meters (Mlynarski 1976 pp.50-51). Made the type for its own family Desmatochelyidae. The poorly known genera *Atlantochelys* and *Neptunochelys* were provisionally included (Hay (1908) p 184) but are more likely *incertae sedis*, perhaps synonyms of better known or more common species. For some time of uncertain evolutionary relationship, it has been placed in the Cheloniidae *incerta sedis* (Mlynarski 1976) and with *Corsochelys* as the subfamily Desmatochelyinae in the family Dermochelyidae. Cladistic analysis shows it to be a member of the Protostegidae (Hirayama 1998, Kear & Lee 2006), and it is sometimes grouped with *Rhinochelys*, a much smaller animal of a similar grade. As well as being known from (wherever) fossil remains of the genus, have been found in the Trent River Formation (Santonian-Campanian) of the Comox Basin of eastern Vancouver Island (Nicholls 1992), which extends the stratigraphic and geographic range extensions for the genus Desmatochelys to the Pacific coast . It is quitre likely that, like modern sea turtles, these animals had an ocean-wide distribution.

Rhinochelys Seeley 1869

Range: Cenomanian of England, France, and Lebanon

Phylogeny: "Protosteginea" : *Desmochelys* + Protosteginae + *

Comments: The following is edited and adapted from a Google translation of the French Wikipedia

Rhinochelys is known mainly

Rhinochelys nammourensis, Cenomanian of Lebanon. Specimens like this showed the synonymy of *Rhinochelys* (known only from the skull) and *Cimochelys* (known only from the shell). Photo by Ghedoghedo, GNU Free Documentation/Creative Commons Attribution license, via Wikipedia

from fossil skulls found in the early Late Cretaceous (Cenomanian) of England and France in the 19th century and described by Owen, Seeley, and Lydekker. In all, more than twenty species have been named and described, mostly by Seeley in 1889. The genus was revised by Collins in 1960 (Collins, 1960), who recognised only three English species - the type species *Rhinochelys pulchriceps* (Owen, 1851), *R. cantabrigiensis* Lydekker, 1889, *R. elegans* Lydekker , 1889, and the French *R. amaberti* Moret, 1935. The rest are ether synonyms or scrappy. The skulls are from rather small sea turtles, generally 4 to 6 cm in length (Mlynarski 1976 p.39) Collins also mentions *Cimochelys benstedi* , known only by its shell, but found in the same strata as*Rhinochelys*, although it is possible these two genera are the same. Based on a diagnosis of post-cranial characters, Collins included *Cimochelys benstedi* among Protostegidae, along with *Chelosphargis*.

The identity of *Cimochelys* and *Rhinochelys* was accepted by Hirayama in his revision of the family Protostegidae in 1994 (Hirayama, 1994). He also synonymises Collins' four species under the name *Rhinochelys pulchriceps* , to which he adds *Rhinochelys benstedi* (the former *Cimochelys*).

In 2006, Tong et al 2006 described specimens from Lagerstätte of Nammoura at Lebanon as a new species *Rhinochelys nammourensis* . The fossils, very well preserved and nearly complete, undoubtedly belong to *Rhinochelys* given their cranial characters, although they differ enough to justify placing them in a new species. The shape of the carapace, also very similar to that of *Cimochelys*, confirming that both genera are the same. - Wikipedia

Given the identity of *Cimochelys* and *Rhinochelys*, the present author (MAK) fails to see the reason for retaining *R. benstedi* as a separate species. That leaves only two species, *Rhinochelys pulchriceps* (Owen , 1851), and *Rhinochelys nammourensis* Tong et al 2006.

Mlynarski 1976 pp.38-9) places *Rhinochelys* with *Calcarichelys* and *Chelosphargis* in Zangerl, 1953a's paraphyletic (Hooks 1998) subfamily Chelospharginae MAK130313

Links: French Wikipedia, Mikko's Phylogeny Archive (retains four species)

Protosteginae **:** *Archelon, Calcarichelys, Chelosphargis, Microstega*, and *Protostega*

Range: Coniacian to Mid Campanian

Phylogeny: "Protosteginea" **:** *Desmochelys* + *Rhinochelys* + * **:** *Chelosphargis* + (*Calcarichelys* + Protostegini)

Characters: Prefrontal-postorbital contact present; scar for M. latissimus dorsi and teres major located at middle of shaft; star-shaped, hyo–hypoplastra. (Hirayama 1998); absence of the foramen palatinum posterius; a basioccipital with knob-like processes fitting into sockets on the posterior end of the pterygoids; the presence of only one suprapygal; and a T-shaped entoplastron that is not sutured to the other plastral elements - Hooks 1998 (as "Protostegidae")

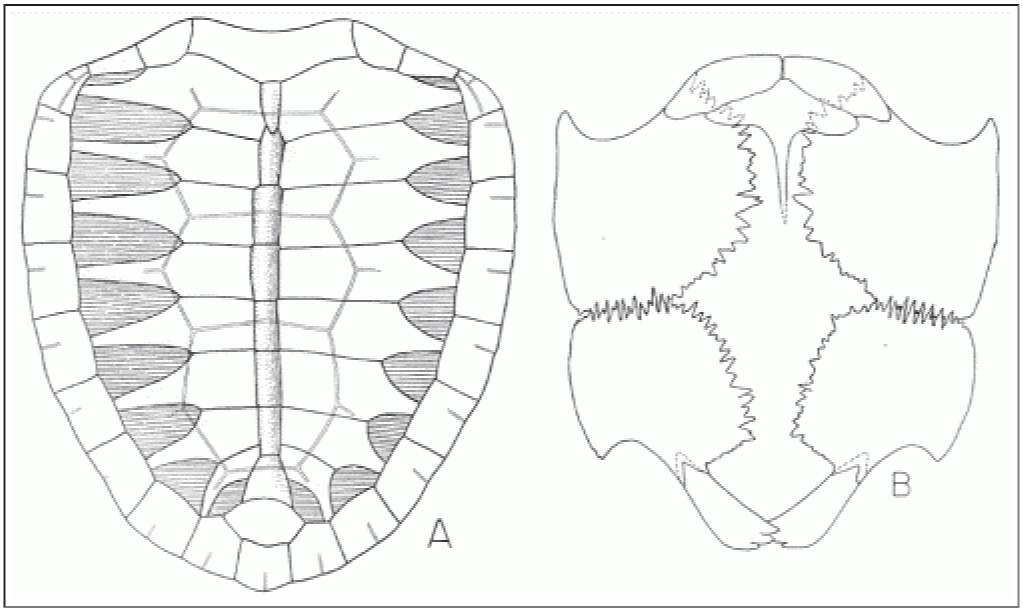
Comments: As evidenced from theire respective character and genus lists, Hirayama and Hooks, writing in the same year, define the same clade using different synapomorphies, and in Hooks' case two extra genera, *Calcarichelys* and *Microstega*. Hooks refers to this clade under the name Protostegidae, but as that family ranking is now universally applied to a more diverse range of taxa we have referred to it as the subfamily Protosteginae. MAK130313

Chelosphargis advena (Hay)

Range: Coniacian/Santonian to Early Campanian of North America

Horizon Niobrara Chalk, Kansas and Mooreville Chalk, Alabama

Phylogeny: Protosteginae **:** (*Calcarichelys* + Protostegina) + *



Chelosphargis advena, No complete specimens are known; this is a reconstruction of the carapace (left) and plastron (right) from available materials. The left side represnets the juvenile shell, the right the adult. From Zangerl, 1953a fig 26, p.87

Description: " Primitive genus of Protosteginae of small or medium size. Skull with blunt, straight premaxillary beak. Frontal bones large and with lateral processes toward the orbital rims. Prefrontals excluded from sagittal contact by nasal bones. Otic and exoccipital area very similar to condition in cheloniid turtles. Lower jaw with long symphysis; rami fused, even in juvenile specimens. A slight, but sharp sagittal crest on triturating surface of lower jaw. Carapace laterally with fontanelles of moderate size in juvenile specimens. Neural bones forming blunt, low keel in midline. Peripheral edge of carapace even. Pygal plate entirely separating eleventh pair of marginals." - Zanger 1953a p.80

Comments: The most primitive of the Protostegines, Primitive genus of Protosteginae of small or medium size. The species is quite common, but is represented mostly by very young individuals. Formerly *Protostega advena* Hay (1908); the over-all appearance and the major proportions of the skull of this species are very similar to those of *Protostega*. Zangerl, 1953agroups *Calcarichelys* and *Chelosphargis* in a new subfamily Chelospharginae. Cladistic analysis by Hooks 1998 shows the latter to be a paraphyletic taxon, which makes it invalid as a cladistic taxon but not as a Linnaean or Evolutionary taxon. MAK130313

Calcarichelys gemma Zanger 1953

Range: Santonian to Early Campanian of North America

Horizon: Mooreville Chalk, Alabama; and Niobrara Chalk, Kansas.

Phylogeny: Protosteginae **:** *Chelosphargis* + (Protostegini + *)

Characters: a small specialized protostegid closely allied to Chelosphargis, but with uniquely specialized neural keel and strongly serrate peripheral margin (except in front). Unusually high, sharply pointed neural plates alternate with nearly flat saddle-shaped ones. Last keel-thorn located on suprapygal. Pygal plate very narrow. Hypoplastron nearly rectangular. - Zanger 1953a p.119, 129

Comments: This small (shell about 30 cm) but bizarre protostegid was equipped with a row of spines along the dorsal mnidline of the shell, alternating with more typically smooth plates. The spines doubtless were defence against predators, as unlike many other protstegids this little animal couldn't rely on sheer size. It was first discovered Burkville near Montgomery in Alabama, by CM Barber in 1946 and described in 1953 by Rainer Zangerl. Zanger's diagnosis of Calcarichelys gemma is based on the study of another fossil discovered in 1949 by Barber Greene, which was particularly complete and well preserved, nicknamed "the rock" by its discoverer, and which is at the origin of name of the species. (French Wikipedia) . Along with the closely related *Chelosphargis* it has been found in both the Niobrara Chalk of Kansas and in the Mooreville Chalk of Alabama, although unlike *Chelosphargis* it is best know from the latter locality. Zanger 1953a includes the two monospecific genera in a new subfamily Chelospharginae, represneting a more primitive level of protostegid organization, although with certain specialized features paralleling those in the Protosteginae (= Protostegini) (Zanger 1953a p.131). It is interesting that these smaller and more morphological primitive animals ranged widely from the inland sea to the open Atlantic, whereas the giant and highly derived protostegids are so far known only from the inland sea, although there is no reason why they could not have had a wider distribution. So far, no protostegines have been found beyond North America, indicating either a lack of suitable starta, or that these great turtles were limited in distribution to the Cretaceous inland sea of mid-west North America. *Protosphargis* is a convergent but unrelated form from the Latest Cretaceous of Europe. MAK130401

Protostegini Hooks 1998

Range: Santonian to Mid Campanian of North America

Phylogeny: Protosteginae **:** *Chelosphargis* + (*Calcarichelys* + * **:** *Microstega* + Protostegina

Comment: The "higher" protostegines. As with Hominidae/inae/ini/ina this taxon's suffic is based on the cladistic sequence of branching, rather than Linnaean tribes which although having the same suffix pertain to a different taxonomic system

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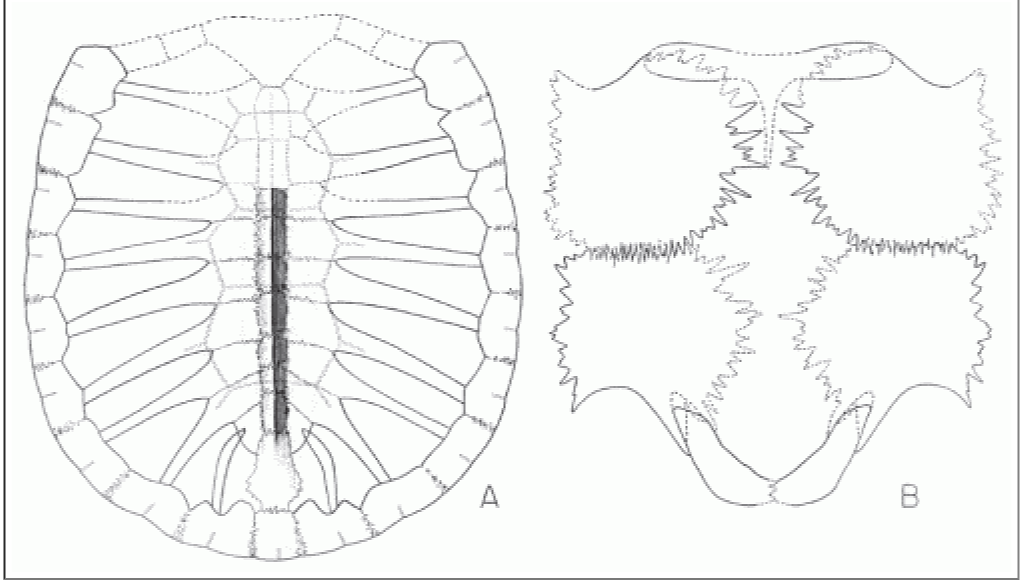
Microstega copei (Wieland 1909)

Synonyms: *Archelon copei*, *Protostega copei*

Range: Santonian or Early Campanian of North America

Phylogeny: Protostegini **:** Protostegina + *

Comments: Based on a disarticulated skeleton of moderate size (YPM 1787),



Microstega copei, carapace (left) and plastron (right). From Zangerl, 1953a fig 20, p.79

this species was described by Wieland, 1909 as a new species of *Protostega*. Zangerl, 1953a noted the even keel formed by the neural series of bones in the carapace is similar to that of *Archelon ischyros*, unlike the uneven, interrupted keel of *Protostega*. He therefore transferred the species to *Archelon*, as a more primitive species of that genus.. Hooks 1998 using cladistic analysis discovered this species is more basal than both *Archelon ischyros* and *Protostega gigas*.and gave it its own genus as well as making it sister taxon of the Protostegina. As there is very little morphological difference between *Protostega* and *Archelon* it probably really doesn't matter what genus this species is allocated to MAK130315

Protostegina Hooks 1998

Range: Santonian to Mid Campanian of North America

Phylogeny: Protostegini **:** *Microstega* + * **:** *Protostega gigas* + *Archelon* (= *Protostega ischyros*)

Protostega gigas. Photo by Claire H. from New York City, GNU Free Documentation/Creative Commons Attribution license, via Wikipedia

Description: "Marine turtles with the fore limbs converted into flippers resembling those of the Cheloniidae. Carapace greatly reduced, the disk extending not one-half the distance toward the distal ends of the ribs. Peripherals present. Plastron loosely connected with the carapace and with a large median fontanel. Entoplastron T-shaped, with the lateral wings elongated and distally expanded. Epiplastra not certainly known. Xiphiplastra short and bent. Skull large, temporal region broadly roofed over. Region in front of the orbits elongated. Jaws with large crushing-surfaces. Choanae far forward; not underfloored by the surrounding bones." - Hay (1908) p.189

Comments: The above is Hay's description of Protostegidae sensu *Protostega* + *Archelon*. These were the last and largest of the Protostegids Zangerl, 1953a makes this the subfamily Protosteginae (Mlynarski 1976 pp.39-40), while Hooks 1998, using cladistic analysis, gives this clade the Linnaean rank of subtribe as Protostegina. But in asmuch as *Protostega* and *Archelon* represent a morphological and stratigraphic sequence, only attachment to the coolness factor associated with the name *Archelon*, and the cladistic phylogenetic reluctance to attribute more than one species to each genus, prevents *Archelon* from becoming a junior synonym of *Protostega*, as *Protostega ischyros* (Wieland), and in fact Williston (1897) did use this binomial, although it seems that no-one followed him in this. Hooks (1998) placed the contemporary *Archelon copei* in a new, somewhat more basal genus, *Microstega* (Hooks 1998), although ll three species are probably similar enough to be considered congeneric. MAK130313

Protostega gigas Cope 1872

Protostega gigas, life reconstruction by Dmitry Bogdanov, GNU Free Documentation/Creative Commons Attribution

Horizon: Type specimen: Smoky Hill Chalk of western

Kansas (Santonian)

license, via Wikipedia

Phylogeny: Protostegina **:** *Archelon (= Protostega ischyros)* + *

Description: Descending parietal plates well developed. Carapace intermediate between Dermochelyidae and Chelonidae, with several primitive characters regarded as ancestral to both. Plastron with larger bones and a much smaller fontanelle than in *Dermochelys*. Body elongate, the posterior end truncated; limbs paddle-shaped. Post-axial border of humerus more orhis genus less deeply emarginate. (Zittel, Eastman, et al (1902) pp.198). Premaxillary beak less developed than in Archelon. Maxilla with a rather broad grinding surface, which extends backward to behind front of orbit. Lower jaw with the rami early co-ossified. Entoplastron T-shaped, with the middle third of the anterior border concave from side to side, the distal ends convex. Radial process of humerus large. Hay (1908) p.190,

Comments: Differs from Archelon only in somewhat smaller size and earlier stratigraphic horizon, this is clearly an ancestral species top the latter. Average plastron length of 1.2 meters (Mlynarski 1976 p.39), maximum overall length upto 3 m. Like the similar-sized modern leatherback sea turtle, with an overall length of upto 2.7 m, *Protostega*'s carapace lacked scutes, making it weaker but also lighter. (Wikipedia). *Protostega* most likely fed on plegaic molluscs such as belemnites

A number of species have been attributed to to this genus. *Protostega copei* is a valid taxon from the Niobora of Kansas and has been given a distinct generic name by Hooks 1998; see *Microstega*. *Protostega dixie* from Selma Formation (Mooreville Chalk), of Alabama is considered a distinct species by Zangerl, 1953a but a synonym of *Protostega gigas* by Hooks 1998. *Protostega potens* Hay is based on a partial and weathered skeleton (AMNH 180), also from the Niobora formation. Zangerl, 1953a considers it a distinctive species but Hooks 1998 makes it a junior synonyms of *Protostega gigas*. The fossil indicates a turtle larger than any known specimen of *P. gigas*, but considerably smaller than the giant type specimen of *Archelon ischyros*. It may simily be a very large *P. gigas*. "Protostega" *eaglefordensis* is a large but poorly known protostegid known from partial remains from the Eagle Ford Formation, Texas. The limbs and girdles are more primitive than in any known large protostegid Zangerl, 1953a p.89. The phylogenetic relationships are unresolved but according to (Hooks 1998) it does not belong in the genus *Protostega*. MAK130313

Links: Oceans of Kansas, Wikipedia (stubby article but comprehensive bibliography).

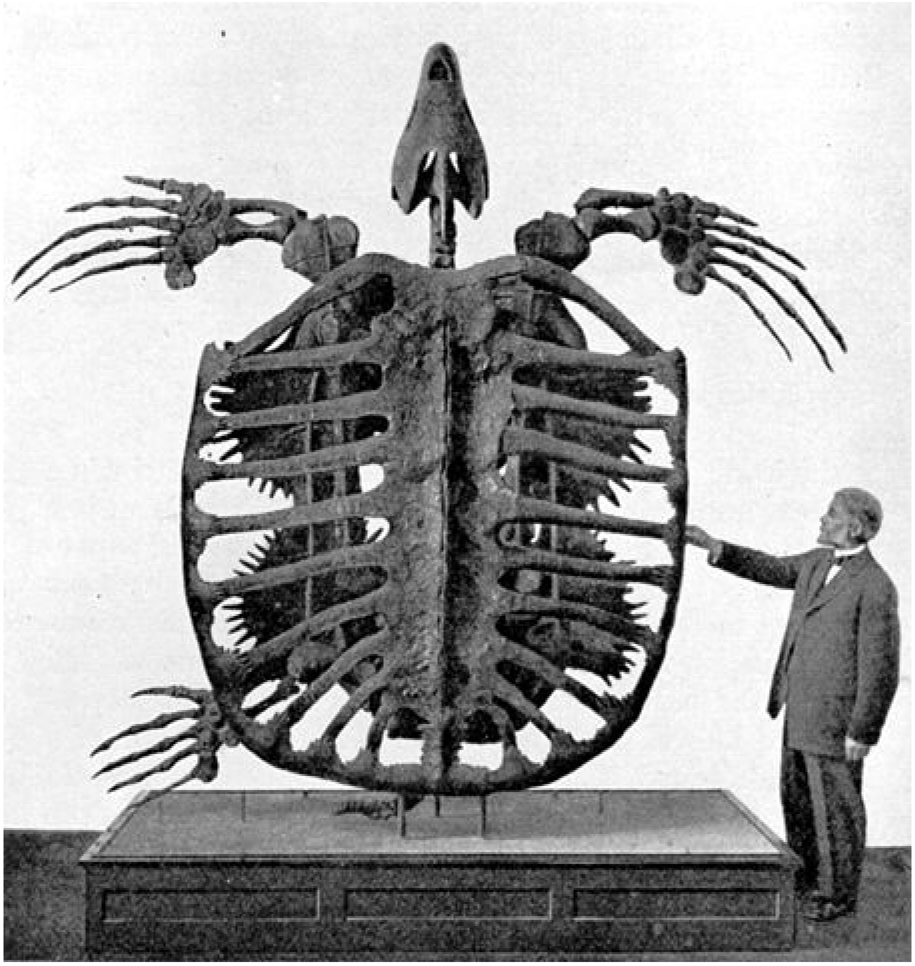
Archelon ischyros Wieland. 1896

Range: Upper Pierre shale (Mid Campanian) of South Dakota and Wyoming.

Phylogeny: Protostegina **:** *Protostega* + *

Description: Premaxillary beak strongly developed. Crushing-surface of upper jaw mostly on the premaxillaries; that on the maxillae extending back only to opposite the choanae. Lower jaw with the rami not co-ossified at symphysis; at least, not until old age. Entoplastron T-shaped, with the anterior border concave from end to end. Radial process of humerus feeble. Hay (1908) p 202

Comments: The appropriately named *Archelon* ("ruler") is with the poorly known *Gigantatypus* the largest sea



Type specimen (YPM 3000) of *Archelon ischyros* in the Yale Peabody Museum, Yale University. Amazingly enough, this giant animal's skeleton represents by no means the largest known Archelon. From Frederic A. Lucas, 1902, *Animals of the past*, copyright expired , public domain, via Wikipedia

turtle that has ever been described, although the freshwater *Stupendemys* may have grown even larger. The type specimen of Archelon (YPM 3000) was collected from the Pierre Shale of South Dakota by Dr. G.R. Wieland in 1895 and described by him the following year (Wieland, 1896) This and other specimens were recovered near the South Fork of Cheyenne River in South Dakota, in the upper Pierre formation, below the Judith River formation (Mid Campanian). From the length of the neck and the carapace Wieland estimates that the total length of type specimen was about 3.5 meters. The estimated total length of the carapace of the original animal is about 1.9 meters. The width, exclusive of the peripherals, must have been about 2 meters; including the peripherals, about 2.5 meters. Hay (1908) pp 202-203. Wieland also described another, more fragmentary specimen of similar size from the same formation and locality, which he named *Archelon marshii*, and which is clearly a synonym of *A. ischyros*

An even larger *Archelon* fossil was found in the Pierre Shale of South Dakota in the 1970s, is more than 4 metres long, and about 4.9 metres wide from flipper to flipper. Since only the tiniest fraction of organisms that ever lived are fossilised, and given that some recent sea turtle specimens are of larger than average size, it is similarly very likely that there were even larger Archelons, in keeping with exaggerated measurements in non-technical literature of flipper to flipper span of 5.5 meters.

Apart from larger size, *Archelon* is anatomically very similar to its predecessor *Protostega gigas*, and Williston 1897 includes it in the same genus; a reasonable approach that is not acted on because of the romantic trendency to make genera of large impressive animals monospecific (*Baronyx* and *Suchimimus* are two other examples of genera that are only distinct at the species level)

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Unlike most turtles, *Protostega* and *Archelon* did not have a solid shell, but instead had a skeletal framework

Archelon ischyros, mounted cast, closeup of head, Canadian Museum of Nature, Ottawa, Ontario, Canada. The upper jaw's very large beak is evident Photo D. Gordon E. Robertson, Creative Commons Attribution license, via Wikipedia

supporting a leathery or bony carapace. In these and other respects they are convergent with Cenozoic and modern Dermochelyds or leatherback turtles. Other distinguishing features include a pointed tail, a narrow skull, a relatively narrow, high-vaulted shell, and a pronounced overbite. The live weight of an Archelon ischyros is estimated at more than 2,200 kg. The bite was probably very strong, optimized for feeding on pelagic mollusks such as squid and belemites. The specimen exhibited by the Museum of Natural History in Vienna is estimated to have lived to be a century old (Wikipedia).

The head alone was enormous, upto a meter long, and the formidable beak, with its broad crushing-surface, indicates a diet of mollusks and crustaceans. Associated with the fossil were various genera of belemnite tetrabranchiate cephalopods, and the jaws of this giant turtle seem to have been well adapted to pick up and crush such objects. Hay (1908) p.208,

Archelon's beak more strongly developed than in *Protostega* Hay (1908) p 202), presumably as the result of allometric growth (like large deer which grow proportionally larger antlers with lareger body size).

MAK130313

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Chelonii: Centrocryptodira

Abbreviated Dendrogram

```
ANAPSIDA ?
 `--o CHELONII
    |--Odontochelys
    `--Testudinata
       `--+--Proganochelys
          `--+--Kayentachelys
             `--+--Meiolanoidea
                `--+--Pleurodira
                   |--Paracryptodira
                   `--+--Protostegidae
                      `--+==Xinjiangchelyidae
                         `--o Centrocryptodira
                            |--+--Hoyasemys
                            |  `--Sinemydidae
                            |--Osteopygis
                            |--Trionychoidea
                            `--o Durocryptodira
                               |--+--Kirgizemys
                               |   `--+--+==o
Macrobaenidae
                               |      |   |-
-Judithemys
                               |      |   `-
-Macrobaena
                               |      `--o
Chelonioidea-Chelydridae-Kinosternoidea Clade
                               |         |--+-
-Chitracephalus
                               |         |  `-
-Chelonioidea
                               |         `--+-
-Chelydridae
                               |            `-
-Kinosternoidea
                               `--Testudinoidea
```

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3. Durocryptodira
4. *Hoyasemys* X
5. *Judithemys* X
6. *Kirgizemys* X
7. *Macrobaena* X
8. Macrobaenidae X
9. *Osteopygis* X
10. Sinemydidae X

Centrocryptodira, Durocryptodira, Morphology and Molocules

The names Centrocryptodira and Durocryptodira nicely represent the conflict between morphology and molecules in turtle evolution; neither is used much now.

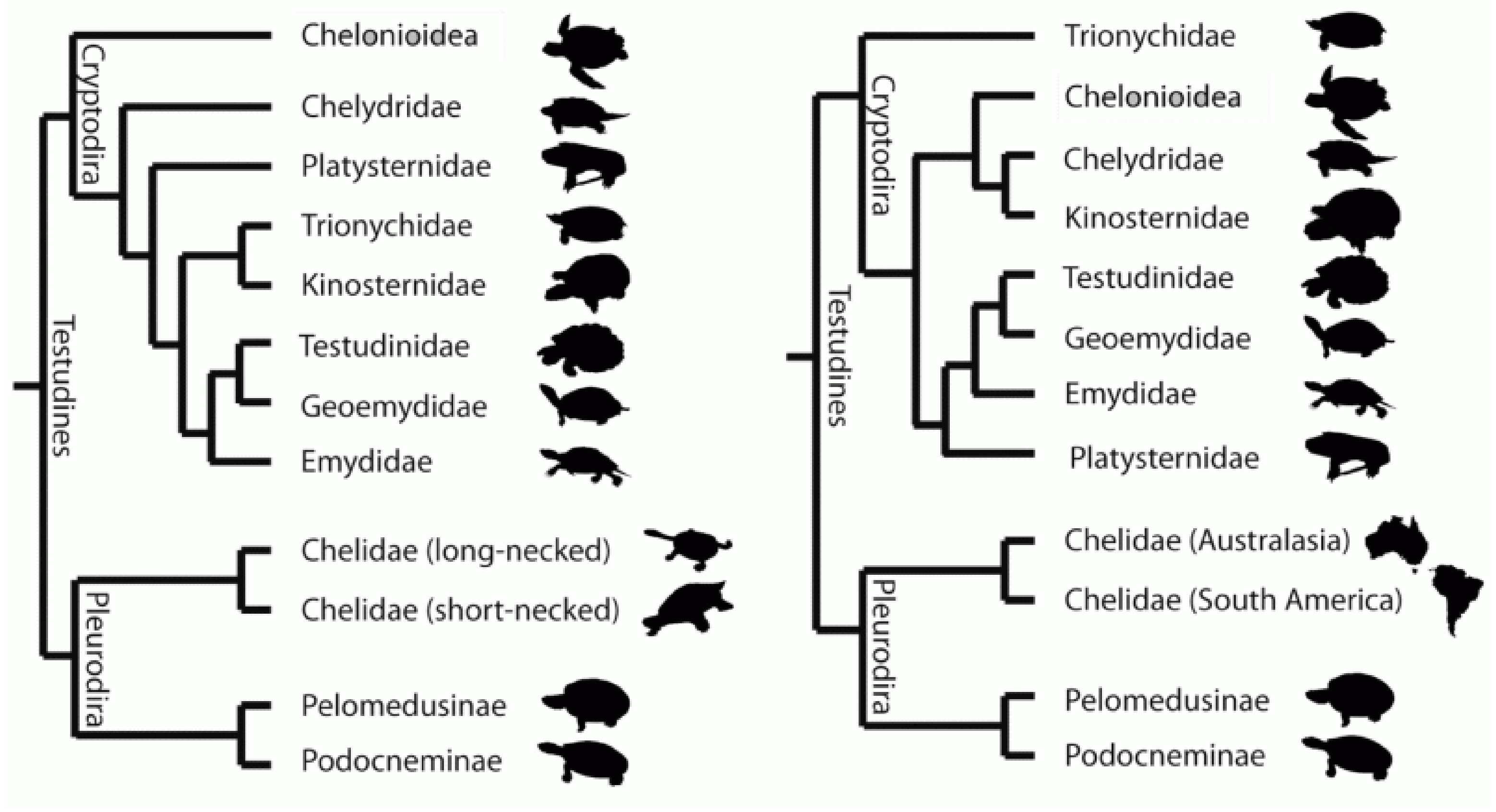
The morphology-based Hennigian cladistic taxon Centrocryptodira was named by Gaffhey and Meylan, 1988 to include Chelonians with pronounced cervical articulations, which includes the Meiolaniidae, the paraphyletic Sinemydidae-Macrobaenidae assemblage, and the Polycryptodira (Gaffney, 1996).

The Meiolaniidae have since been considered a stem Chelonian by more recent workers (Hirayama et al, 2000, Joyce 2007, Sterli 2008, and Anquetin 2009); this difference would seem to be due to the replacement of Hennigian cladistics with statistical-computational parsimony analysis, and phylogenetic nomenclature such as restricting morphology based definitions to crown-groups only (in this regard, Joyce's 2007 paper is as important and revolutionary as Gaffhey 1975 and Gaffhey and Meylan, 1988.

This more recent paradigm means the rejection of cladograms based on a smaller number of well-known characters with those based on a greater number of less analysed and atomistic treated characters. This shift in emphasis is itself the result of the development of cheaper and more powerful computing. For this reason, in every field of cladistic paleontology, the Hennigian "hand-coded" method has been replaced by trees based on huge matrixes and supermatrixes of the sort that could only be calculated by powerful computers.

Both methodologies agree however that the various Cretaceous to Paleocene semiaquatic and mostly Asiamerican turtles of the families Sinemydidae and Macrobaenidae are a paraphyletic assemblage or grade of forms more advanced than Jurassic Asian Xinjiangchelyidae, and from which recent or crown group cryptodires evolved. Here the Polycryptodira Gaffney and Meylan, 1988 are synonymous with "Crown Group Cryptodira" of statistical-computational and phylogeny-nomenclature based current cladism, and includes the superfamilies Chelydroidea, Chelonioidea, Trionychoidea and Testudinoidea.

For Gaffney and Meylan and co-workers and students therefore the series goes Xinjiangchelyidae + (Meiolaniidae + (paraphyletic Sinemydidae and Macrobaenidae + (Chelydroidea + (Chelonioidea + (Trionychoidea and Testudinoidea)))). While for later workers, it is Xinjiangchelyidae + (paraphyletic Sinemydidae and Macrobaenidae + (Chelonioidea + (Chelydroidea + (Trionychoidea and Testudinoidea)))). The only differences is that for the latter the Meiolaniidae are not cryptodires but placed outside the crown group testudines altogether, and Chelonioidea are the most basal taxon of crown group cryptodoires. Developmental biology supports the latter, with Chelonioidea more basal than Chelydroidea, and Trionychoidea and Testudinoidea the most derived Werneburg & Sánchez-Villagra 2009. But when matched with the fossil record there is very little congruence. Of advanced cryptodires only the trionychoidea goes back to the early-Late Jurassic, all the other clades are represented by extensive ghost lineages until at least the late Cretaceous



Alternative testudine phylogenies. (A), morphology-based, according to Joyce 2007, with cheloniidea as the most basal extant cryptrodires. This is also supported by developmental biology (Werneburg & Sánchez-Villagra 2009). (B) molecular-based, according to Shaffer 2009, with Trionychia as the most basal extant clade, which is supported by the fossil record (Danilov & Parham, 2006). Diagram from Jones et al, 2012 fig 1; Creative Commons Attribution

Molecular sequencing presents a totally different picture. Beginning with Shaffer et al. (1997) and ubiquitously verified by every paper since (e.g. Fujita et al, 2004, Krenz et al 2005, Shaffer, 2009, Barley et al. 2010, (more)). In contrast to morphological analyses, it finds both the Trionychoidea and Chelydroidea to be polyphyletic. In this phylogeny, the big headed turtle *Platysternon megacephalum* turns out to be more closely related to the Testudinoidea. Equally surprisingly, the traditional Trionychoidea splits into two groups, one of these, consisting of the families Trionychidae and Carettochelyidae (the Trionychia), being resolved as the most basal extant cryptodires, and only very distantly related to the other (the Kinosternoidea). What is surprising is that morphologically these are very specialised and similar animals; whether using Gaffney's Hennigian cladistics or the more popular current computational-statistical method of Joyce and later workers, the Trionychoidea (as Trionychia + Kinosternoidea) is universally resolved as a highly derived monophyletic taxon.

The consensus molecular phylogeny therefore would be Pleurodira + (Trionychia + (Chelydridae + Chelonioidea + Kinosternoidea) + Testudinoidea incl. *Platysternon*). Even if the details of relation between the Chelydridae + Chelonioidea + Kinosternoidea, and of Testudinoidea and *Platysternon* (whether the latter is a sister group to the Testudinoidea as a whole or included within the group as the sister clade to Emydidae) might vary slightly, all agree on the fundamental position of the Trionychoidae at the base of the cryptodire family tree. In view of the great morphological similarity between the Trionychoidae and the Kinosternoidea, it seems mind-boggling that evolution should follow such identical nodes independently even after a hundred million years or more of seperate evolution.

Could the apparent basal position of the Trionychoidae then simply be an artifact of molecular sequencing? It is striking that the Trionychoidae have the longest branches of extant chelonians, which shows that their apparent basal position may be the result of sequencing artifacts, specifically the common problem known as long branch attraction. Sterli, (2010) tested the validity of the long branches of the Pleurodira as the adjacent group to Trionychoidae, with analyses excluding Pleurodira, Trionychoidae, and Kinosternoidea. The results show that the phylogenetic position of each clade is stable and does not vary when one is excluded from the analysis. As further confoirmation, the five genes were tested separately in Bayesian analyses and maximum likelihood. In all the cases the topologies retrieved Trionychoidae as the adjacent group of Pleurodira, as distinct from all other cryptodires (Sterli, (2010) p.103)

Support for the ancient status of the Trionychoidae comes from the stratigraphic sequence; an appearance as far back as the Oxfordian (early Late Jurassic) (Danilov & Parham, 2006) makes them the earliest known crown cryptodire lineage, the only extant clade whose unambiguous fossil record predates the late Cretaceous. Although many cladists dislike stratigraphy as it gets in the way of nice and tidy morphological analyses, the present author (MAK) considers excessive appeal to ghost lineages to be a cop out in the case of groups with an already extensive fossil record. Since even terrestrial testudines are easily and frequently fossilised, one needs to ask why so many clades are totally unknown as fossils for more than half their purported stratigraphic range.

Another intriguing piece of evidence is the presence of transitional forms, as well as exterme homoplasy. *Basilochelys* combines Xinjiangchelyid attributes with those of Adocusia. The mid Cretaceous proto-Carettochelyid *Kizylkumemys* has very archaic (paracryptodire-like) characteristics. *Sandownia* is another form that may be either a stem-eucryptodire-like trionychoidan or an unrelated animal convergent on trionychoidans. Cladistic analysis by Tong et al. 2009 reveals rampant homoplasy among testudines and several characters occuring only in Trionychoidae (Crown Trionychoidae, Adocus and Nanhsiungchelyidae) and some macrobaenid–sinemydid turtles, which suggests the Trionychoidae might have a more stemward position among eucryptodiran turtles. This would explain both their very early stratigraphic occurrence in contrast to Kinosternoidae, Chelydroidea or Testudinoidea; and the results of molecular phylogenies (Tong et al. 2009 pp.168).

Based on a combination of paleontology and molecular phylogeny, Danilov & Parham, 2006 and 2008 propose a scenario in which Pleurodira, Trionychoidae, and non-trionychoidan cryptodires, the latter grouped together in the new clade Drurocryptodira (meaning hard shelled cryptodires, to distinguish them from the soft-shelled Trionychoidae), diverge during the middle to late Jurassic.

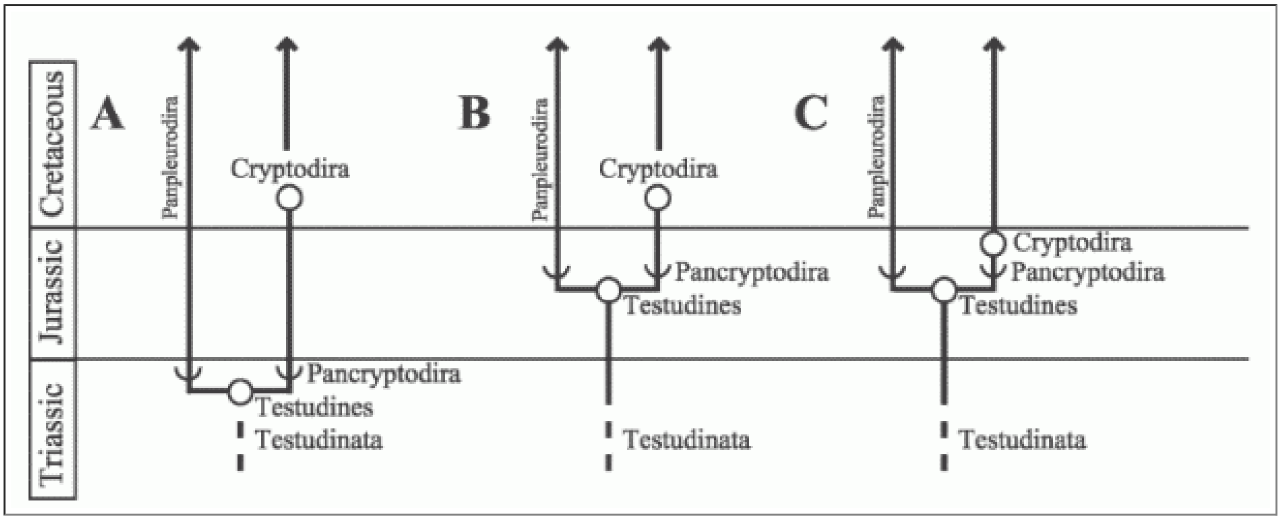


Diagram shopwing three hypotheses of testudine evolution and the origins of the stem group or Pancryptodira and the crown group (here Cryptodira) of Cryptodire turtles. **A**, Traditional hypothesis (e.g., Gaffney and Meylan, 1988; Shaffer et al., 1997) which posits a very early split between Pleurodires and Cryptodires, and then long stem lineages with both; **B**, Stastistical-Parsimony cladistic methodology (e.g. Joyce 2004, Joyce 2007,) which posts both a long stem testudine lineage and a long pancryptodire stem prior to diversgence opf crown groups; **C**, Molecular-Stratigraphic hypothesis which has a long stem-testudine lineage but a very early division of higher cryptodires (Trionychoidae + Durocryptrodira). as proposed by Danilov & Parham, 2006 and 2008. Taxa are stem based (open semi-circle) or node based (circle). Diagram from Danilov & Parham, 2006 p.578, fig 7

Both explanations cannot be correct. If hennigian morphological, statistical morphological, and developmental parsimony analyses are all to be preferred over stratigraphy and molecular evolution, Trionychoidae remarkably molecularly divergent from all other extant cryptodires of which *all* major groups must be represented by extended ghost lineages going deep into the Jurassic. That means that all other higher cryptrodire lineages unknown from fossils for about half their history, despite turtles otherwise having an excellent fossil record. This recalls the dilemma with *Archaeopteryx* and the dromaeosaurs. The late Jurassic *Archaeopteryx* is clearly more advanced than its early Cretaceous "ancestors". In this case late Jurassic ancestors like *Anchiornis* are known. Moreover, not only is the fossil record almost totally unreliable in recording the first appearance of even well-fossilised taxa, but molecular sequencing is also shown to have a very poor phylogentic signal, full of misleading artifacts such as basal Trionychoidae and Testudinoid Platysternids

But if molecular phylogeny is reliable, then so is stratigraphy, with the Pleurodires and the Trionychoidae well known from the late Jurassic, confirming their early branching in the molecular tree. Trionychans would be convergent with higher hard shelled turtles, especially the Kinosternoidea, the most extraordinary degree, much more so than protostegidae and dermochelyidae, since unlike protostegids, trionychoidans do not retain primitive features. This means that one after another unique adapation would have to occure independently in both lineages to arrive at morphologically convergent but phylogenetically distinct highly specialised forms; a bit like the humanoids of Star Trek, the vulcans, klingons, and so on who all independently evolved to almost identricxal human-like end forms (link). Morphologically this makes very little sense. It is one thing to imagine an ichthyosaur looking roughly like a dolphin, it is quite another for them to be so similar as to be included in the same superfamily, molecular phylogeny is full of convergences of this sort that don't make sense given the random nature of selection and evolution; another example are the Heliozoa (more). It also means that even molecular development follows molecular convergence, with very little useful phylogenetic signal. Similarily, molecular phylogeny recovers many morphological nonsensical clades, such as the Afrotheria, Cyclostomia, and archosaurian turtles

In the end we are left with two equally persuasive yet also equally inconclusive and problematic scenarios. Perhaps new fossil discoveries and new methodological insights can shed light on this enigma. There being no easy solution at present, we have included both phylogenies under each entry, MAK130126

The Sinemydid-Macrobaenid Grade

The Sinemydids and Macrobaenids are a paraphyletic assemblage of basal eucryptodiran turtles of a more advanced (derived to use the technical term) grade than the Xinjiangchelyids (themselves most likely also a paraphyletic grade). In cladistic analyses they are usually resolved as successive sister taxa of Polycryptodira (Gaffney) or Crown Cryptodira (Joyce etc) (Parham and Hutchison 2003, Gaffney et al. (2007), Joyce 2007, Rabi et al 2010), although some analyses seem to suggest grades or subgroups, although tree topologies differ according to whether one follows a Hennigian (e.g. Joyce) or a statistical (e.g. Joyce) cladistic methodology.

They include mostly terrapin-like semi-aquatic forms that first appeared during the Late Jurassic in China and are best known from the Cretaceous to Paleogene of Asia and North America. During the early Cretaceous, they seem to have outcompeted the similarily terrapin-like pleurodires (check ref, biogeography), who retreated to South America and Australasia. By the middle to late Cretaceous the Sinemydid-Macrobaenids had radiated into a number of distinct lineages; these became the Cenozoic testudine groups, the Chelonioidea, Kinosternoidea, Chelydridae, and Testudinoidea. Like the paracryptodira, the sinemydid-macrobaenids easily surived the K-T mass extinction, continuing to flourish in Paleogene Laurasian before giving way to more modern faunas. MAK130119

Descriptions

Centrocryptodira Gaffhey and Meylan, 1988: Crown Group Cryptodira and their fossil relatives

Range: Late Jurassic to Recent, Cosmopolitan

Phylogeny: Xinjiangchelyid - Crown Cryptodire clade **:** *Chengyuchelys* + Xinjiangchelyidae + *Larachelus* + * **:** Sinemydidae + Trionychoidea + Durocryptodira.

Range: Late Jurassic to Recent

Characters: Characteristics include formed (concave or convex) articulations (procoelous and opisthocoelous vertebrae) between succeeding cervical vertebrae. These well developed articulation surfaces constitute a more advanced condition then in more primitive Eucryptodires, and were made a defining feature of the Centrocryptodira. A thick floor of the canalis caroticus internus in the pterygoid is also a feature of this group. (Gaffney, 1975, Meylan 2001). This characteristic also developed independently in both the Pleurodira and Baenidae.

Comments: Gaffney co-workers' placement of the Meiolaniids is controversial, statistical-computational trees place them further towards the base of the testudine tree than other chelonians. For this reason, apart from the Gaffney school the term Centrocryptodire is no longer used. Although statistical morphological analyses support Sinemydidae as basal to extant cryptodires, molecular phylogeny instead favours a separate origin for the Trionycha, which would make the Centrocryptodira as originally defined polyphyletic MAK130119

With the increasing popularity of quantitaive methodologies and the replacement of morphology-based Hennigian cladistics and apomorphy-based clades with statistical-computational parsimony analysis and stem and crown based cladistic nomenclatural preference of restricting a familiar and morphologically well-defined taxon to the crown group only, apomorphic terms like Centrocryptodora and Polycryptodira have been rejected in favour of simply as "Cryptodira". The problem is that excessive reliance of crown clade terminology can lead to ambiguity. A well known example of this is the many definitions of Tetrapoda. In order to avoid confusion we have appended the phrase "crown group", to distinguish this taxon from the morphological (or apomorphic) Cryptodira. MAK130119

The Centrocryptodora or Crown Group Cryptodires represent a group of derived eucryptodires that are first known from the Late Jurassic of China. Of the two lineages, *Yehguia tatsuensis* and *Sinaspiderites wimani* are pantrionychids (or trionychoidea) known from Sichuan, whereas *Sinemys lens* is the earliest known Sinemydid , from Shandong (Rabi et al 2010 p.266). If at least some and perhaps all of the Sinemydids are durocryptodires it would solve the otherwise annoying problem of excessive ghost lineages even if it means a gread deal of convergent evolution. Chinese Jurassic eucrptodire diversity was extremely high; the different localities may imply different geographic and ecological regions.

Lourenço et al (2012), using molecular clocks calibrated with fossil taxa place the divergence between trionychoidans and non-trionychoidan cryptodires (in their paper, here Durocryptodira) at around 144.0 Mya, or in other words the Jurassic-Cretaceous boundary (Lourenço et al 2012 p.502). This would seem to be a little young as both the oldest Sinemydids and stem trionychans date to the late Jurassic. But the incongruence between the mammal fossil record and molecular clocks does not surport the premise of an invariant random mutation rate, and the same seems to be the case here.

Links: Taxon diversity

Durocryptodira: hard shelled cryptodires Danilov & Parham, 2006. Molecular, node-based definition: LCA of Testudo graeca Linnaeus, 1758, Kinosternon scorpioides (Linnaeus, 1766), Chelonia mydas (Linnaeus 1758), and Chelydra serpentina Linnaeus, 1758, but excluding Trionyx triunguis (Forskål, 1775) and Carettochelys insculpta Ramsay, 1887. From duro-, Latin for hard, and cryptodira- for cryptodires. Danilov & Parham, 2006p.577. If the molecular-phylogeny is incorrect then Durocryptodira becomes paraphyletic (or synonymous with crown group Cryptodira.

Range: fr the Early Cretaceous. Late Jurassic stem forms may have been present but had not yet evolved into extant lineages (Danilov & Parham, 2006, p.579)

Range: Fr the Late Cretaceous

Phylogeny: Centrocryptodira : Some Sinemydidae + Trionychoidea + * : Some Sinemydidae + (*Kirgizemys* + (Macrobaenidae + Testudinoidea + Chelonioidea-Chelydridae-Kinosternoidea clade)

Comments: Apart from Danilov and Parham, the use of the term Durocryptodira has not caught on. It is retained here only because there seems to be no other name for this molecular-sequenced clade. The absence of clear morphological traits among molecular taxa such as Durocryptodira is a well recognised feature in many higher mammalian clades derived from molecular sequencing. MAK130118

It is not unlikely that stem representatives lie among the Late Jurassic and Cretaceous Sinemydidae and Macrobaenidae, which help to fill the long stratigraphic gap betrween the early late Jurassic and the late Cretaceous. In this molecular-stratigraphic scenario, during the later middle to early late Jurassic, the testudines underwent a dramatic evolutionary radiation. Five long-lived clades emerged at this time, the Meioliinids or terrestrial horned tortoises, a primitive lineage first known from the Cretaceous, the Pleurodira or side-necked semi-aquatic forms, the Paracryptodira or unspecialised forms, the Cretaceous to Paleogene Sinemydidae-Macrobaenidae group that became the ancestors of either all extant cryptodires or of the extant hard-shelled types (Durocryptodira), and the Trionychia or advanced soft-shelled turtles, which are remarkably morphologically convergent with the durocryptodiran Kinosternoidea. Even so the position of the Trionychoidea in the phylogeny given here is extremely provisional, pending more analysis of and insights into Sinemydid and Macrobaenid phylogeny.

During the mid Cretaceous the durocryptodires seem to have undergone a sudden bursts of evolution. Lourenço et al 2012 using molecular dating, posits a rapid evolutionary radiation involving the origin of the extant Kinosternidae, Chelydridae, Chelonioidea and Testudinoidea at between 120 and 90 Mya (mid-Cretaceous), shown by the short internal branches between these clades in their phylogram. MAK130403

Hoyasemys

Horizon: Early Cretaceous of Spain

Phylogeny: Centrocryptodira : ((*Kirgizemys* + (Macrobaenidae + Chelonioidea-Chelydridae-Kinosternoidea Clade) + Testudinoidea)) + Trionychoidea + (Sinemydidae + *))

Comments: the western-most record of a Sinemydid-Macrobaenid grade chelonian.

Sinemydidae: *Dracochelys, Manchurochelys, Ordosinemys, Sinemys*

Range: Late Jurassic to Cretaceous of Asia

Phylogeny: Centrocryptodira : ((*Kirgizemys* + (Macrobaenidae + Chelonioidea-Chelydridae-Kinosternoidea Clade) + Testudinoidea

) + *Osteopygis* + Trionychoidea + (*Hoyasemys* + *

Characters: completely formed central articulation on the cervical vertebrae.

Comments: cervical vertebrae represent a more advanced condition than *Xinjiangchelys* (Hirayama et al 2000 p.189). Paraphyletic as normally defined. However a smaller grouping, including *Dracochelys, Manchurochelys, Ordosinemys*, and *Sinemys*, would seem to be monophyletic, according to some statistical analyses.

In contrast to the "true" Macrobaednids, *Annemys* spp., *Ordosemys* spp., *Dracochelys bicuspis*, *Hangaiemys hoburensis* and *Sinemys* spp. still retain an open carotid fenestra and reduced basipterygoid process of the basisphenoid, a primitive feature homologous with that of basal turtles using topology and intermediates. (Rabi & Joyce 2012)

Graphic: *Manchurochelys liaoxiensis*, via Wikipedia

Osteopygis

Range: Late Cretaceous to Early Paleocene of North America (New Jersey)

Phylogeny: Centrocryptodira : (*Hoyasemys* + Sinemydidae) + Trionychoidea + (Testudinoidea + (*Kirgizemys* + (Macrobaenidae + Chelonioidea-Chelydridae-Kinosternoidea Clade))) + *

Comments: According to Parham 2005, specimens referred to *Osteopygis* from Late Cretaceous to Early Paleocene marine sediments of the USA represent a chimera (parts of two species confused as the same animal), combining the head of the marine turtle *Euclastes* with the shell and post-crania of macrobaenids. *Osteopygis emarginatus* can be distinguished from *Judithemys* and most Asian "macrobaenids" by its larger size (shell lengths of upto 70cm), thicker shell, and the presence of plastral fontanelles. (Parham 2005 p.76). This species represents the eastern-most extent of the "macrobaenids".

Kirgizemys

Synonym: *Hangaiemys* (see note)

Range: Early Cretaceous of Asia

Phylogeny: Centrocryptodira : Sinemydidae + *Osteopygis* + Trionychoidea + (Testudinoidea + ((Macrobaenidae + Chelonioidea-Chelydridae-Kinosternoidea Clade) + *)

Comments: Basal centrocryptodiran/durocryptodiran, possibly related to panchelonoidea (Danilov & Parham, 2008), although the open open carotid fenestra (assuming synonymy of *Hangaiemys* and *Kirgizemys*) makes this a more primitive form.

[1] "I. G. Danilov, A. O. Averianov, P. P. Skutschas, A. S. Rezvyi (St. Petersburg) reported new data on the morphology of the 'macrobaenid' genus *Kirgizemys* known from the Early Cretaceous of

Kirghizia, Buryatiya (Russia) and China. New material from the Early Cretaceous of Buryatia allowed study of the previously unknown skull of *Kirgizemys*. In skull and shell morphology, Kirgizemys is indistinguishable from Hangaiemys from the Early Cretaceous of Mongolia. The authors consider *Hangaiemys* as a junior subjective synonym of *Kirgizemys*." Fossil Turtle Newsletter Jan 2004

Macrobaenidae

Horizon: Late Cretaceous to early Tertiary of Asia and North America

Phylogeny: Centrocryptodira : Sinemydidae + Trionychoidea + (Testudinoidea + (*Kirgizemys* + (Chelonioidea-Chelydridae-Kinosternoidea Clade + * : *Judithemys* + *Macrobaena*)))

Comments: As conventionally defined, the Macrobaenids are a grade of freshwater and estuarine stem cryptodires that originated in the Early Cretaceous and dies out in the late Paleocene. They consist of a range of forms more advanced than basal forms like the Baenidae and Xinjiangchelyidae, but not yet at the morphological stage of modern cryptodires, an assemblage, a grade rather than a clade, of mostly Asian, Cretaceous to early Cenozoic, taxa that would seem to be clearly related to each other, as well as to crown group cryptodira. The Macrobaenidae especially seem to be an artificial grouping of morphologically and ecologically similar types (Parham (2005)). Some recent cladistic analysis shows that the ancestors of marine turtles may be found among terrestrial forms like Sinemydids and Macrobaenids (Sterli 2008 and 2010, Pérez-García (2012)). In another tree the Sinemydids are even crownward of the chelonioidea (Slater et al (2011), p.1407). What seems to be clear is that they represent an ancestral lineage from which modern cryptrodires evolved. If the trionychoidans branched from the cryptodire stem before most other centrocryptodires, as molecular phylogeny and stratigraphy both imply, then the sinemydids and macrobaenids are included in the cryptodire crown group. And even in morphology-only analysis, some or all Sinemydids at least still seem to be crown group cryptrodira.

A narrower definition can be supposed for a smaller group such as *Macrobaena* and *Judithemys* which can be tentatively interpretred as stem chelonioid/kinosternoids and which feature a reduced carotid fenestra. This is in contrast to other Sinemydid-Macrobaenid cryptrodires which retain the more primitive or basal condition (Rabi & Joyce 2012). The closure of the carotid fenestra occurred at least three times in crown Cryptodira (the other two being trionychoids and testudinoids), although a reduced carotid fenestra is also present is primitive eucryptodires (plesiochelyids, eurysternids, and protostegids) (*ibid*) showing additional instances of homoplasy and phyloparallelism.

Judithemys sukhanovi

Horizon: Late Cretaceous (Campanian) Dinosaur Park Formation of Alberta, Canada

Phylogeny: Macrobaenidae : *Macrobaena* + *

Comments: "The morphology of *Judithemys* reiterates a suite of characters (large size, well-differentiated neurals reduced to eight, and greater overlap of the twelfth marginal scales onto the second suprapygal) common to Late Cretaceous-Paleocene ''macrobaenids'' and distinct from Early Cretaceous members" (Parham, J.F. & Hutchison, J.H. 2003), although its exact phylogenetic position, as for that matter that of other Asian Cretaceous-Paleogene turtles of Sinemydid/Macrobaenid grade is uncertain. It seems to be closely related to, but more advanced than, *Kirgizemys*

Macrobaena

Horizon:

Phylogeny: Macrobaenidae : *Judithemys* + *

Comments:

Chelonioidea-Chelydridae-Kinosternoidea clade

Range: Fr the Late Cretaceous

Phylogeny: Centrocryptodira : Sinemydidae + Trionychoidea + (Testudinoidea + (*Kirgizemys* + (Macrobaenidae + * : Panchelonioidea + (Chelydroidea + *Emarginachelys* + Kinosternoidea)))

Comments: Revealed through molecular phylogeny only. Descended from ancestral Durocryptodira. Molecular phylogeny reveals a very early branching for the Trionychoidea, in which case some Sinemydids and Macrobaenids were stem durocrptodires MAK130403

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Chelonii: Trionychoidea (= Trionychoidae)

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Pleurodira
         |--Paracryptodira
         `--+--Protostegidae
            `--+==Xinjiangchelyidae
               `--o Centrocryptodira
                  |==Sinemydidae
                  |--+--o Trionychoidea
                  |  |--Basilochelys
                  |  `--+--o Adocusia
                  |     |  |--Yehguia
                  |     |  `--+--o Adocidae
                  |     |     |   |-- Adocus
                  |     |     |   `--
Shachemydinae
                  |     |     `--o
Nanhsiungchelyidae
                  |     |         |-
-Kharakhutulia
                  |     |         `--+-
-Hanbogdemys
                  |     |            |--o
"Nanhsiungchelyinae"
                  |     |            |  |-
-Anomalochelys
                  |     |            |  `-
-Nanhsiungchelys
                  |     |            |-
-Zangerlia
                  |     |            `-
-Basilemys
                  |     `--+--Peltochelys
                  |        `--o Trionychia
                  |           |-
-Carettochelyidae
                  |           `--o Trionychidae
                  |              |--+-
-Plastomeninae
                  |              |  `-
-Cyclanorbinae
                  |              `-
-Trionychinae
                  `--o Durocryptodira
                     |--+--Chelonioidea
                     |  `--+--Chelydridae
                     |     `--Kinosternoidea
                     `--Testudinoidea
```

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9. *Hanbogdemys* X
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11. *Kizylkumemys* X
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The African or Nile softshell turtle, *Trionyx triunguis* (Forskål, 1775), a modern representative of this most ancient of cryptodiran lineages. Photo by Dan Schwartz, Creative Commons Attribution license, via Wikipedia

The Trionychoidea are phylogenetically the most controversial turtle taxon, since molecular phylogeny has them diverging very early from the rest of the cryptrodires, whereas some morphological analyses place them next to the Kinosternoidea.

Stratigraphically, they are oldest extant cryptodire clade. An extensive Mesozoic record includes the Cretaceous genera *Adocus*, *Basilemys*, *Nanhsiungchelys*, and *Peltochelys*, (Joyce et al 2004, p.1002), and *Yehguia tatsuensis*, late Jurassic (Oxfordian) of China (Danilov & Parham, 2006). The early Cretaceous *Sandownia harrisi* is sometimes included here (Meylan et al 2000), although it could equally belong to a distinct and more primitive eucryptodire lineage, the Angolachelonia (Mateus et al 2009)

Molecular evidence also supports the very early appearance of Trionychia (Shaffer, 2009), which either branched off very early from the rest of the Cryptodira, or are a paraphyletic group from which other extant cryptodires developed (Krenz et al 2005). In any case it seems that pleurodires, trionychoids, and non-trionychid cryptodires (Durocryptodira Danilov & Parham, 2006) represent a trichotomy that emerged during the mid Jurassic (Krenz et al 2005 p.189). Yet if the Trionychoidea and Kinosternoidea are distinct taxa that deverged early in eucryptodire history, the number of morphological convergences required that would consistently place them together in any cladistic parsimony analysis is simply incredible (although no worse than other moleciular phylogenies when considered morphologically, e.g. Squamata, Artiodactyls, etc). Also remarkable would be the absense of primitive characteristics in extant forms (in contrast to the Protostegidae which while converging on Chelionoidea also have a number of primitive features). On the other hand, the absense of any non-trionychoidan crown cryptodire clades prior to the Latest Cretaceouys is also remarkable. If this morphological interpretation is correct than the cryptodires have so many Jurassic-to-Mid Cretaceous ghost lineages that they seem as Cretaceous whales or rodents. Another alternative, which no-one has apparently suggested, is that the diverse and abundant Mesozoic clade Adocusia are not stem-Trionychia at all, but convergent due to similar lifestyle, in the manner of protostegids and dermocheylids. For now we have gone with the molecular and stratigraphic hypothesis over the morphology-only one. MAK130302

Descriptions

Trionychoidea Gray, 1825 sensu Mlynarski, 1976

Synonyms: Trionychidea Bell, 1828, Trionychida Gray, 1870, Trionychoidae Meylan & Gaffney 1989, Pantrionychia Joyce et al 2004

Range: late Jurassic (Oxfordian) to Recent

Phylogeny: Centrocryptodira **:** Durocryptodira + * **:** *Basilochelys* + (Adocusia + (*Peltochelys* + Trionychia))


Chinese softshell turtle *Pelodiscus sinensis*. Photo from here, via CKT.

Comments: "Trionychoidea" is used here instead of "Trionychia" because it includes extinct as well as crown taxa, and instead of "Trionychoidae" to conform to the standard Linnaean suffix for superfamily. The Trionychoidea are a well defined and specialised assemblage of cryptodire turtles that first appear in the fossil record in the late Jurassic, they are by many tens of millions of years the oldest lineage of extant cryptodires, by the late Cretaceous they were a ubiquitious element in Laurasian freshwater faunas. Among the many lineages from this time are the Nanhsiungchelyidae, Adocidae, Carettochelyidae, and Trionychidae, along with a number of monogeneric groups. The Nanhsiungchelyids are particularily intersting as they independently evolved as large terrestrial forms, equivalent to Cenozoic testudinids.

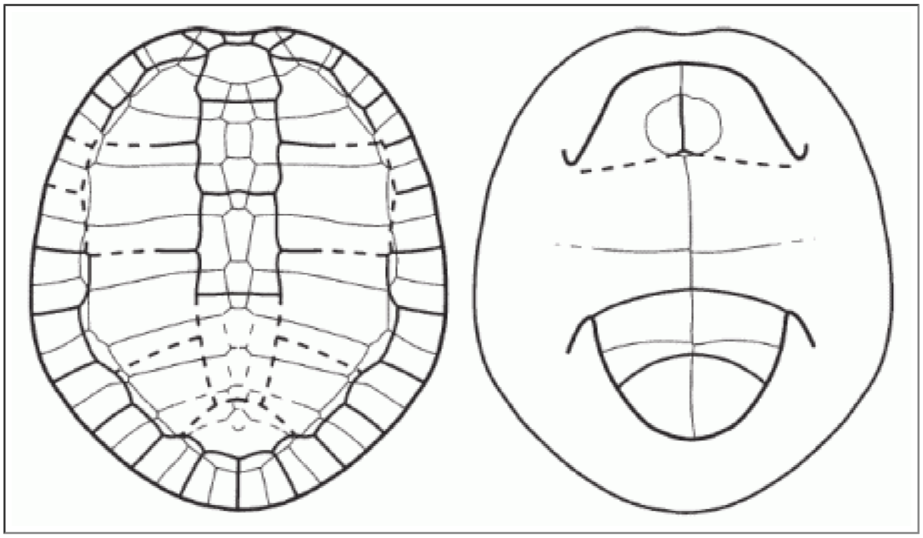
Hennigian morphological analysis places them as a specialised clade, e.g. Gaffney, 1975, Meylan 2001, Gaffney & Meylan 1988, Meylan and Gaffney (1989), and Meylan 2001, on the basis of the following characters: Small stapedial artery, with large palatine artery and canalis caroticus lateralis; significant contribution of palatine to side-wall of braincase; tenth body vertebra free from costals; thelial process present; maxillary 'tooth' present; caudifibularis muscle present (Gaffney & Meylan 1988 via CKT110603). Gaffney and Meylan propose the phylogeny Centrocryptodira **:** +

* : Kinosternoidea + Trionychoidae. More recent computational-statistical phylogenetic found much less morphological support for this clade; according to Joyce 2007 p.69, the clade Trionychoidea is only weakly supported in this analysis by a single character, listed above, the contribution of the palatine to the lateral brain case wall. He found the additional characters to be either problematic or the result of homoplasy. Molecular phylogeny goes further and has unanimously fails to support its monophyly. Beginning in the late 1990s, molecular sequencing (Shaffer et al. (1997), Cervelli et al. 2003; Fujita et al, 2004, Krenz et al 2005, Parham et al. 2006) found the Dermatemydidae and Kinosternidae to be unrelated to the Trionychidae and Carettochelyidae, and reject the monophyletic Trionychoidea sensu Gaffney and Meylan (1988), which becomes a diphyletic taxon in which the Trionychoidea and Kinosternoidea as only very distantly related. A smaller group, Trionychia or Pantrionychia is instead used for the extant Trionychidae and Carettochelyidae and the related fossil forms (the pan- prefix being added by Joyce et al (2004) to include the stem group), these are considered totally unrelated to all other recent Cryptodira (Böhme, 2005, p.410) for which Danilov & Parham, 2006 coined the clade Durocryptodira. Most of these analyses place the Trionychia as the basalmost clade within the cryptodires (Shaffer, 2009). As regards the pattern of chelonian cranial arterial circulation, the Trionychoidea and Kinosternoidea differ from the more widespread Testudinoid condition. This supports a monophyletic Trionychia/Trionychoidae, whereas the more inclusive Trionychoidea taxon sensu Gaffney and Meylan is not supported (Jamniczky & Russell, 2007). In the present work we've followed the molecular phylogenetic position, as this is supported by stratigraphic priority of Trionychoidea, which appear in the fossil record some fifty to a hundred million years before any non-trionychoidan crown cryptodires MAK130302

Basilochelys macrobios

Horizon: latest Jurassic-earliest Cretaceous Phu Kradung Formation of NE Thailand

Phylogeny: Trionychidae : (Trionychinae + (Cyclanorbinae + Plastomeninae)) + *



Reconstruction of the shell of the basal trionychoidan *Basilochelys macrobios* from the Latest Jurassic or Earliest Cretaceous of Thailand. Length 90 cm. From Tong et al. 2009 p.162

Comments: This large cryptodire (shell length upto 90cm) known from skull, shell and other postcranial elements, would seem to be the most basal member of the Trionychoidea, with a combination of primitive eucryptodire and derived characters. It constitutes a transitional form with many features shared with both Xinjiangchelyidae, Adocidae and Nanhsiungchelyidae. The amphicoelous cervical vertebrae are like those of *Xinjiangchelys* and *Thalassemys*, although it differs from the xinjiangchelyids and plesiochelyids by a derived character (posterior portion of the canalis caroticus internus is covered by bone), a Centrocryptodiran synapomorphy. There are also several characters shared with Early Cretaceous Sinemydidae and Macrobaenidae, such as *Ordosemys*. Several features of the shell are shared with Trionychoidea and Testudinoidea, and the first thoracic vertebra has an anteroventrally facing anterior central articulation, which is a feature of the neck retraction mechanism characteristic of advanced cryptodires. This implies these large turtles were probably capable of retracting the head inside the shell, an advanced feature in cryptrodire evolution (Tong et al. 2009 pp.164-5) Tong et al. 's cladistic analysis resulted in a single tree of 177 steps with a consistency index of 0.47 and retention index of 0.74, suggesting rampant homoplasy in the dataset. The combination of primitive and derived characters in *Basilochelys* suggests that the Trionychoids may have originated from xinjiangchelyids and their close relatives (Tong et al. 2009 p.168), which supports the molecular and stratigraphic evidence of an early divergence for this group. Cladistic analysis by Syromyatnikova 2012 interprets as a basal Adocusia rather than stem Trionychoidea. In any case, given the ambiguity and homoplasy of the material, any interpretation either way must only tentative. For now we have followed Tong et al. in placing Basilochelys as a stem trionychoidan (Trionychoidea in their paper). MAK130211

Adocusia: the most inclusive clade including *Adocus beatus* (Leidy, 1865) and *Nanhsiungchelys wuchingensis* Yeh, 1966

Range: Late Jurassic to Oligocene of Asia, Late Cretaceous to Paleocene of North America.

Phylogeny: Trionychoidea : *Basilochelys* + ((*Peltochelys* + Trionychia) + * : Adocidae + Nanhsiungchelyidae + *Yehguia*)

Characters: Sinuous midline plastral sulcus; Osseous connection between the plastron and carapace (evolved independently within Adocusia, Pankinosternoidea, and Pantestudinoidea, the primitive condition for Cryptodira is ligamentous); sculptured shell.

Comment: stratigraphically by far the oldest trionychoidan group. The phylogeny is still disputed. Hennigian cladistic study (Gaffney & Meylan, 1988; Meylan & Gaffney, 1989)) show the Adocidae as the sister group to the clade (Nanhsiungchelys + (Trionychidae + Carettochelyidae)). Statistical-computational analysis instead reveals a monophyletic clade Adocusia (Adocidae + Nanhsiungchelyidae + Yehguia) as sister group to Crown Trionychoidea (Danilov & Parham, 2006, 2008; Joyce 2007; Sterli, 2010), although not all agree on the monophyly of the Adocusia (Tong et al., 2009). Primitive features of morphology are characteristic of basal level eucryptodires such as the Xinjiangchelyidae (Syromyatnikova 2012) It may be that this is a paraphyletic assemblage of stem forms rather than a true clade (by analogy with Ceratosauria within theropoda; previously considered to be sister taxon to the Tetanura it is now recognised to be a grade of early theropods), in which case, phylogenetically speaking, Adocusia would equal Trionychoidea, and adocusian synapomorphies are actually shared primitive features modified or lost in more advanced trionychoidans. Alternatively, in contradiction to all current parsimony-blased cladograms, if the Adocusia are not trionychoidans but evolved by convergence, this would explain both why the most morphologically primitive Trionychoidea like *Kizylkumemys* and perhaps *Sandownia*, are found in the crown group, as well as tidying up the ridiculous number of ghost lineages. MAK130128

Yehguia tatsuensis

Range: late Jurassic (Oxfordian) of China

Phylogeny: Adocusia : Adocidae + Nanhsiungchelyidae + *

Comments: Previously included under *Plesiochelys*, closer analysis revealed this archaic turtle to be the earliest known trionychoidan by Danilov & Parham, 2006. However Lourenço et al 2012 using molecular dating place the divergence between trionychoidans and non-trionychoidan cryptodires at around 144.0 Mya, or in other words the Jurassic-Cretaceous boundary (Lourenço et al 2012 p.502) . They therefore interpret late Jurassic forms like *Yehguia* as early crown Cryptodira rather than a trionycha

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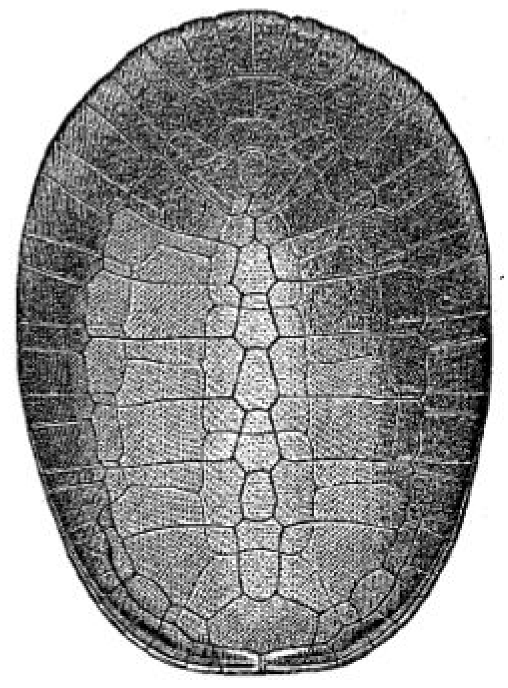
Adocidae Cope, 1870

Range: Late Cretaceous to Paleocene (Cenomonian to Danian) of NAm & Asia

Phylogeny: Adocusia : Nanhsiungchelyidae + *Yehguia* + * : *Adocus* + Shachemydinae

Characters: Weakened costal ribheads (Danilov & Parham, 2006)

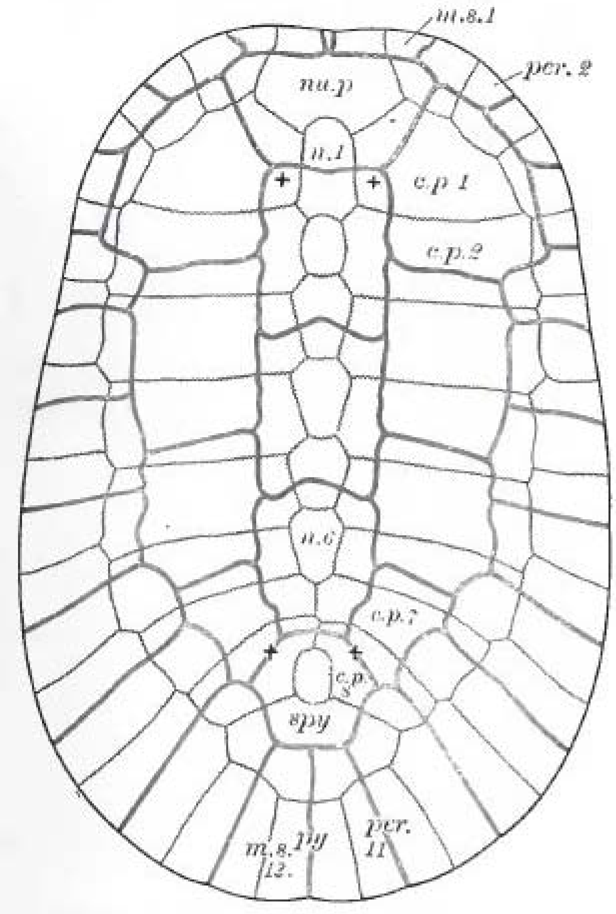
Comments: A group of large fresh-water aquatic turtles from the Late Cretaceous of Asia and North America. In Asia the Adocidae were more numerous than Nanhsiungchelyidae and often dominated Late Cretaceous complexes turtles. They were mainly confined to the humid subtropical climate



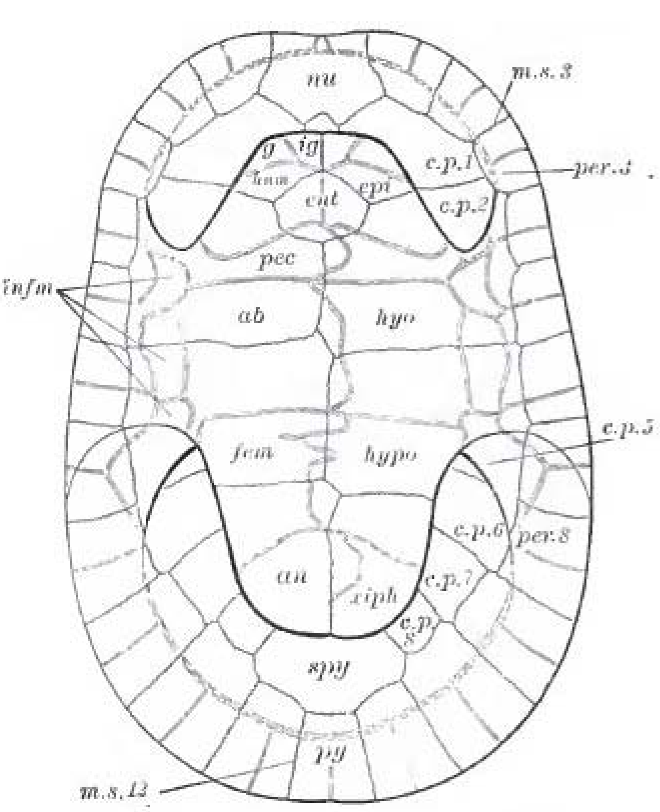
Shell of *Adocus punctatus*, image by Othniel C. Marsh, 1890, public domain. Via Wikipedia

conditions on the outskirts of Asia with extensive coastal lowlands (Syromyatnikova 2012). The entire surface of the carapace is finely sculptured with a very regular arrangement of minute tubercles. (Scheyer 2007, p.104)

Originally, through the influential classifications of Lydekker (1889) and Zittel (1889), adocids were placed in the family Dermatemydidae with the extant turtle *Dermatemys mawii*, based on the absence of mesoplastra, the presence of a complete row of inframarginals, and a well-ossified plastron. However, Meylan and Gaffney (1989) argued on cladistic grounds that these are paraphyletic (shared primitive) features among cryptodires, and that most similarities between adocids and Dermatemys mawii should be interpreted as plesiomorphies or homoplasies. They transferred the adocids to the Trionychoidea, a morphology-only clade that is not supported on molecular grounds. As the phylogenetic relationships of adocids can only be determined using fossil skeletal morphology, Danilov & Parham 2008 reanalysed the morphological dataset of Joyce (2007), using a topological constraint that forced the current molecular consensus and the nonmonophyly of Trionychoidea. Their resulting cladograms placed adocids as the sister group to Trionychia, as basal cryptodirans. (Zelenitsky et al)



Adocus punctatus, carapace of type. Length 53 cm, width 39 cm. c.p.1, c.p.2, c.p.8, costal plates; m.s.1, m.s.12, marginal scutes; nu.p, nuchal plate; per 2, per 11, peripheral bones; py, pygal; spy, suprapygal ; n.1, n.6, neural bones.



Adocus punctatus, plastron. ab, abdominal scute ; an, anal scute ; c.p.1, c.p.2, etc., costal plates; ent, entoplastron ; epi, epiplastron ; fem, femoral scute; g, gular scute; hum, humeral scute ; hyo, hyoplastron; hypo, hypoplastron; ig, intergular scute; infm inframarginal scutes ; nu, nuchal bone; pec, pectoral scute; per.3, per.8, peripheral bones; py, pygal; spy, suprapygal; xiph, xiphiplastron. From Hay (1908) p.237-8, figs 296-7; public domain (copyright expired).

Adocus Cope, 1868 ((monotypal Subfamily Adocinae Cope, 1870)

Range: Late Cretaceous of Kazakhstan, Central Asia, Late Cretaceous to the Late Paleocene in North America North America, upto Eocene of Asia

Phylogeny: Adocidae : Shachemydinae + *

Description: - Hay (1908) p.237-8,

Comments: Medium to large omnivorous-herbivorous freshwater turtles, in large animals the shell could reach up to 80cm. Aquatic and probably a good swimmer, shell delicately sculptured, flat and long, smoothly contoured, the plastron has large openings to allow free motion of the limbs. May have resembled, but not related to, the Mesoamerican river turtle *Dermatemys*. Jehle, 2006, with which they were for a long time grouped (e.g. Zittel, Eastman, Woodward, et al(1932), Mlynarski 1976). Known from the Late Cretaceous (Coniacian to Maastrichtian) of North America, extending to the Early Palaeocene (Puercan) (Hell Creek Formation and overlying Tullock Formation) of Montana (Scheyer 2007, p.105) continuing to the Late Paleocene . A number of species are known from the Late Cretaceous (early Cenomanian to early Campanian) of central Asia and Kazakhstan. (Syromyatnikova & Danilov, 2009)

Shachemydinae: Khosatzky, 1977,: *Ferganemys*, *Shachemys*

Range: Late Cretaceous of Asia

Phylogeny: Adocidae * : *Adocus* + *

Characters:. entoplastron is shortened and truncated anteriorly. (Danilov & Parham, 2006), some plastral kinesis

Comments: Shachemys and Ferganemys are both characterized by a short, relatively elongated and streamlined skull, while Adocus it is higher and shorter. The orbits are shifted upward, while for Adocus located on the sides of skull. These differences are likely to be dietary: the presence of relatively high skull suggests greater bite force and power over moving objects for Adocus. In *Shachemys skharakternoy* a reduction or disappearance of neural plates, also found in some Chelidae (Chelodina and Emydura) is associated with a reduction of the space for the passage of the longissimus dorsi muscle (*m. longissimus dorsi*). This means these animals were less able to lunge with the neck, and, thus, does not allow to make sharp and fast attacks its prey.Feeding more likely involved relatively passive capture and swallowing of prey. Underdeveloped neck muscles are also associated with the presence of the hinge at the front of plastron, providing additional protection for the head with weakly mobile neck. Shachemys is only known from coastal areas (Syromyatnikova 2012)

Nanhsiungchelyidae Yeh, 1966

Basilemys sp., photo © Royal Tyrrell Museum

Range: Cenomanian to Maastrichtian of Asia (Mongolia, China, and Japan) and Campanian to Maastrichtian of N Am

Phylogeny: Adocusia : Adocidae + *Yehguia* + * : *Kharakhutulia* + (*Basilemys* + *Nanhsiungchelys* + *Zangerlia*)

Characters: reduced number of phalanges; thelial process absent (Meylan & Gaffney, 1989)

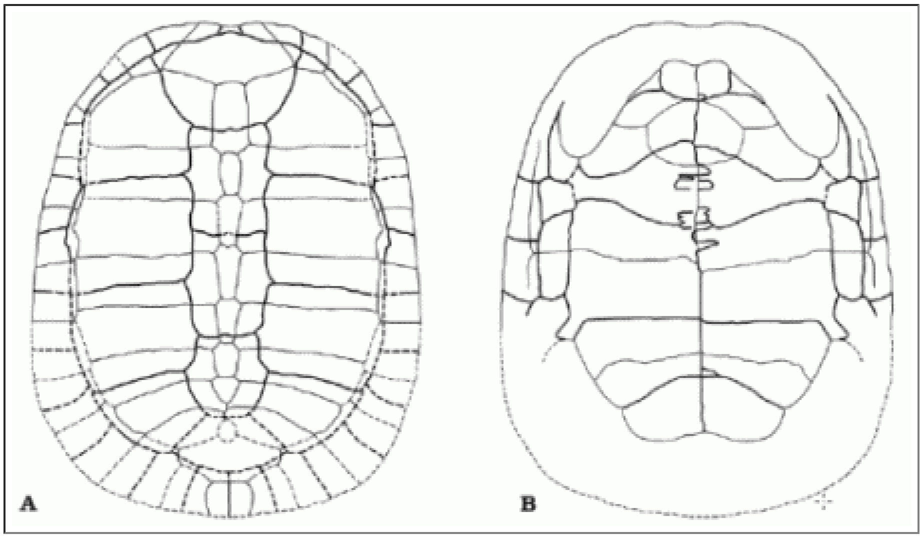
Comments: A uniquely East Asian - North American Cretaceous group of large testudines (with shells generally around 50 to 90 cm in length (Hirayama et al. 2001) characterised by a combination of aquatic and terrestrial features, although a terrestrial lifestyle seems more likely, making them testudinid precursors (Syromyatnikova 2012). They include the genera *Zangerlia, Hanbogdemys, Anomalochelys, Nanhsiungchelys* and *Basilemys*. In contrast to the Adocidae, the Nanhsiungchelyidae preferred inland arid climates, most remains being found in eolian deposits, suggesting they live in hot and dry desert landscapes (Syromyatnikova 2012). The morphology is still poorly known, and the systematic position of a number of forms unclear. This is especially true of Asian species, which are described mainly on the basis of a few fragmented materials (Syromyatnikova 2012) As with the Adocids they were originally included under the Dermatemydidae. (Mlynarski 1976) The external surfaces of the shell bones of *Basilemys, Zangerlia* and *Nanhsiungchelys* share a regular pock-marked sculpture (Scheyer 2007, p.105), although sculpturing can be distinguished from those of the Adocidae by the relatively bigger and more irregular pits and grooves (Sukhanov et al 2008 p.602). Cladistic analysis shows the Nanhsiungchelyids to be close to the Adocidae. Some cladograms show an early split between the Asian forms like *Nanhsiungchelys* and the American *Basilemys* (Gaffney & Meylan, 1988, Joyce & Norell, 2005); others have a number of lineages, with *Kharakhutulia* as the most basal, , implying that the North American *Basilemys* is derived from Asian ancestors, although it is not clear which lineage *Basilemys* is closest to (Sukhanov et al 2008, Syromyatnikova 2012). MAK130222

Kharakhutulia kalandadzei Sukhanov et al 2008

Horizon: Lower part of the Bainshire Formation, Cenomanian or lower Turonian of Khara Khutul, Mongolia

Phylogeny: Nanhsiungchelyidae : (*Basilemys* + *Nanhsiungchelys* + *Zangerlia*) + *

Comments: The most basal Nanhsiungchelyid, smaller than most other members of the family (shell only 23 to 25 cm long), in overall morphology transitional between Adocidae and more advanced members of the Nanhsiungchelyidae (Sukhanov et al 2008 p.610) MAK130205



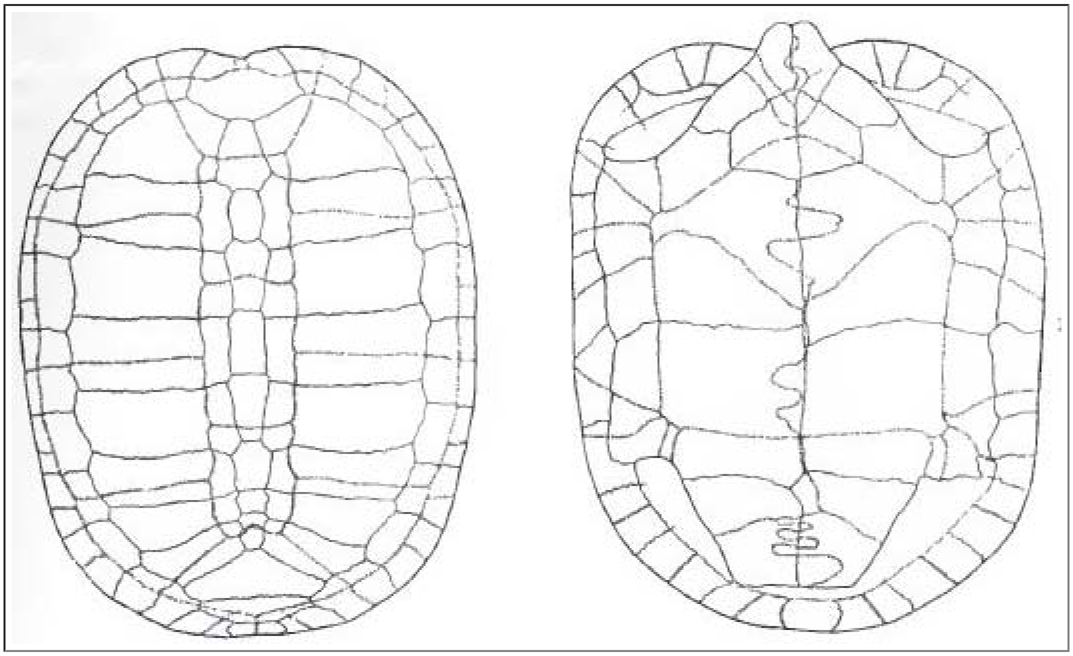
Reconstruction of the shell of the basal Nanhsiungchelyid, *Kharakhutulia kalandadzei*, in dorsal (**A**) and ventral (**B**) views. Length about 25 cm. From Sukhanov et al 2008 p.610

Basilemys Hay, 1902

Range: Late Cretaceous (Campanian to Maastrichtian) of North America

Phylogeny: Nanhsiungchelyidae : *Kharakhutulia* + (*Nanhsiungchelys* + *Zangerlia* + *)

Description: Shell highly sculptured. Epiplastra much thickened. Bridge wide. Intergular scutes present. Pectorals greatly expanded at the midline, narrowed laterally. An axillary and an inguinal scute but no other inframarginals - Hay (1908) p.226



Basilemys sinuosa. Carapace and plastron, length 71.5 cm, breadth 58.5 cm. From Hay (1908) p.229, figs 288 and 289; public domain (copyright expired).

Comments: A specialised Laurentian lineage of Nanhsiungchelyids, evolving in isolation from the various Asian forms. The pock-marked sculpturing extends into the interior of the shell openings, with the internal surfaces of bones adjacent to these openings also heavily sculptured. Several morphological features, such as robust elephantine limbs and stubby feet, ossified limb armour, strong epiplastral projections, and triturating surfaces of maxilla, show that Basilemys were the ecological equivalent of terrestrial and herbivorous tortoises (Scheyer 2007, p.105). This distinguishes it from the predominantly freshwater semi-aquatic turtles of the time. However the shell was low and sleek rather than domed as with the testudinidae (Acorn 2007, p.14). Several species are known; *Basilemys variolosa* is from the Campanian and *B. imbricaria, B. nobilis*, and *B. sinuosa* from the Maastrichtian. The latter is known from a nearly complete carapace and plastron holotype from the Maastrichtian of Montana. and also

known from North and South Dakota, and Wyoming, had an average carapace of 70 by 56.5 cm, giving an estimated body mass of 38.5 kg Paleobase. The largest specimens of this genus have shells exceeding 1 meter in length. Their large size and terrestrial habitat meant that these was among the few testudine groups that succumbed to the K/T mass extinction (Jehle, 2006).

A purported Asian species, *B. orientalis* Sukhanov and Narmandakh, 1975, from the Bainshire Formation [upper Turonian or Santonian] of Baishin Tsav, Mongolia (Sukhanov et al 2008), turned out to be unrelated and has been given its own genus, becoming *Hanbogdemys orientalis*. *Hanbogdemys* is common in Asia in the range of Cenomanian - Campanian (Syromyatnikova 2012). A single nuchal from Khara Khutul (Cenomanian or lower Turonian) may belong to a distinct but related species (Sukhanov et al 2008 p.612), perhaps an ancestral form. MAK130205

Nanhsiungchelys

Range: *Nanhsiungchelys wuchingensis* from the Maastrichtian of China. Related form (*Anomalochelys angulata*) from Cenomanian of Japan

Phylogeny: Nanhsiungchelyidae : *Kharakhutulia* + (*Basilemys* + *Zangerlia* + *)

Comments: A distinctly Asian lineage with a relatively large skull and long tubular snout, Lucas, 2001, pp.182-3 suggests this was likely for rooting out food like the extant tropical Australasian pig-nosed turtle *Carettochelys*. A more likely explanation is an adaptation to arid climate from the Asian end-Cretaceous. A similar structure is known for the Aldabra giant tortoise *Aldabrachelys* from the Seychelles. Large nasal cavities which are adapted to the absorption of water through the nostrils which was adapted to living in arid conditions. Syromyatnikova 2012). *Anomalochelys angulata* Hirayama et al. 2001 from the Cenomanian of Japan (Hirayama et al. 2001) seems to be a closely related form (Sukhanov et al 2008 p.602), indicating that this was a long lived lineage throughout East Asia. MAK130222

Zangerlia

Range: Campanian of Mongolia

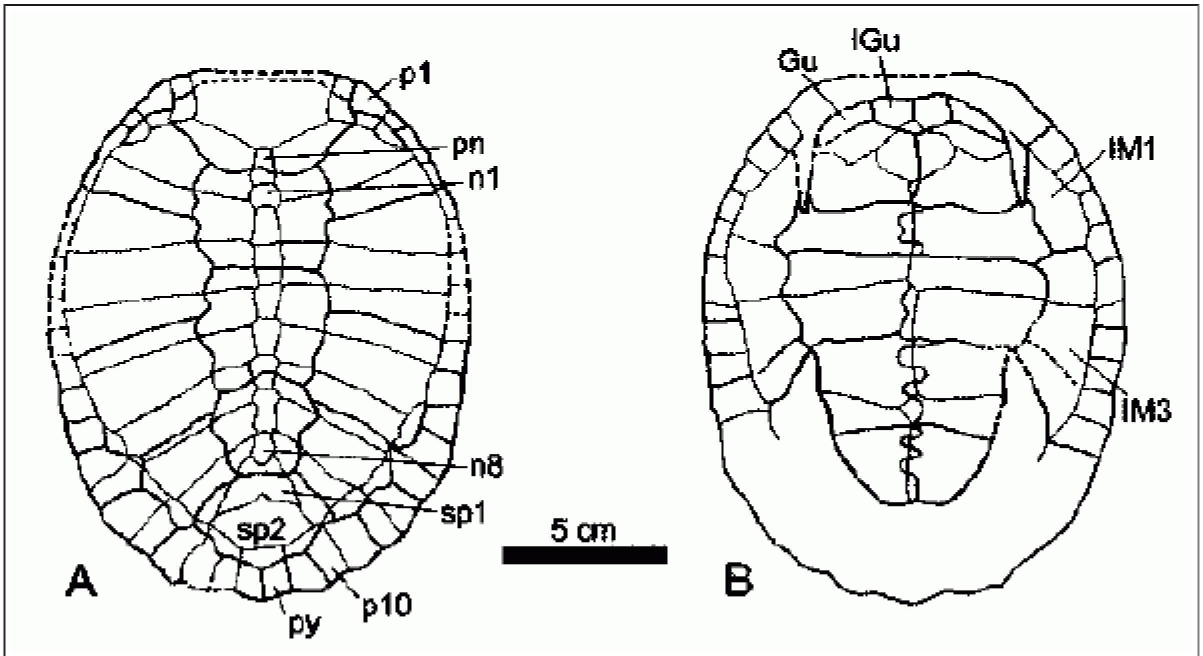
Phylogeny: Nanhsiungchelyidae : *Kharakhutulia* + (*Basilemys* + *Nanhsiungchelys* + *)

Comments: A primitively or secondarily small genus known from several species (Sukhanov et al 2008). *Zangerlia* may have fiolled the same ecological role as small testudinids. A number of species are placed here, although this may be a paraphyletic or polyphyletic taxon. MAK130301

Fossil of *Zangerlia neimongoliensis*, at the *Musee d'Histoire Naturelle*, Brussels. Photo by Ghedoghedo Creative Commons Attribution, Wikipedia

Peltochelys duchastelli **Dollo, 1884**

Range: Wealden (Barremian/Aptian) of Belgium



Peltochelys duchastelli, Early Cretaceous of Beligium. Shell in Dorsal (left) and Ventral (right) view. Drawing from Böhme, 2005, p.413.

Phylogeny: Trionychoidea : *Basilochelys* + (Adocusia + (Trionychia + *))

Comments: A basal trionychoidan, and the oldest representative of the Trionychoidea outside Asia. The clade Trionychia + *Peltochelys* is supported by a reduction of the number of peripherals to 10 pairs (Anquetin, 2009 p.204). It shows that this clade had diverged from Adocusian trionychoidans by or around the Barremian age

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Trionychia

Florida Soft-shell Turtle, *Apalone ferox*, as seen in Everglades National Park, Homestead, Florida, USA.. Photo by Johnskate17, GNU Free Documentation/Creative Commons Attribution license, via Wikipedia

Range: Mid Cretaceous (Aptian) to Recent.

Phylogeny: Trionychoidea : *Basilochelys* + (Adocusia + (*Peltochelys* + * : Trionychidae + Carettochelyidae))

Characters: peripherals not sutured to costals; ribheads strongly sutured to vertebral centra; premaxillae fused; radius and ulna in contact adjacent to manus; number of clawed digits three or fewer; coracoid longest of three pectoral processes; carapace not sutured to plastron (Meylan & Gaffney, 1989)

Further description: "Dorsal vertebrae and ribs fused with the dermal plates to form an incompletely ossified carapace ornamented with coarse vermiculating sculpture; no epidermal shields. Neck bending by a sigmoid curve in e vertical plane. Skull with descending parieto-pterygoidal processes. Pterygoids broad throughout, separated from each other, the basisphenoid joining the palatines. Cervical vertebrae without transverse processes. Sacral and caudal ribs generally attached to well-developed transverse processes of the neural arches. Pelvis free from the carapace and plastron. Limbs modified into

paddles, the fourth digit with at 1not four phalanges, and only the three inner digits clawed. Marginal hones absent or forming an incomplete series, not connected with the ribs. Nine plastral elements; epiplastra separated from the hyoplastra by the V-shaped entoplastron." - Zittel, Eastman, et al (1902) pp.195-6

Comments: [1] "The group of three-clawed mud-turtles, which appears first in the Upper Cretaceous of the United States, and next in the lowest Tertiary strata of both Europe and North America, exhibits the most generalised structure of all Chelonians. The shell is incompletely ossified, and the plastral elements remain separate throughout life. Vacuities persist in the carapace, and various portions of the skeleton afford evidence of imperfect ossification. There are no free nasals, and no parieto-squamosal arch ; the descending processes of the prefrontal may or may not be connected with the vomer, the epipterygoids are free, and the dentaries distinct. The stapes is entirely surrounded by the quadrate. The pterygoid is broad, without lateral expansions, separating the quadrate and basisphenoid. Only one family is recognised." - Zittel, Eastman, et al (1902) pp.196

[2]. Lourenço et al 2012 using molecular dating place the divergence of crown Trionychoidea into Carettochelyids and Trionychids at 128.7 Mya, or Barremian age of Early Cretaceous.

The Pig-nosed Turtle *Carettochelys insculpta*, Dvur Králové Zoo, Czech Republic. Photo by Karelj. Public domain. via Wikimedia

Carettochelyidae:

Range: Mid Cretaceous (Albian) to Recent of Asia

Phylogeny: Trionychia : Trionychidae + *

Characters: paired articulation between 8th vertebra and the nuchal bone, limbs terminate in paddles. (Jack R Holt)

Comments: Medium-sized, freshwater turtles Pignose Turtles. The carapace is leathery; and they have an elongate, pig-like snout. The fossil record of the group is almost exclusively found in the Northern Hemisphere, with fossil forms from North America, Europe, and Asia. Divided into the more basal Anosteirinae with *Kizylkumemys* Nessov, 1977, *Anosteira* Leidy, 1871 and

Pseudanosteira Clark, 1932, and the larger and more advanced Carettochelyinae which includes *Carettochelys* Ramsay, 1887, *Allaeochelys* Noulet, 1867, *Burmemys* Hutchison et al., 2004 and *Chorlakkichelys*. The oldest representative of Carettochelyidae is *Kizylkumemys schultzi* from the middle Cretaceous (Albian and Cenomanian) of central Asia. It also has a number of primitive features. "In 2003, I. G. Danilov and A. O. Averianov (St. Petersburg, Russia) presented new data on the morphology of *Kizylkumemys*, which appears to be more primitive than *Carettochelys* with similarities to trionychoid turtles. The new data supports the monophyly of the (crown) clade Trionychia (Carettochelyidae + Trionychidae), although the carotid morphology of *Kizylkumemys* is closer to the baenid condition (internal carotid canal is floored anteriorly, no foramina basisphenoidales present), which argues for the Trionychia outside of Eucryptodira." (check quote) Fossil Turtle Newsletter Jan 2004 p.7. This supports molecular phylogeny, which posists a very early split between the (pan)Trionychia and all other extant cryptodires. Even older material, mentioned in Hirayama et al. (2000), from the Early Cretaceous (Hauterivian) of Japan, likely represents the phylogenetic stem of Carettochelyidae. During the Eocene, Carettochelyidae had its greatest diversity in Asia, Europe and North America. Today, the only surviving species is *Carettochelys insculpta* Ramsay, 1887, found in freshwater and brackish water rivers and lagoons in New Guinea and Australia. (Joyce et al 2004, p.1002; Scheyer 2007, pp.106-7) MAK130222.

Trionychidae:

Range: Mid Cretaceous (Aptian) to Recent,

Phylogeny: Trionychia : Carettochelyidae + * : *Basilochelys* + ((Plastomeninae + Cyclanorbinae) + Trionychinae)

Characters:. [1] Fleshy lips over the keratin beak, no articulation between the centra of the last cervical and first thoracic vertebrae, temporal region open, ; webbed feet, claws only on the middle three digits (hence the name - "Trionyx" - Three Clawed). Most of the carapace is lost, replaced by flexible leathery covering instead of scutes; the plastron is also reduced, with the connection through ligaments instead of as bony bridge. The shell is very flattened and the head has elongate rostra (nostrils in a projecting snout)." - Jack R Holt

Further description: "Skull depressed, the small orbits directed more or less upwards and approximated towards the nares; temporal fossae completely open, and squamosal and supra-occipital with very long posterior processes. Plastron totally distinct from the carapace, with large vacuities. Humerus much curved." - Zittel, Eastman, et al (1902) pp.196

Trionyx messelianus from Messel Pit Fossil Site (Middle Eocene of Germany) at the Naturmuseum Senckenberg. *T. messelianus* can reach a length of about 60 cm and it is the largest species of turtles of Messel Pit Fossil Site. Carapace and plastron are not connected by bony prominences and the plastron show bony plates reduced to small protrusions. According to see Karl (1998) *Trionyx messelianus* is a synonym of *Rafetoides austriacus* (Peters, 1858). - Wikimedia. Photo by Hectonichus, GNU Free Documentation/Creative Commons Attribution license, via Wikimedia

Comments: Freshwater riverine (rarely brackish water) mainly carnivores turtles feeding on fish, crustaceans, and insects, fast swimmers. The neck and snout are elongated for prey ambush. They lay 4 to 100 brittle, spherical eggs ref. Trionychidae originated in Asia in the late Early Cretaceous, *Aspideretoides allani, Aspideretoides foveatus, Aspideretoides splendidus*, and *Apalone latus* from the Late Cretaceous (middle Campanian) of North America are likely trionychids, thus extending the age of the crown back to the lastest Cretaceous. (Joyce et al 2004, p.1002, Scheyer 2007, p.109). During the Tertiary they spread to all other continents with exception of Antarctica. Most fossil forms placed in the extant genus *Trionyx* have been described from Eocene and Miocene Europe, although there is the tedemcy now to give them distinct generic names. *Axestus* and *Plastomenus* Cope, from the Eocene of Wyoming and New Mexico, are closely related genera.

Chitra Gray is known from the Pliocene and Recent (Zittel, Eastman, et al (1902) pp.196). 23 species and 14 extant genera of extant soft-shelled turtles are known from temperate and tropical areas of North America, Eurasia, Africa and New Guinea (Joyce & Lyson 2010 p.241)

Plastomeninae: ***Hutchemys*****,** ***Plastomenus*****, *****?Helopanoplia***

Range: Late Cretaceous (Campanian) to Eocene of North America (possibly also Kazakhstan)

Phylogeny: Trionychidae : *Basilochelys* + (Trionychinae + (Cyclanorbinae + *))

Characters:. Well ossified plastron and the central fontanella of the plastron is small or even absent

Comments: Phylogenetic analysis reveals that plastomenids are stem cyclanorbines, either an early branching clade of stem Cyclanorbinae, or a paraphyletic grade that gave rise to modern cyclanorbines. This significantly reduces the previous ghost range (in this case the result of a research bias rather than absense of fossils) of the total group Cyclanorbinae from some 80 to about 30 million years. Although abundant, their fossil record is still too poorly understood. Joyce & Lyson 2010. As the Plastomenidae are now includsed in the total clade Cyclanorbinae, we have downgraded them from family to subfamily ranking (alternatively the Cyclanorbinae can be elevated to family rank).

References: Scheyer 2007, pp.110; Joyce et al 2009, Joyce & Lyson 2010

Fossil of *Plastomenus* sp. in the Field Museum of Natural History, Chicago. Photo by Smokeybjb, GNU Free Documentation/Creative Commons Attribution license, via Wikipedia

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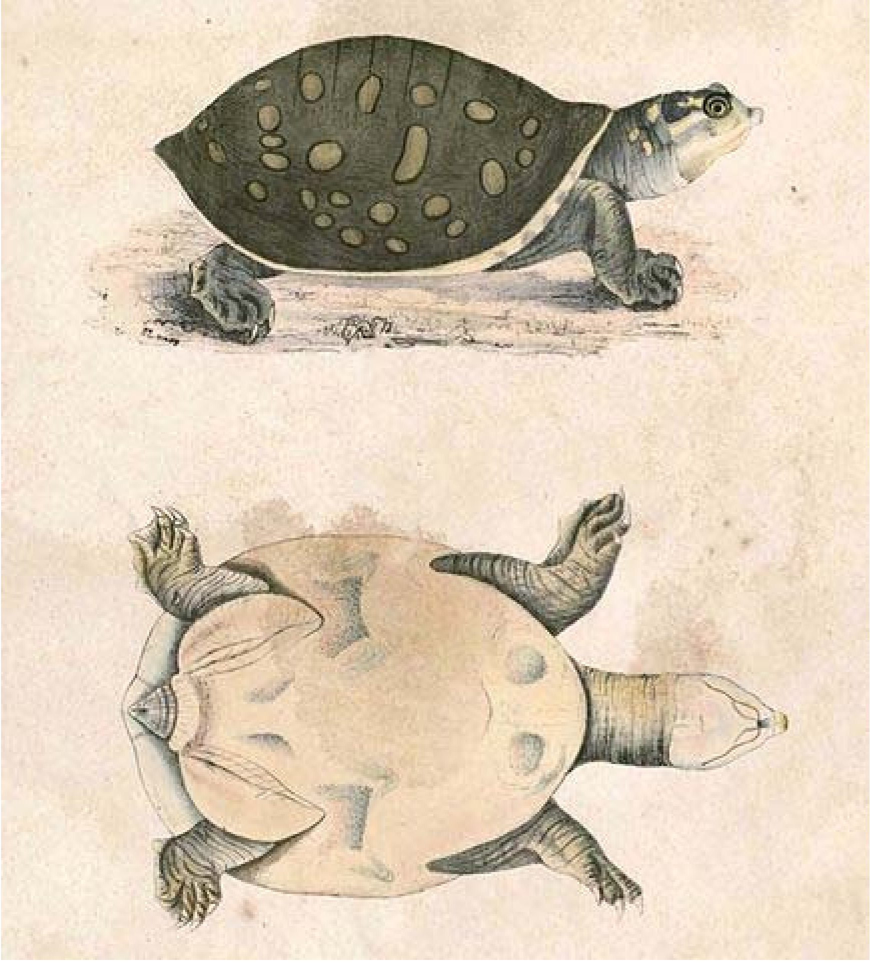
Cyclanorbinae: ***Cyclanorbis*****,** ***Cycloderma*****,** ***Lissemys***

Range: Miocene to Recent

Phylogeny: Trionychidae : *Basilochelys* + (Trionychinae + (Plastomeninae + *))

Characters:. massively ossified shell and fused hyo- and hypoplast

Comments: Evolved from plastomenine ancestors Joyce & Lyson 2010. Three recent genera - *Cyclanorbis*, *Cycloderma*, and *Lissemys* - with two species each. *Lissemys* still retains small bone elements in the periphery of the soft dermal part of the shell, and is considered the most basal extant representative of the Trionychidae. The shells are also more extensively ossified than trionychines, a set of traits that is generally considered to be morphologically less specialised (and hence closer to the ancestral condition). Joyce & Lyson 2010 p.241The subfamily is known in the fossil record from the Miocene of Saudi Arabia and the Pliocene of Africa and India. (Scheyer 2007, pp.110)



Lissemys punctata (Indian flapshell turtle). Illustrations of Indian Zoology - volume 2, Thomas Hardwicke. Public domain. via Wikimedia

Trionychinae: Extant genera ***Amyda, Apalone, Aspiderestes, Chitra, Dogania, Nilssonia, Palea, Pelochlys, Pelodiscus, Rafetus, Trionyx***.

Range: Mid Cretaceous (Aptian) to Recent

Phylogeny: Trionychidae : *Basilochelys* + (Cyclanorbinae + Plastomeninae) + *)

Characters:. plastral bones not firmly fused but loosely bonded by connective dermal tissue

Eastern Spiny Softshell Turtle (*Apalone spinefera*). Photo by Kim Pardi, Creative Commons Attribution license, via Wikipedia

Comments: Medium-sized, freshwater turtles, known from the Mid Cretaceous of North America onwards (Scheyer 2007, pp.110-111). In contrast to cyclanorbines, trionychines exhibit a number of traits that are typically interpreted as derived, including "a reduction in the ossified carapacial disk to the point that the pelvis is not covered by bone, the resulting development of an extensive leathery carapacial perimeter with the formation of extensive free rib ends, and the reduction in the plastral callosities, particularly those of the entoplastron and epiplastra" Joyce & Lyson 2010 p.241

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Pleurodira
         |--Paracryptodira
         `--o Eucryptodira
            |--Protostegidae
            `--+--Plesiochelyidae
               `--+==Xinjiangchelyidae
                  `--o Centrocryptodira
                     |==Sinemydidae
                     |--Trionychoidea
                     `--+--+==Macrobaenidae
                        |   |--o
Panchelonioidea
                        |   |  |-
-Chitracephalus
                        |   |  `--o
Chelonioidea
                        |   |     |--o
Toxochelyidae
                        |   |     |  |-
-Toxochelys
                        |   |     |  `-
-Porthochelys
                        |   |     |--+-
-Mesodermochelys
                        |   |     |  `?--o
Allopleuroninae
                        |   |     |      |-
-Allopleuron
                        |   |     |      `-
-Protosphargis
                        |   |     `--o Crown
Group  Chelonioidea
                        |   |        |--o
Pancheloniidae
                        |   |        |  |-
-Mexichelys
                        |   |        |  `--+-
-Lophochelyinae
                        |   |        |      `--o
Cheloniidae
                        |   |        |
|--Euclastes
                        |   |        |
|?--Gigantatypus
                        |   |        |
|--Argillochelys
                        |   |        |
|--Eochelone
                        |   |        |
|--Itilochelys
                        |   |        |
`--+--Pacifichelys
                        |   |        |
`--+--Puppigerus
                        |   |        |
`--o Cheloniinae
                        |   |        |
|--+--Chelonini
```

Contents

```
|   |--Syllomus           |    |         |
|   |--Chelonia           |    |         |
|   `--Natator            |    |         |
`--o Carettini            |    |         |
|--Eretmochelys           |    |         |
`--+--Procolpochelys      |    |         |
|--Caretta                |    |         |
`--Lepidochelys           |    |         |
Dermochelyidae            |    |         `--o
-Corsochelys              |    |            |-
Dermochelyidne            |    |            `--o
-Eosphargis               |    |               |-
+--Psephophorus           |    |               `--
`--Dermochelys            |    |
                          |    `--+--Chelydridae
-Kinosternoidea           |       `-
                          `--Testudinoidea
```

Taxa on This Page

1. Allopleuroninae X
2. *Allopleuron* X
3. *Argillochelys* X
4. *Caretta*
5. Carettini
6. *Chelonia*
7. Cheloniidae
8. Cheloniinae
9. Chelonini
10. Chelonioidea
11. *Chitracephalus* X
12. *Corsochelys* X
13. Crown Group Chelonioidea
14. Dermochelyidae
15. Dermochelyinae
16. *Dermochelys*
17. *Eochelone* X
18. *Eosphargis* X
19. *Eretmochelys*
20. *Euclastes* X
21. *Gigantatypus* X
22. *Itilochelys* X
23. *Lepidochelys*
24. Lophochelyinae X
25. *Mesodermochelys* X
26. *Mexichelys* X
27. *Natator*
28. *Pacifichelys* X
29. Pancheloniidae
30. Panchelonioidea
31. Procolpochelys X

32. *Protosphargis* X
33. *Psephophorus* X
34. *Puppigerus* X
35. *Syllomus* X
36. *Porthochelys* X
37. *Toxochelys* X
38. Toxochelyidae X

The Chelonioidea or sea turtles are among the most distinctive of reptiles, and have been characteristic of marine ecosystems since the late Cretaceous. They are easily distinguished from other testudines by their flipper-shaped limbs. with the fore-pair the larger and low streamlined shell. As with some freshwater aquatic forms like the Trionychoidae there is the tendency to reduce the bony shell, so that in the leatherback turtle this has becomes little more than numerous bony platelets situated in thick, leathery skin. Unlike other cryptodires, they cannot retract their head into the shell. As with the Mesozoic ichthyosaurs and plesiosaurs, the marine turtles have a worldwide pelagic distribution.

Despite the strong similarity with the Cretaceous Protostegids, the Chelonioidea are only very distantly related; both groups independently evolved paddles, a reduced, streamlined shell, and large size from different semi-aquatic terrapin-like ancestors. The dramatic evolutionary radiation of the chelonioids during the Late Cretaceous (Late Campanian age) may be due to the availability of ecological opportunities vacated by protostegids, which had became extinct by this time (Parham & Pyenson 2010 p.242). During the latest Cretaceous through the Cenozoic they diversified into a range of ecological roles. Now after 75 million years of highly succesful evolution, these large, charismatic, and highly specialised reptiles, like every other species of large wild animal, are themselves facing extinction due to human predation, poaching, and ecological enroachment MAK130224

Descriptions

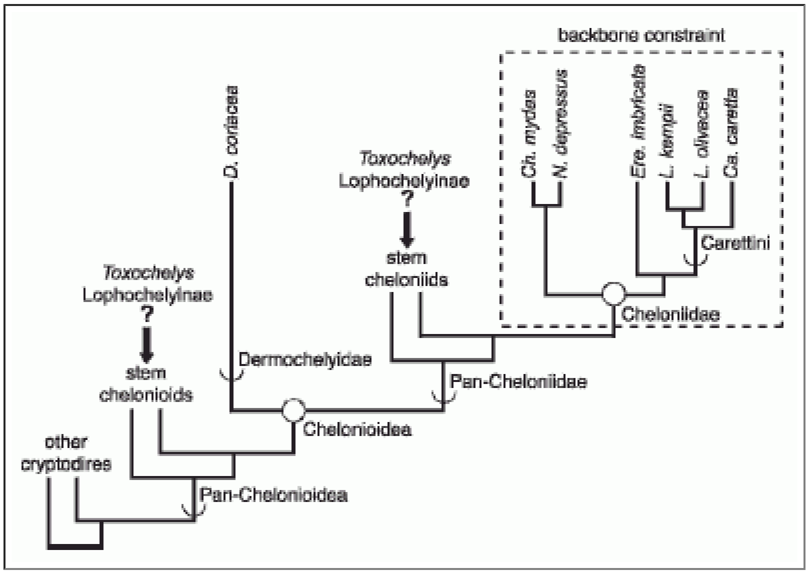
Panchelonioidea (= Panchelonioidea of Joyce et al 2004, = Superfamily Chelonioidea) **:** Sea Turtles and their fossil relatives

Range: Cretaceous to Recent

Phylogeny: Chelonioidea-Chelydridae-Kinosternoidea clade : (Chelydridae + *Emarginachelys* + Kinosternoidea) + * : *Chitracephalus* + Chelonioidea

Characters: "xiphiplastral fontanelle, which involves the reduction of the xiphiplastra in narrow struts that frame it" - Pérez-García 2012 p.577,

Comments: The name Panchelonioidea is used by Joyce et al 2004 to refers to the clade that includes both extant Chelonioidea and a number of extinct and ancestral lineages. It basically means Chelonioidea as usually defined. The Pan- prefix as a signifier of a phylogenetic stem group and crown taxa. As yet it has not caught on outside testudine studies, and we have retained the Linnaean superfamily for the sake of consistency. MAK130301



Phylogenenetic taxonomy (Joyce et al 2004 and later) and cheloniid molecular sequenced (Naro-Maciel et al 2008 and later) constraint tree. Full circles represent node-based definitions whereas semi-circles represent stem-based definitions. showing the uncertain position of the fossil taxa *Toxochelys* and the Lophochelyinae as either stem cheloniids or stem chelonioids; the same ambiguity applies to other fossil taxa e.g. *Mesodermochelys*, Allopleuroninae. From Parham & Pyenson 2010 fig.1

Chitracephalus dumonii, from sketch in Pérez-García & Murelaga (2012). Note the very long neck and almost circular shell

Chitracephalus dumonii Dollo, 1885

Synonym: *Salasemys pulcherrima*

Range: Hauterivian/Barremian to Barremian/Aptian of Belgium and Spain.

Phylogeny: Panchelonioidea **:** Chelonioidea + *

Description: "Cranium much elongated and depressed, with an extremely short facial region, and temporal fossae not roofed. Cervical vertebrae without transverse processes. Pleurals narrowed at their outer ends, with vacuities within the well-developed border of the peripherals. Plastral elements similar to those of Chelone. Digits clawed, not greatly elongated." - Zittel, Eastman, et al (1902) pp.198

Comments: Originally of uncertain placement (classification Testudinata incertae sedis) cladistic analysis of this long necked semi-aquatic turtle by Pérez-García 2012, shows that Chitracephalus is actually a basal Chelonioidean. Together with *Hoyasemys*, *Chitracephalus* forms part of an Early Cretaceous European clade that includes macrobaenid, sinemydid, and panchelonioidean turtles. MAK130306

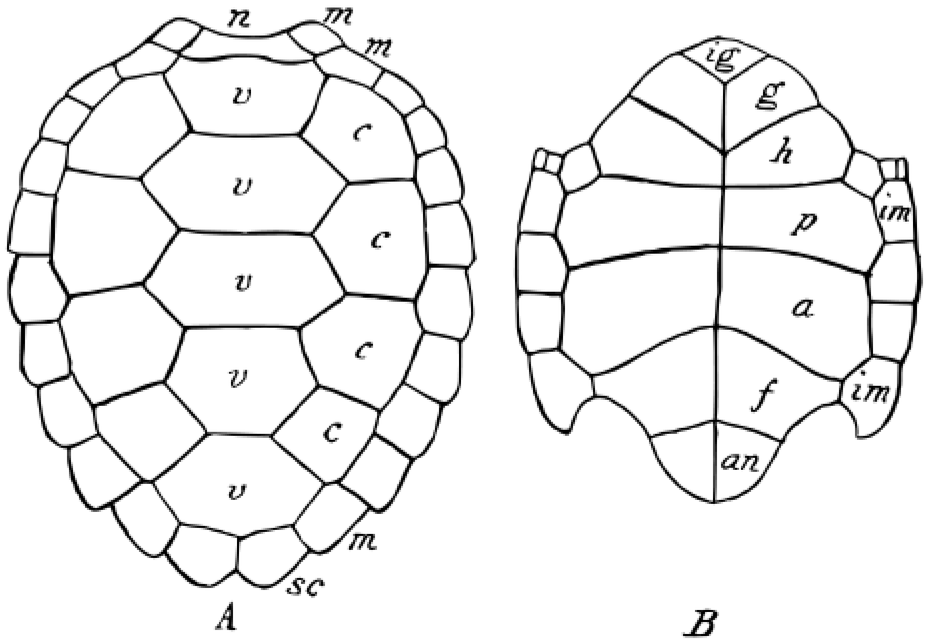
Chelonioidea : Sea Turtles and their fossil relatives

Range: Cretaceous to Recent

Phylogeny: Panchelonioidea : *Chitracephalus* + * : (*Mesodermochelys* + ?Allopleuroninae) + Toxochelyidae + Crown Group Chelonioidea)))

Characters: "raised pedestal on the visceral surface of the nuchal for the articulation with the neural spine of the eighth cervical vertebra present; reduction of costal ossifications, central plastral fontanelle retained in adult individuals; epiplastra elongate in shape; and paddles present" - Anquetin, 2009 p.202. "well developed costal fontanelles" Pérez-García 2012 p.577, Anquetin, 2009 p.202

Comments: The precise phylogenetic position of Cretaceous taxa like *Toxochelys* and *Mesodermochelys* is uncertain, but the general consensus now is that they represent stem taxa (with *Mesodermochelys* and *Toxochelys* forming a polytomy with Crown Group Chelonioidea (Anquetin, 2009 p.202), or *Mesodermochelys* may be more basal than *Toxochelys* (Pérez-García 2012) rather than early representatives of the Cheloniidae and Dermochelyidae.



Shell of *Chelone mydas*, with epidermal horny shields.

A. Carapace
B. Plastron.

a. Abdominal.
an. Anal.
c. Costal.
f. Femoral.
g. Gular.
h. Humeral.
ig. Intergular.
im. Inframarginal.
m. Marginal.
n. Nuchal.
p. Pectoral.
sc. Supracaudal.
v. Vertebral.

The anterior inframarginal is also termed *axillary*, and the posterior *inguinal*.

Carapace terminology, showing *Chelonia*. The shape, arrangement, and type of scutes and its distinctive jargon is essential for understanding testudine paleontology and phylogeny (see also our Primer on Turtle Shell Anatomy. From G.A. Boulenger, *Fauna of British India. Amphibia and Reptilia*. 1890, public domain, via Wikipedia

MAK130301

Links: Wikipedia; Oceans of Kansas (late Cretaceous forms);

Toxochelyidae Baur (1896) (ref)

Toxochelys?, Smithsonian National Museum of Natural History: Hall of Fossils Photo by Ryan Somma, via Wikipedia, with caption, Creative Commons Attribution-Share Alike 2.0

Range: Late Cretaceous (Coniacian to Earliest Maastrichtia) of North America

Phylogeny: Chelonioidea **:** (*Mesodermochelys* + ?Allopleuroninae) + Crown Group Chelonioidea + * **:** *Toxochelys* + "Thinochelyinae"

Description: "Skull somewhat depressed. (flat) Temporal region extensively roofed. Quadrate notched for the columella. Choanae situated well forward; not underfloored by the palatines. Palatines extending forward to the vomers and forming the outer boundaries of the choanae. Hay (1908) p.163 Anterior vomer area wide and smooth. Carapace circular, rarely cordiform.(Zangerl, 1953b p.173) with eleven pairs of peripherals, in addition to the nuchal and pygal. Neuralia flat (i.e. no keel along the bones of the midline of he carapace). Nuchal not furnished with costiform processes. Epidermal shields present. Plastron loosely articulated with the carapace, not extending forward to the third peripheral and backward hardly to the eighth. Fore foot with at least 2 claws; the phalanges furnished with condyles; the limb as a whole resembling that of the Trionychidae."

Comments: A group of late Cretaceous near shore marine turtles that show a number of primitive features that distinguish them from the Cheloniidae. Although some cladistic analyses show *Toxochelys* (and by implication related Toxochelyidae) to be stem-cheloniids (e.g. Hirayama 1998), the consensus now is that they represent a lineage of stem chelonoidea, prior to the cheloniid-dermochelyd divide (e.g. Gaffney & Meylan, 1988, Kear & Lee 2006, Anquetin, 2009, Pérez-García 2012), They seem to have been geographically limited to the American Cretaceous inland sea. As well as *Toxochelys*, other genera like *Porthochelys*, and *Thinochelys* have also been placed here. *Toxochelys* is known from several species. These turtles were probably not particularly good swimmers; unlike the Cheloniidae the shell is not excavated above the forelimbs (Zittel, Eastman, Woodward, et al (1932), p.316), so there is more limited range of motion. Their eyes face to the top, not outward and slightly forward as in modern sea turtles. These animals may have been bottom dwellers in very shallow sea, perhaps somewhat comparable in habits to the soft-shelled and snapping turtles of freshwater streams and ponds. (Jehle, 2006). Falling sea levels during the early Maastrichtian may have been an environmental factor contributing to their demise. MAK130310

Toxochelys Cope

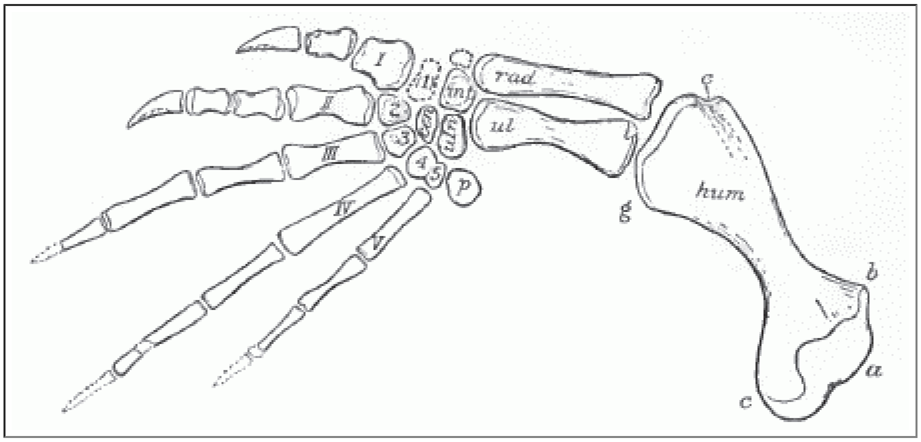
Range: Late Cretaceous (Coniacian to Earliest Maastrichtia) of North America

Phylogeny: Toxochelyidae **:**

Description: Like Cheloniidae except no secondary palate, fore-foot with at least two claws, phalanges with condoyles (Zittel, Eastman, Woodward, et al (1932), p.316); "Skull longer than broad. No nasal bones. Carapace with large lateral fontanels. None of the peripherals in contact with the disk of the carapace. Midline with prominent carina rising at intervals into tubercles, some of which are distinct bones. Tail with a series ot compressed tubercles above.

Plastron with median and lateral fontanels."- (Hay (1908) p.163)

Comments: This genus gives its name to the family Toxochelyidae. The type species *Toxochelys latiremis* Cope 1873 is the most common fossil turtle in the Smoky Hill Chalk, Niobrara Formation, western Kansas, of late Cretaceous Santonian age (at the time a shallow inland sea). Although some specimens may only be 15 cm in length (Mlynarski 1976, p.41), these obviously reprent juveniles, adults having a carapace of around a meter in length (Hay (1908) p.169; Oceans of Kansas ref). It was contemporary with *Ctenochelys*, which was closer to modern turtles.

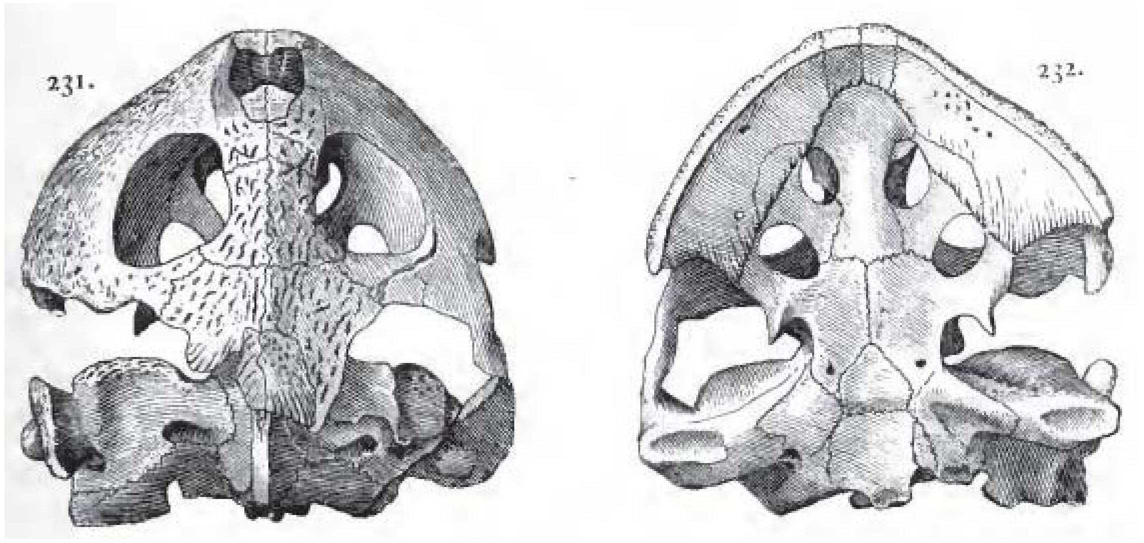


Toxochelys latiremis. Front limb. x 0.28 life-size. Specimen in Yale Univ. collection. a, head of humerus; b, radial process; c, ulnar process; cen, centrale; e, ectepicondylar groove; g, entocondyle; hum, humerus; intj, intermedium; pj pisiforme; rad, radius; ul, ulna; uln, ulnare; I, II, etc., metacarpals; 1, 2, 3, etc., distal carpal bones. Figure by Wieland. From Hay (1908) p.166, fig 200; public domain (copyright expired). The limb is only slightly paddle-like, unlike more specialised marine turtles like *Archelon* or *Carretta*

The Early Campanian *T. moorevillensis* Zangerl, 1953 from the Mooreville Chalk, Alabama was convergent on the modern Green Sea Turtle *Chelonia* and on a number of distinct fossil forms in having thin dentaries with large symphyseal ridges (Zangerl, 1953b p.176) ; it was probably the first of the herbivorous chelonoids, associated with the evolution of sea grasses (Parham & Pyenson 2010). The stratigraphically oldest species of *Toxochelys* is *T. latiremis* from the Niobrara, is also the most highly specialized. The less specialised Early Campanian T. moorevillensis, T. barberi Schmidt; from the late Campanian Marlbrook Marl, Arkansas, and T. atlantica Zangerl, 1953 from the Upper Greensand, New Jersey.represent a series that occur along the open waters of the Gulf and Atlantic coasts, whereas T. latiremis lived in a semi-isolated inland basin, and hence may have underwent specialization earlier and at a faster rate than its relatives along the Gulf coast (Zangerl, 1953 p.270). *T. browni* Hay is a very large species from the Early to Mid Campanian Pierre Shale, South Dakota and Wyoming is much larger than *T. latiremis*. here is some disagreement regarding synonymy, the Paleobiology Database includes every species but under *Toxochelys latiremis*) *Toxochelys weeksi* Collins; Ripley Formation, Tennessee.; from the earliest Maastrichtian, is the last known member of the genus (Karl & Lindow, 2009).

Link: Oceans of Kansas.

Porthochelys laticeps Williston



Porthochelys laticeps. Skull of type, half life size. Niobrara formation (Santonian), Kansas. From Hay (1908) p.181, figs 231 and 232; public domain (copyright expired).

Range: Santonian to Early Campanian of North America

Phylogeny: Toxochelyidae : *Toxochelys* + *

Description: "Skull as broad as long (*right*). Nasal bones present. Lateral fontanels of the carapace obsolete. All of the peripherals articulating closely with the costals. No carina along the middle of the back and no tubercles. Plastron with small median and lateral fontanels." - Hay (1908) p.180

Comments: Like *Toxochelys*, *Porthochelys* seems to be a near coastal species, in contrast to the protostegoids (Hay (1908) p.38). The skull of Porthochelys is much more robust and much wider than that of Toxochelys. The strength of construction and width are correlated with the greater masticatory surface areas on upper and lower jaws (Zangerl, 1953 p.173). The different-shaped head implies different feeding strategies and lifestyle, hence the co-existence of these two similar species. As is so often with fossil forms, it is likely that the many named species are junior synonyms of the type, with differences due to intra-specific variation and post-mortem and geological distortion.. This was a reasonably large animal, the nearly circular carapace of the type specimen being 78.5 cm wide and 73 cm long Hay (1908) p.182

The Informal name "Thinochelyinae" (Mikko's phylogeny) might be used for several species, especially *Porthochelys laticeps* Williston, 1901, *Thinochelys lapisossea* Zangerl, 1953, assuming they are more closely related to each other than *Toxochelys*. MAK130310

Mesodermochelys undulatus Hirayama & Chitoku, 1996

Range: Santonian to Early Maastrichtian of Japan

Phylogeny: Chelonioidea **:** Toxochelyidae + Crown Group Chelonioidea + (?Allopleuroninae + *)

Comments: *Mesodermochelys undulatus* is usually considered a Cretaceous relative or ancestor of *Dermochelys coriacea* (e.g., Hirayama & Chitoku, 1996; Hirayama 1998, Kear & Lee 2006). Cladistic analysis by Joyce, 2007 found only very weak support for this, in the form of partial loss of carapacial scales. Anquetin, 2009 p.202 analysis recovered *Toxochelys latiremis*, *Mesodermochelys undulatus*, and Crown Chelonioidea as an unresolved polytomy at the base of panchelonioids, while Pérez-García 2012, incorporating *Chitracephalus dumonii* in a modified data set of Joyce (2007) found *Mesodermochelys* to be even more basal than *Toxochelys*.

Mesodermochelys firest appears in the early part of the Late Cretaceous. An unnamed primitive species with a carapace of less than a meter long was the most dominant sea turtle known from the Santonian of Hokkaido Prefecture, Japan. The larger *Mesodermochelys undulatus* from the Campanian to Early Maastrichtian of Japan (Hirayama 2012). As with more specialised sea turtles, *Mesodermochelys* had elongated front flippers. This species is particularly abundant in the Maastrichtian Hakobuchi Group of Hokkaido Prefecture, although it is also known from the Late Campanian to Early Maastrichtian Izumi Group of Hyogo and Kagawa Prefectures, western Japan. This was a large animal, with a carapace reaching 1.3 to 1.5 metres in length. An isolated humerus is about 50 cm long, suggesting an individual with almost 2 m long carapace. (Hirayama 2012) Only the neural or spinal scutes, or individual plates, of the carapace are well grooved. (Wikipedia) MAK130301

Allopleuroninae

Range: Maastrichtian of Europe.

Phylogeny: Chelonioidea **:** Toxochelyidae + Crown Group Chelonioidea + (*Mesodermochelys* + * **:** *Allopleuron* + *Protosphargis*)

Comments: The subfamily Allopleuroninae is sometimes used to include a number of Late Cretaceous to Early Cenozoic genera (*Allopleuron, Eosphargis, Glyptochelone* and *Protosphargis*) (Bishop 2007) considered early Dermochelyidae. Of these, *Eosphargis* can confidentally be placed in the Dermochelyidae, but the others are of iuncertain phylogenetic position. They may be specialised stem Cheloniids convergent with Dermochelyids, or perhaps equally or more likely a distinct line or lines of stem Chelonoideans. Parham & Pyenson 2010 informally place *Allopleuron hoffmanni* near *Mesodermochelys undulatus*. As well as being near contemporaries, both have a reduced, Dermochelyid-like shell and thin dentaries with large symphyseal ridges which imply a possibly herbivorous diet (Parham & Pyenson 2010), although of course these could easily have simply been convergences. These turtles replaced the *Toxochelys moorevillensis*, which disappeared around the end of the end of the Campanian. MAK130310

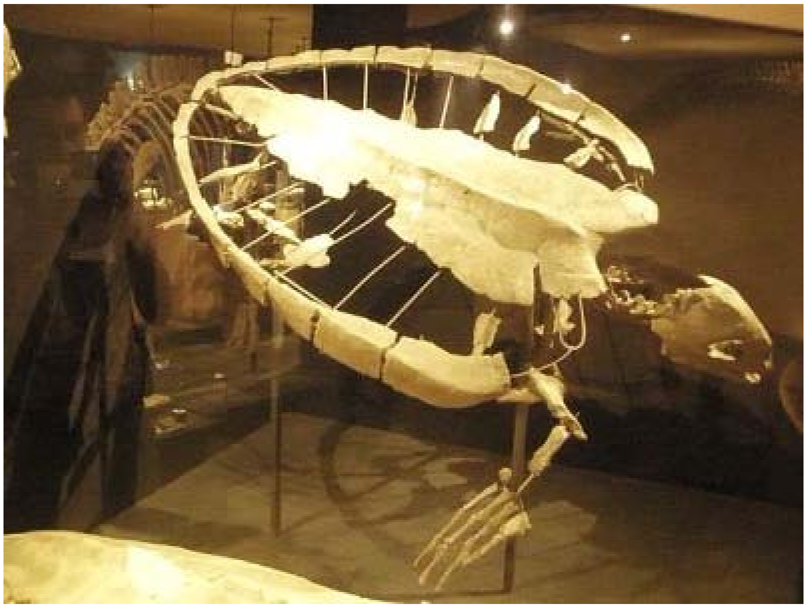
Allopleuron hoffmanni (Gray, 1831)

Range: Late Maastrichtian of Netherlands

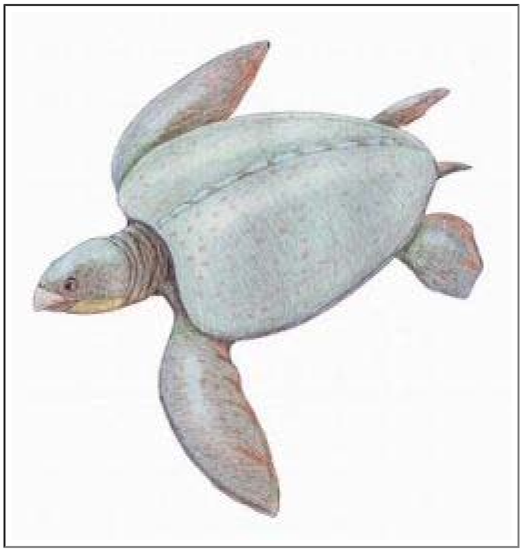
Phylogeny: Allopleuroninae **:** *Protosphargis* + *

Description: Carapace long and narrow, nuchal deeply emarginate, neurals short and wide with a long keel; marginals long and slender. Zittel, Eastman, et al (1932) p.198

Comments: A fairly large, highly specialised sea turtle, with a plastron length of about 1.2 meters (Mlynarski 1976 p.51). The carapace is greatly reduced, making it unlikely to be an ancestor of Cenozoic cheloniidae. - Hay (1908) p.209. May or may not be related to either or both *Protosphargis* and *Mesodermochelys*. Included by Gaffney and Meylan, 1988 in the Euchelonioidea MAK130311



Allopleuron hoffmanni, at Natural History Museum of Maastricht, photo by Ghedoghedo, Creative Commons Attribution license, viavia Wikimedia



Protosphargis veronensis Capellini , 1884, from the Latest Cretaceous (Maastrichtian) of Northern Italy. Artwork by Dmitry Bogdanov, GNU Free Documentation/Creative Commons Attribution license, via Wikimedia

Protosphargis veronensis Capellini , 1884

Range: Maastrichtian of Italy

Phylogeny: Allopleuroninae **:** *Allopleuron* + *

Description: Body skeleton similar to that of *Protostega*, but bones of plastron more slender, and median fontanelle larger. Zittel, Eastman, et al (1902) pp.198

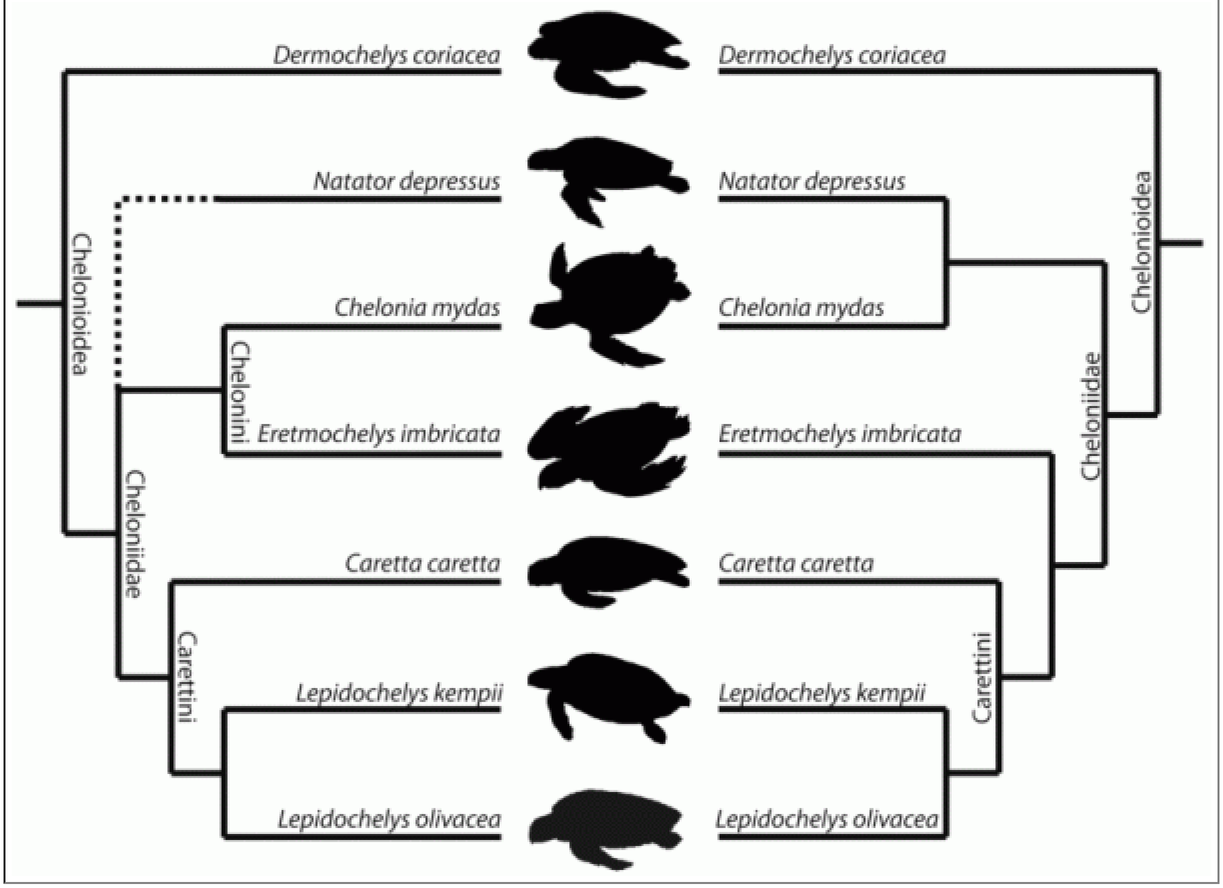
Comments: This animal was probably very similar to today's leatherback turtle (*Dermochelys coriacea*), and it is thought that *Protosphargis*' shell, which could exceed two meters in length, may have been similarly equipped with longitudinal ridges along the back, which help these animals to move quickly in the water. The reduction of the shell is greater than that of the Protostegidae, and more reminiscent of *Dermochelys*. The bones of the limbs also show a remarkable specialization to marine life. Either a primitive dermochelyid or an unrelated but convergent form. MAK130316

Links: Wikipedia (Italian) Wikipedia (Dutch)

Crown Group Chelonioidea

Range: Fr the Late Cretaceous

Phylogeny: Chelonioidea : Toxochelyidae + (*Mesodermochelys* + ?Allopleuroninae) + * :



Alternative relationships of chelonioid species according to (*left*) the morphology-based phylogeny of Gaffney and Meylan 1988 (*Natator depressus* was not included in that analysis) and (*right*) the molecular-based phylogeny of Thomson and Shaffer 2010. Names of higher taxa follow Gaffney and Meylan 1988. Silhouettes not to scale. Diagram from Jones et al, 2012 fig 1; Creative Commons Attribution.

Pancheloniidae + Dermochelyidae))

Characters: "nasal absent; parietal-squamosal contact present, temporal emargination poorly developed; foramen palatinum posterius absent; and rostrum basisphenoidale rod-like, thick and rounded" - Anquetin, 2009 p.202.

Comments: Gaffney and Meylan, 1988 erected the clade Euchelonioidea for the Cheloniidae, and a clade uniting *Notochelone*, *Allopleuron*, *Desmatochelys*, and the Dermochelyoidae (Dermochelyidae and Protostegidae). The tendency now (according to statistical-computational cladistics) is towards interpreting these Dermochelyid-like taxa as the result of evolutionary convergence. The name Euchelonioidea can be still be used in a more limited context as a synonym to or alternative for the confusing (because the ambiguity in regards to the Linnaean-based taxonomy) phylogenetic use of "Chelonoidea" and the the clumsy "Crown Chelonoidea" MAK130311

Extant Chelonioidea include two families and eight species of extant sea turtles, the monospecific Dermochelyidae (*Dermochelys coriacea*) and the Cheloniidae. Both lineages are represented by a number of fossil forms from the late Cretaceous and Cenozoic. They are pelagic animals with a worldwide distribution. Diet varies according to species, the giant leatherback turtle (*Dermochelys*) feeds mainly on jellyfish, ridleys and loggerheads (*Caretta* and *Lepidochelys*) on crabs and other benthic invertebrates, and green turtle (*Chelonia mydas*), the only herbivorous species, adults feeding on kelp [*Thalassia testudinium*]

Although they are widely protected, every living species is endangered by human activities, whether poaching, oceanic pollution, being caught in nets, injury through boat propellers, or loss of nesting sites through urbanization of coasts and their encasement in seawalls and revetments, and increasingly efficient fisheries.

Links: Geologic History of Sea Turtles, Wikipedia

Pancheloniidae Joyce, Parham & Gauthier, 2004

Range: Fr the Late Cretaceous, pan-oceanic

Phylogeny: Crown Group Chelonioidea **:** Dermochelyidae + * **:** *Mexichelys* + (Lophochelyinae + Cheloniidae)

Characters: (from Gaffney & Meylan 1988): Secondary palate formed by broad maxilla with contributions from palatine, choanal passages separated by ventral plate of vomer forming prominent part of palate; foramen caroticum laterale and canalis caroticus lateralis much larger in diameter than foramen anterius canalis carotici interni and medial branch of canalis caroticus internus. - via Taxon Diversity - CKT

Comments: As with Panchelonioidea, the name Pancheloniidae is used by Joyce et al 2004 to refer to the stem-group that includes crown Cheloniidae and a number of extinct and ancestral lineages (although technically speaking in cladistics you are not supposed to say "ancestors" because it cannot be proved that one species is an ancestor, we are using the term in the colloquial sense). Alternatives are "Chelonioinea" and Cheloniidae Gray, 1825 sensu Hirayama, 1997. We have retained the original Cheloniidae to refer to both more advanced stem and also crown taxa. Cheloniidae in this definition is represented by such taxa as *Puppigerus* and *Euclastes* (Joyce et al 2004 p.1001). The boundaries between (Pan)Cheloniidae and more primitive or ancestral stem (Pan)Chelonoidea are blurred. On the one hand, Lophochelyines and *Euclastes* (as "*Osteopygis*") have been included in the Toxochelyidae (Carroll, 1988, p.616); on the other, *Toxochelys* and *Ctenochelys* from the Late Cretaceous of North America have also been included in the Cheloniidae (Hirayama, 1998). As several recent cladistic analyses shows *Toxochelys* to be more distantly related (Joyce, 2007, Anquetin, 2009, Parham & Pyenson 2010 fig.3, Pérez-García 2012) , it is here considered basal Chelonioidea. MAK130310

Mexichelys coahuilaensis (Brinkman, Aquillon- Martinez, de Leon Da´vila, Jamniczky, Eberth, and Colbert, 2009)

Range: Late Campanian of Mexico.

Phylogeny: Pancheloniidae **:** (Lophochelyinae + Cheloniidae) + *

Comments: Previously included under *Euclastes*, this is a much more primitive animal, either a stem chelonioid or a very basal cheloniid, and only distantly reelated to Cenozoic cheloniids . It is distinguished from both both stem-chelonioids such as *Toxochelys* and stem-cheloniids like *Ctenochelys* (Lophochelyinae) by an extensive secondary palate, an advanced feature that allows simultanous breathing and feeding. *Mexichelys* fed on hard-shelled prey (durophagy). These animals were among the first that replaced the protostegids during the Campanian, but by the Maastrichtian they had in turn been replaced by convergently durophagous stem-cheloniid lineage that continued into the middle Miocene. (Parham & Pyenson 2010)

Lophochelyinae

Range: Coniacian to Mid Maastrichtian of North America.

Phylogeny: Pancheloniidae **:** *Mexichelys* + (Cheloniidae + *)

Comments: The Lophochelyinae are a family of Late Cretaceous primitive sea turtles that represented a distinct and apparently geographically limited lineage. They range in size from the small *Lophochelys*, with a plastron length of about 20 cm, to the large *Ctenochelys*, with an equivalent length of aboout a meter, and the very large Prionochelys, witha shell of about 1.5 meters (Mlynarski 1976 pp.43-4). The fossil remains of these animals have been found in Alabama, Arkansas and New Jersey. They have been various placed in the Toxochelyidae (Zangerl, 1953b, Mlynarski 1976, Kear & Lee 2006), the stem Chelonoidea (Gaffney and Meylan, 1988), and the Pancheloniidae (Parham & Pyenson 2010). We have tentatively followed the latter's phylogeny but it should remain provisional at best. MAK130316

Cheloniidae Gray, 1825

Range: Fr the Latest Cretaceous, pan-oceanic

Phylogeny: Pancheloniidae **:** *Mexichelys* + (Lophochelyinae + * **:** *Euclastes* + *Gigantatypus* + *Argillochelys* + *Eochelone* + *Itilochelys* + (*Pacifichelys* + (*Puppigerus* + Cheloniinae))

Characters:

Comments: Here used rather informerly to include *Euclastes* grade sea turtlles and above, which heps to reduce the long phylogenies listed above. There probably isn't a clear distinction between Cheloniidae and Pancheloniidae, unless it's an apomorphic one (defined by specific characteristics not found in Lophochelyines etc) MAK130311

Lytoloma elegans from the Latest Cretaceous of Morocco. Photo copyright Roger Perkins

Euclastes Cope, 1867 and related forms

Synonyms: *Rhetechelys*, *Osteopygoides*, *Osteopygis* (crania only)

Range: Latest Cretaceous to Eocene of North America. *Lytoloma* Cope, 1869 is a closely related genus, it is known from the Latest Cretaceous of England, as well as Morrocco and possibly the Eocene of Tunisia.

Phylogeny: Cheloniidae **:** *Gigantatypus* + *Argillochelys* + *Eochelone* + *Itilochelys* + (*Pacifichelys* + (*Puppigerus* + Cheloniinae)) + *

Characters: Skull resembling that of *Caretta*. Carapace rounded posteriorly, vacuities of shell smaller than in *Caretta*s; epiplastrals narrow; exposed portion of entoplastron very short, xiphiplastrals uniting extensively in the median line. Zittel, Eastman, et al (1902) pp.198. Broad, flat extensive secondary palate; wide, dentary bone with an elongated symphysis and flat triturating surface; low tomial ridge on the beak, and primitive humerus (Lynch and Parham 2003

"*Osteopygis*" (= *Euclastes*) life reconstruction. Copyright John Maisano

Comments: Head broad and flattened, with eyes far forward, like the living loggerhead turtle (Zittel, Eastman, Woodward, et al(1932), p.315). Unlike the contemporary *Toxochelys* and *Eochelone*, *Euclastes* had a secondary palate, although not as developed as in *Ctenochelys*. The widened palate and dentaries jaws were suitable for crushing hard-shelled organisms, (Lynch and Parham 2003, wikipedia), they represent one of a number of distinct ecologically and morphologically convergent hyper-durophagous cheloniids, the Maastrichtian *Euclastes wielandi;* (Hay, 1908) replacing the earlier but similar Late Campanian *Mexichelys* (Parham & Pyenson 2010). The carapace is rounded at the rear, vacuities (gaps in the shell, a common marine turtle feature) not as large as in modern forms (Zittel, Eastman, Woodward, et al(1932), p.315). *Lytoloma elegans* from the Late Cretaceous/Early Paleocene phosphate bed deposits near Khouribga, Morocco is a closely related form. These near-shore and marine turtles inhabited the opening Atlantic coastline of West and North Africa and Western Europe. The well-known *Osteopygis* is a chimera based on the head of *Euclastes* and the post-crania of macrobaenids. Durophagous (feeding on hard-shelled invertebrates) '*Osteopygis*'-like turtles are known from many localities including South America and Africa (Parham 2005 p. 75).

The genus is something of a wastebasket taxon. Lynch and Parham 2003 attempted to phylogenetically define *Euclastes* as those taxa that share a more recent common ancestor with the latest Creteacous type species *Euclastes platyops* Cope 1867 than to extant sea turtles or well-known Paleogene taxa, but the only specimen of *E. platyops* is too incomplete for phylogenetic analysis (Parham & Pyenson 2010). Parham & Pyenson 2010 assign only three species to the genus, *E.. platyops*, *E. acutirostris* Jalil, de Lapparent de Broin, Bardet, Vacant,Bouya, Amaghzaz, and Meslouh, 2009 and *E. wielandi*, as, unlike other durophagous stem cheloniids, all three show dorsally facing orbits, implying perhaps a specialised, shallow water lifestyle. Other species are transferred to distinct genera, including the new genera *Mexichelys* and *Pacifichelys* (Parham & Pyenson 2010), The Mid Eocene *Glossochelys planimentum* is a specialised durophagous form with a high vaulted skull (Parham & Pyenson 2010 p.235) that may or may not be related, All these stem cheloniids are very similar, and in the past the various genera have been synonytmised (Zittel, Eastman, et al (1932)) MAK130310

Gigantatypus salahi Kaddumi, 2006

Gigantatypus, at Eternal River Museum, photo by Ghedoghedo, Creative Commons Attribution license, viavia Wikimedia

Range: late Maastrichtian of Jordan

Phylogeny: Cheloniidae **: :** *Euclastes* + *Argillochelys* + *Eochelone* + *Itilochelys* + (*Pacifichelys* + (*Puppigerus* + Cheloniinae)) + *

Comments: Known only from an enormous humerus, this gigantic sea turtle lived in the southern regions of the Tethys Ocean about 100-120 kilometres off the north eastern margins of Cretaceous Africa. Estimated total length is over 3.5 metres in length, equivalent to that of *Archelon* Wieland, 1896. (Parham & Pyenson 2010). We have tentatively followed the latter's phylogeny but it should remain provisional at best. MAK130316

Eochelone brabantica Dollo 1903

Range: Middle Eocene of Belgium.

Phylogeny: Cheloniidae **:** *Euclastes* + *Gigantatypus* + *Argillochelys* + *Itilochelys* + (*Pacifichelys* + (*Puppigerus* + Cheloniinae)) + *

Comments: This genus lends its name to the paraphyletic subfamily Eocheloniinae, which includes a number of stem cheloniids. The skull of *Eochelone* is broad and flattened, the eyes are to the side rather than to the front as in more advanced forms. The carapace is elongated and does not have a keel. (Zittel, Eastman, et al (1932)). This was a small sea turtle, with a plastron length of about 60 cm (Mlynarski 1976 p.46)

Itilochelys rasstrigin Danilov, Averianov & Yarkov , 2010

Horizon: Beryozovaya beds (Danian) of Rasstrigin 2 locality, Dubovsky, Volgograd Oblast, Russia.

Phylogeny: Cheloniidae **:** *Euclastes* + *Gigantatypus* + *Argillochelys* + *Eochelone* + (*Pacifichelys* + (*Puppigerus* + Cheloniinae)) + *

Comments: From Wikipedia: Itilochelys rasstrigin is known only from three fossils, the holotype, specimen number "ZIN PH 1/118" and two referred specimens, numbers "ZIN PH 2/118" and "ZIN PH 3/118" . The type specimen is composed of a grouping of cervical vertebrae I-III, partial skull, and disarticulated lower jaw. Specimen ZIN PH 2/118 is an isolated section of dentary while ZIN PH 3/118 is a right humerus. The fossils were all recovered by A. A. Yarkov from fossiliferous outcrops of the Beryozovaya beds exposed at the Rasstrigin 2 locality.[1] As of 2011, the type and referred specimens are preserved in the Paleoherptological collections housed at the Zoological Institute of the Russian Academy of Sciences, in Saint Petersburg, Russia. Itilochelys was first studied by I. G. Danilov and A. O. Averianov of the Zoological Institute along with A. A. Yarkov of the Natural History, Humanitarian Institute in Volgograd. Their 2010 type description of the genus and species was published in the journal Proceedings of the Zoological Institute RSA. The generic name was coined by Danilov, Averianov, and Yarkov as a combination of the medieval Arabian/Persian name of the Volga River, Itil, along with the Greek "chelys", meaning turtle. The specific epithet rasstrigin is in reference to the type locality of the specimen.

Itilochelys rasstrigin is one of three fossil cheloniid sea turtle taxa which have been recovered from the Volgograd region and the most complete specimen recovered so far. The other two taxa are represented by a specimen of the genus *Euclastes* known from the Karpovka site and a specimen related to the genus *Tasbacka* from the Malaya Ivanovka site.

The placement of *Itilochelys rasstrigin* in the family Cheloniidae is supported by the contact of the squamosal and parietal bones, an emarginated v-shaped crest on the underside of the basisphenoid, and features of the nasal bone structure. Placement of the species as a stem member in the family is based on the structure of the humerus which shows a morphology transitioning towards the derived pelagic structuring of modern cheloniids. (Danilov et al 2010)

Shell of *Argillochelys subcristata* and skull of *Puppigerus crassicostata*, at the Museum für Naturkunde, Berlin. Photo by Ghedoghedo Creative Commons Attribution, Wikipedia

Argillochelys Lydekker in 1889.

Range: Late Paleocene to Early Eocene of England (*A. cuneiceps* (Owen, 1849); and *A. antiqua*); Middle Eocene of Morocco (*A. africana* (Tong & Hirayama, 2008]).

Phylogeny: Cheloniidae **:** *Euclastes* + *Gigantatypus* + *Eochelone* + *Itilochelys* + (*Pacifichelys* + (*Puppigerus* + Cheloniinae)) + *

Description: "skull short and wide, shell and bones of the pectoral arch similar to those of *Caretta*, except that the carapace has but four costal shields, and the xiphiplastrals unite extensively along the median line" - Zittel, Eastman, et al (1902) pp.198

Comments: A small sea turtle, with a plastron length of about 20 cm (Mlynarski 1976 p.48) (unless these fossil forms are huveniles). *Argillochelys* is the third (after *Toxochelys* and *Allopleuron*-*Mesodermochelys*) of four ecologically convergent specialised lineages with thin dentaries with significant symphyseal ridges imply shearing rather than crushing; possibly feeding on plants like sea grasses. (Parham & Pyenson 2010)

Pacifichelys Parham & Pyenson 2010

Range: Miocene of North America.

Phylogeny: Cheloniidae **:** *Euclastes* + *Gigantatypus* + *Argillochelys* + *Eochelone* + *Itilochelys* + ((*Puppigerus* + Cheloniinae) + *)

Comments: Originally described as *Euclastes hutchisoni* is the youngest member of this lineage and is known from the middle Miocene Temblor Formation of California. (Lynch and Parham 2003, Brinkman 2009 p.39). Later phylogenetic analysis by (Parham & Pyenson 2010 shows *Pacifichelys* to be a more advanced form, closer to *Puppigerus*.

Puppigerus Cope in 1870

Fossil of *Puppigerus parkinsonii*, at Teylers Museum, Haarlem. Photo by Ghedoghedo Creative Commons Attribution, Wikipedia

Range: Eocene of United States, England, Belgium, and Uzbekistan. (*P. camperi* is known from the London Clay and Bracklesham Beds of England, as well as the Sables de Bruxelles and the Sables de Wemmel of Belgium. *P. nessovi* is known from the Dzheroi 2 locality of Uzbekistan. *P. crassicostata* may or may not be the same as *P. camperi*).

Phylogeny: Cheloniidae **:** *Euclastes* + *Gigantatypus* + *Argillochelys* + *Eochelone* + *Itilochelys* + (*Pacifichelys* + (Cheloniinae + *))

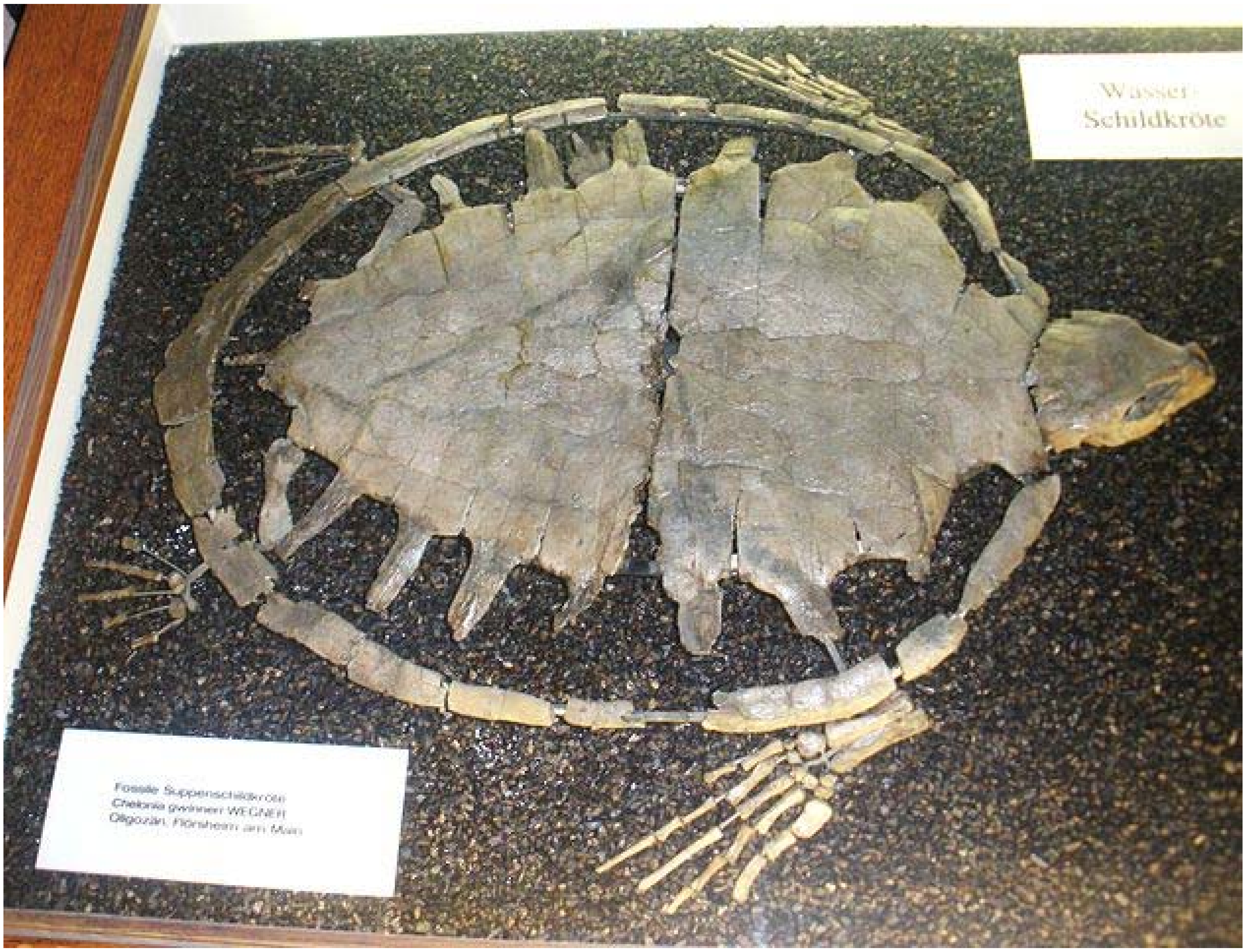
Comments: Another representative of the subfamily Eocheloniinae. From Wikipedia: Fossils show that *Puppigerus* was around 90 centimeters long, and its weight has estimated as being somewhere around 9-14 kilograms. Although cheloniids such as *Puppigerus* first appeared during the Cretaceous, several traits of this genus give it more of a resemblance to modern cheloniids: its "huge" eyes pointed sideways rather than upward, unlike more primitive cheloniids, and its shell was completely ossified. The pygal (rearmost plate of the upper shell) also lacked a notch seen in earlier cheloniids. It was a herbivore, living off marine vegetation, and one of the "best-adapted" prehistoric turtles: its "unusually large" eyes helped it gather as much light as possible, and its specialized jaw structure kept it from accidentally breathing in water. Its front legs were flipper-like, but its hind legs were not developed in this manner, suggesting that it would have spent considerable time on dry land, where females would have laid their eggs.

Cheloniinae : sea turtles (Green, Hawksbill, Loggerhead, Ridley, and their fossil relatives)

Range:

Phylogeny: Cheloniidae **:** *Euclastes* + *Gigantatypus* + *Argillochelys* + *Eochelone* + *Itilochelys* + (*Pacifichelys* + (*Puppigerus* + * **:** *Syllomus* + *Chelonia* + *Natator* + Carettini))

Comments: Included here are six species



Fossil of *"Chelonia" gwinneri*, Wegner 1918, a small marine turtle from the Oligocene (Rupelien) of Flörsheim, Germany. Despite its good preservation, the phylogenetic placement of this species is unclear as it has not been determined cladistically. Many fossils of marine Cheloniids were traditionally identified as "Chelonia". Specimen at Senckenberg Museum of Frankfurt. Photo by Ghedoghedo Creative Commons Attribution, Wikipedia

of extant sea turtles, *Caretta caretta* or Loggerhead, *Chelonia mydas* or green turtle, *Eretmochelys imbricata* or hawksbill, *Natator depressus* or flatback Turtle, *Lepidochelys kempii* or Kemp's Ridley turtle and the related *Lepidochelys olivacea* or Olive Ridley turtle, plus their fossil relatives. Most of these species are capable of hybridising with others in the family (Karl et al 1995) (see also essay on hybridisation among giant tortoises) The female returns to the same nest area every 1-3 years. Determing evolutionary relationships within the Cheloniidae on morphological grounds has been difficult. Much of the problems are due to overall similarity, with species and genera nearly indistinguishable in terms of external morphology (Bowen, 2003 p.8). The various species are distinguished by details such as the prefrontal scales on the head, the number of and shape of scutes on the carapace, and the type of inframarginal scutes on the plastron. Molecular phylogeny however provides a celare picture (Bowen, 2003), and we have followed here the recent consensus (Naro-Maciel et al 2008, Thomson and Shaffer 2010, Guillon et al 2012)

There are a number of early Cenozoic fossil forms that may or may not belong here. A large sea turtle from the Earliest Paleocene (Danian age) of Illinois has been assigned to the recent genus *Chelonia* (green sea turtle), but many such cases fossils assigned to living genera have proven to be mistaken or impossible to confirm, so this identification still requires corroboration (Jehle, 2006), and the very early stratigraphic date makes it dubious. The late Oligocene *Carolinochelys*, from the Chandler Bridge Formation of South Carolina has been suggested as a possible ancestor of the living loggerhead turtle *Caretta caretta*, although this has yet to be confirmed with cladistic analysis. A mounted skeleton at the Science Museum of Minnesota, in a swimming pose, is the first articulated specimen of this kind. It is about one meter long, and was found in association with whales, the dugong *Crenatosiren*, sea birds, the crocodile *Gavialosuchus*, other turtles, and fishes. (Anon 2009). The oldest undisputed cheloniids are an unnamed form from the Early Miocene (Brinkman 2009) of Oregan, and *Procoplochelys grandaeva* from the middle Miocene of eastern North America (Joyce et al 2004 p.1001).

Chelonini

Range: Middle Miocene or Pliocene to Recent, Cosmop.

Phylogeny: Cheloniinae **:** Carettini + * **:** *Chelonia* + *Natator* + Syllomus

Comments: The clade *Chelonia* + *Natator* is supported by molecular phylogeny. *Syllomus* may be an early form. MAK130308

Green turtle, *Chelonia mydas*, Gimp-Savvy.com, US National Oceanic and Atmospheric Administration, Public domain, via Wikimedia

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Syllomus aegyptiacus Lydekker, 1889

Range: .

Phylogeny: Chelonini **:** *Chelonia* + *Natator* + *

Comments: *Syllomus* is a pseudodont Sea Turtle widely distributed in the middle Miocene (Brinkman 2009 p.39), known from Egypt, Japan, the Atlantic seaboard (the Middle Miocene Calvert Formation of New Jersey and Northeastern Virginia, along with *Procolpochelys* and *Psephophorus* (Weems 1974, Anon 2009)), and possibly the Temblor Formation of California (Lynch and Parham 2003). It is clear that, like modern sea turtles, it had a ocean-wide distribution. This was a small sea turtle, with a plastron length of about 60 cm (Mlynarski 1976 p.48) Taxonomically it has been placed, with several similar forms such as *Kurobechelys*, in its own subfamily Syllominae (Bishop 2007). Although fossil material from Japan and North America is relatively complete material and cladistic studies done, the phylogeny placement remains ambiguous, the species being variously interpreted as a sister-taxon to extant Cheloniidae, a basal member of the crown group (Lynch and Parham 2003) or sister taxon of the Flatback Turtle *Natator depressa* (Parham & Pyenson 2010) and hence a member of the tribe Natorini. The genus is more primitive than extant cheloniids in that the canalis caroticus lateralis and base of the canalis caroticus internus were fully encased in bone (Brinkman 2009 p.45), although it is also possible that advanced features developed independently in several lines of cheloniinae. MAK130308

Chelonia (Linnaeus, 1758)

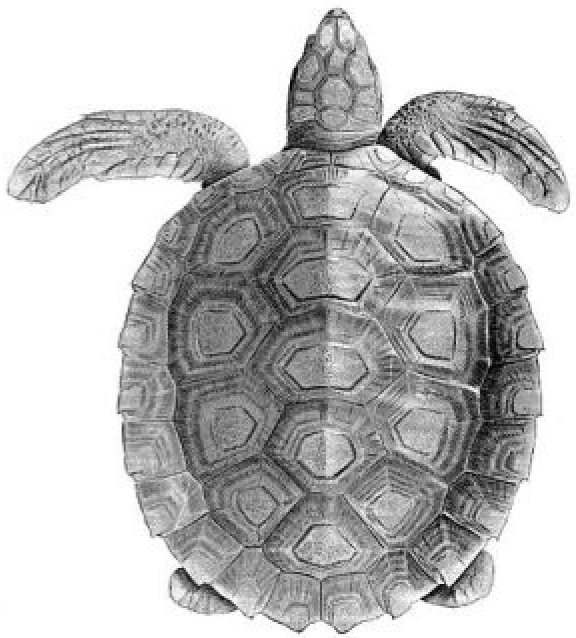
Green turtle, *Chelonia mydas*, Hawaii, Photo by Brocken Inaglory, GNU Free Documentation/Creative Commons Attribution license, via Wikimedia

Range: Late Miocene to Recent, tropical and subtropical Oceans

Phylogeny: Chelonini : *Natator* + *Syllomus* + *

Characters: "Skull comparatively long, narrow, with the orbits lateral. Shell cordiform or pointed al both ends, with four costal shields, the plastral vacuities persisting for a long period. An intergular and a series of inframarginal shields present." Zittel, Eastman, et al (1902) pp.198. One pair of scales between eyes (Bishop 2007)

Comments: The extant green sea turtle, Chelonia mydas, has a range that extends throughout tropical and subtropical seas around the world. Although there are two distinct populations in the Atlantic and Pacific Oceans, these do not qualify as distinct subspecies. Adult green turtles grow to 1.5 metres in length with a weight of 68-190 kg and average carapace length is 78-112 cm, with exceptional specimens larger. Unlike other extant cheloniids,*Chelonia* is mostly a herbivorous, adults usually inhabit shallow lagoons, feeding mostly on various species of seagrasses. Like other sea turtles, green sea turtles migrate long distances between feeding grounds and hatching beaches. Many islands worldwide are known as Turtle Island due to green sea turtles nesting on their beaches. It is listed as endangered by the IUCN and CITES Wikipedia



Natator depressus, illustration from McCulloch 1908, public domain

Natator depressa Flatback Turtle

Range: Recent, northern Australasia

Phylogeny: Chelonini **:** *Syllomus* + *Chelonia* + *

Comments: Unlike other sea turtles which have an ocean-wide distribution, the flatback sea turtle (*Natator depressus*) is endemic only to the continental shelf of northern Australasia. It usually found in bays, shallow, grassy waters, coral reefs, estuaries, and lagoons. The carapace of the adult is on average 90 cm long. It is low-domed, the edge is upturned, and has four pairs of costal scales—fewer than other marine turtles. The upper parts are an olive-grey, and more pale ventrally. A single pair of scales is located at the front of the head, which also distinguish this species. (Wikipedia). No fossils are known. Although initial molecular studies resolved this species as the sister taxon to the Carettini (Bowen, 2003, Iverson et al 2007), the current consensus is that it is more closely related to *Chelonia mydas* (Naro-Maciel et al 2008 Thomson and Shaffer 2010, Guillon et al 2012). It may or may not be related to, and presumably evolved from, the widespread Miocene *Syllomus* (Parham & Pyenson 2010)

Carettini Zangerl and Turnbull, 1955

Range: Early Miocene to Recent, Cosmop.

Phylogeny: Cheloniinae **:** Chelonini + * **:** *Eretmochelys* + (*Procoplochelys* + *Caretta* + *Lepidochelys*)

Characters: presence of two pairs of prefrontal scutes between eyes, four or more pairs of lateral or imbricated scutes

Comments: The clade *Caretta* + *Lepidochelys* is one of the few represented by morphological and molecular congruency. *Procoplochelys* would be an ancestral form from which these two evolved. The phylogenetic position of *Eretmochelys* is more uncertain, it may be a basal member of the Carettini, as indicated by molecular studies (Naro-Maciel et al 2008), or it could be related to *Chelonia*, as morphology suggests (Gaffney and Meylan 1988) MAK130307

Eretmochelys Hawksbill turtle

Range: Recent, Atlantic, Pacific, and Indian Oceans

Phylogeny: Carettini **:** (*Procoplochelys* + *Caretta* + *Lepidochelys*) + *

Characters: Four pairs of lateral or imbricated scutes

Comments: *E. imbricata* is easily distinguished from other sea turtles by its sharp, curving beak with prominent tomium. There is a distinct pattern of thick scutes that make up its carapace. While its

Eretmochelys imbricata. The carapace's serrated margin and overlapping scutes are evident in this individual. Photo by Ecocentrik Guy, GNU Free Documentation/Creative Commons Attribution license, via Wikipedia

carapace has five central scutes and four pairs of lateral scutes like several members of its family, E. imbricata's posterior scutes overlap in such a way as to give the rear margin of its carapace a serrated saw-like appearance of its shell margins. The hawksbill's forelimbs have two visible claws on each flipper. Hawksbill shells slightly change colors, depending on water temperature. While this turtle lives part of its life in the open ocean, it spends more time in shallow lagoons and coral reefs. Adult hawksbill sea turtles have been known to grow up to 1 meter in length, weighing around 80 kg on average. The turtle's shell, or carapace, has an amber background patterned with an irregular combination of light and dark streaks, with predominantly black and mottled-brown colors radiating to the sides. While this turtle lives part of its life in the open ocean, it spends more time in shallow lagoons and coral reefs. A critically endangered species, in the past its shell was used for tortoiseshell jewellry. (Wikipedia). We are here following molecular phylogeny in placing this species in the tribe Carettini.

Hawksbill Turtle off the coast of New Ireland. A close-up of the hawksbill's distinct beak. Photo by Tom Doeppner, July 2000. More photos from that dive. GNU Free Documentation/Creative Commons Attribution license, via Wikipedia

Procoplochelys grandaeva (Leidy, 1851)

Range: middle Miocene of the eastern United States.

Phylogeny: Carettini **:** *Eretmochelys* + (*Caretta* + *Lepidochelys* + *)

Comments: Originally *Chelonta grandaeva* Leidy, the genus *Procoplochelys* was coined by Hay (1908) p.215 from then still fragmentary material. *Procoplochelys grandaeva*, from the middle Miocene Calvert Formation of New Jersey, seems to be closely related to the extant *Lepidochelys* and *Caretta* on the basis of features of the shell, particularly the increased number of neurals (see Zangerl and Turnbull, 1955) as well as cranial features Weems (1974). It can therefore be confidently placed in the Tribe Carettini, "Procoplochelys" *melii* (Misuri, 1910) from the Miocene Pietra Leccese sediments of south-eastern Italy is probably not related (Brinkman 2009 p.39)

Caretta Merrem, 1820 or Stejneger, 1904 **:** Loggerhead

Caretta caretta (Loggerhead Sea Turtle) at Océanopolis, Brest, France. Photo by User:Strobilomyces , GNU Free Documentation/Creative Commons Attribution license, via Wikipedia

Synonym: *Thalassochelys caretta*

Range: Late Miocene/Pliocene to Recent, Cosmopolitan

Phylogeny: Carettini : *Eretmochelys* + (*Procoplochelys* + *Lepidochelys* + *)

Characters: "Carapace completely ossified in the adult, with at least five pairs of costal shields, and vacuities more or less obliterated. A series of inframarginal plastral shields present." Zittel, Eastman, et al (1902) pp.198

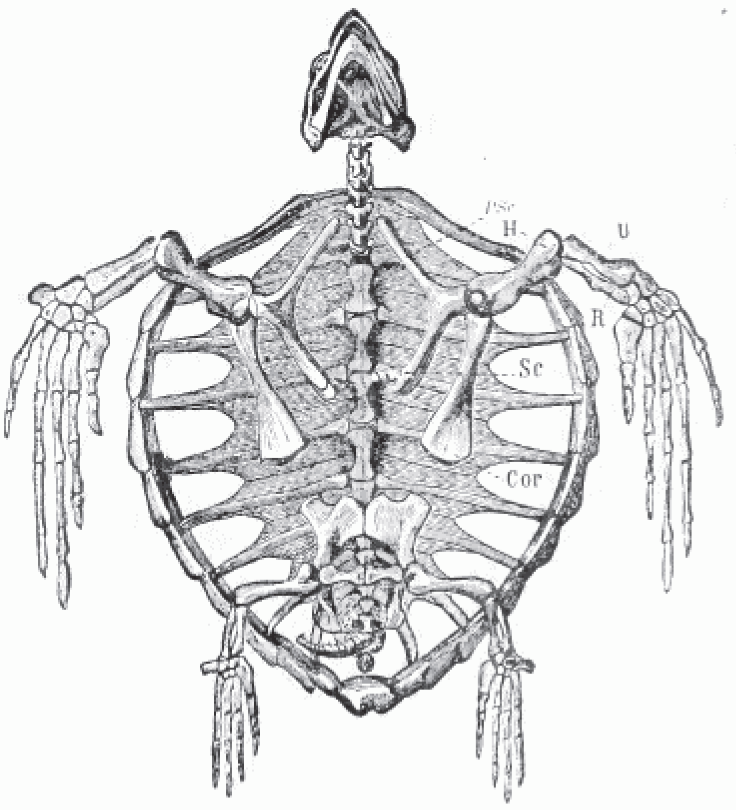
Comments: It's a shame that the old name (e.g. Zittel, Eastman, et al (1902) pp.198-9) *Thalassochelys* - "sea turtle" is no longer used. The loggerhead (*Caretta*), is a sea turtle with a cosmopolitan distribution. It first appears during the late Miocene or Pliocene (Parham & Pyenson 2010). The only well known fossil species is *Caretta patriciae* is a Pliocene species from North Carolina (Zug 2001). "Caretta" *eocaenica* Lydekker 1889 from the Eocene of England does not belong in this genus, but probably represents an unspecified stem cheloniid. *C. caretta* (Linnaeus, 1758) is the only extant species. There is no evidence that it should be divided into the two subspecies *C. c. caretta* and *C. c. gigas* (Bowen, 2003).

The following notes on the evolution and biogeography of the genus are from Wikipedia

---

Around three million years ago, during the Pliocene epoch, Central America emerged from the sea, effectively cutting off currents between the Atlantic and Indo-Pacific Oceans. The rerouting of ocean currents led to climatic changes as the Earth entered a glacial cycle. Cold water upwelling around the Cape of Good Hope and reduction in water temperature at Cape Horn formed coldwater barriers to migrating turtles. The result was a complete isolation of the Atlantic and Pacific populations of loggerheads. During the most recent ice age, the beaches of southeastern North America were too cold for sea turtle eggs. As the Earth began to warm, loggerheads moved farther north, colonizing the northern beaches. Because of this, turtles nesting between North Carolina and northern Florida represent a different genetic population from those in southern Florida (Spotila, 2004 p.167).

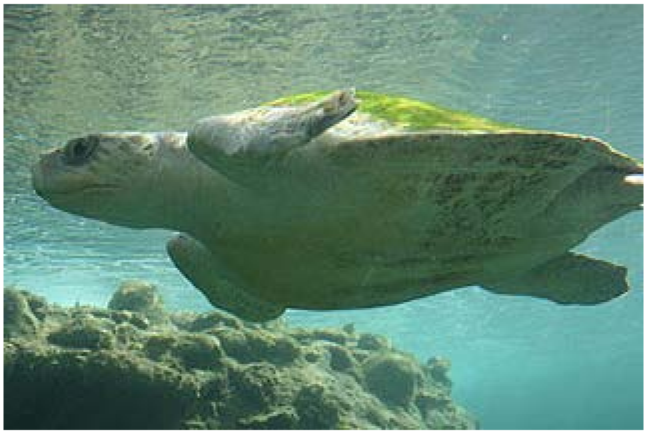
The distinct populations of loggerheads have unique characteristics and genetic differences. For example, Mediterranean loggerheads are smaller, on average, than Atlantic Ocean loggerheads (Spotila, 2004 p.166). North Atlantic and Mediterranean loggerhead sea turtles are descendants of colonizing loggerheads from Tongaland, South Africa. South African loggerhead genes are still present in these populations today (Spotila, 2004 p.167).



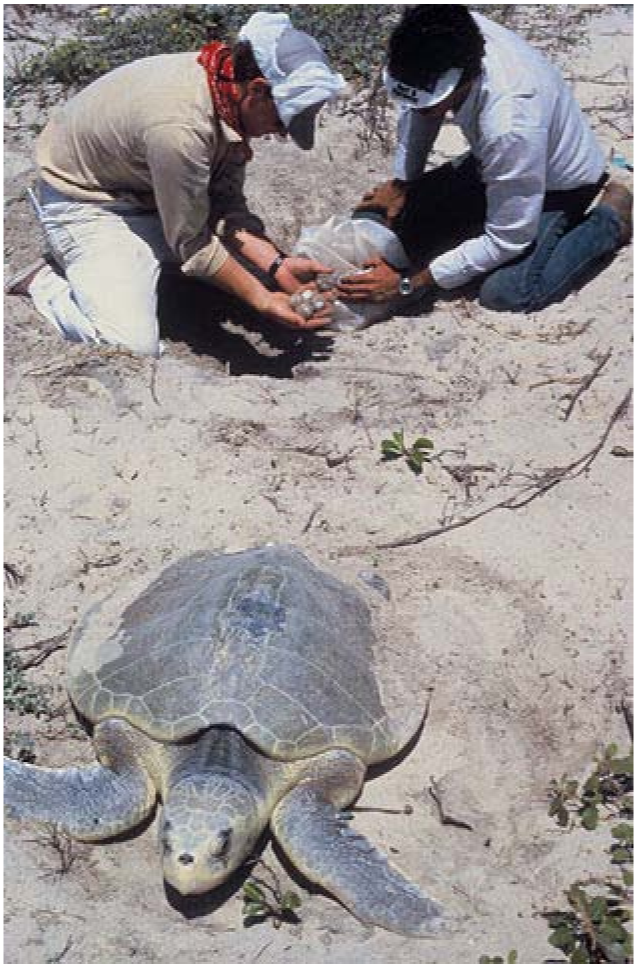
Skeleton of the modern cheloniid *Caretta caretta*, Recent; Mediterranean, showing features of an advanced sea turtle, The lightweight and reduced shell, and the greatly enlarged fore-flippers for use in propulsion, with the smaller rear flippers used for steering, are feature that independently developed in all lineages of advanced sea turtles (including the unrelated Protostegidae) Ventral aspect of skeleton, the plastron removed, cor, Coracoid ; h, Humerus; pre, Precoracoid; r, Radius; sc, Scapula; u, Ulna.- Zittel, Eastman, et al (1932) p.199, public domain

Adults have an average weight range of 80 to 200 kg and a length range of 70 to 95 cm, although some specimens grow much larger (the maximum reported weight is 545 kg and the maximum carapace length is 213 cm). No external differences in gender are seen until the turtle becomes an adult, the most obvious difference being the adult males have thicker tails and shorter plastrons than the females. Wikipedia

Loggerheads can produce intergeneric crosses with most other members of the family Cheloniidae, even ones only distantly related. Molecular sequencing reeveals a long separation between Atlantic and Indian-Pacific populations, and regional clusters of genotypes in the western Pacific and South Atlantic, although this temperate adapted species can occasionally transcend geographic boundaries by transfer of mtDNA lineages between the Atlantic and Indian oceans via southern Africa. (Bowen, 2003)



Lepidochelys olivacea at Réunion. Photo by Thierry Caro, GNU Free Documentation/Creative Commons Attribution license, via Wikipedia



Researchers collect Kemp's ridley (*Lepidochelys kempii*) sea turtle eggs. Washington DC Library. Obtained from http://images.fws.gov/. via Wikipedia, Public Domain

Lepidochelys Fitzinger, 1843 **:** Ridley sea turtels

Range: Late Miocene/Pliocene to Recent, Atlantic, Pacific, and Indian Oceans

Phylogeny: Carettini **:** *Eretmochelys* + (*Procoplochelys* + *Caretta* + *)

Characters: Five or more pairs of lateral scutes

Comments: Ridley sea turtles (*Lepidochelys*) are a genus of medium-sized sea turtles about 50-70 cm long. They feed on crabs, fish, cephalopods, clams, and some marine vegetation (Wikipedia). Both morphology-based cladistics and molecular sequencing agree that ridleys are very closely related to loggerheads, and both may have speciated from *Procoplochelys* during the late Miocene or early Pliocene (Parham & Pyenson 2010). There are two extant species, *Lepidochelys olivacea* or Olive Ridley turtle, and the slightly larger, rare and criticaly endangered *Lepidochelys kempii* or Kemp's Ridley turtle.

Dermochelyidae : leatherback turtles

Range: Late Cretaceous (Campanian) to Recent, Cosmopolitan

Phylogeny: Crown Group Chelonioidea **:** Pancheloniidae + * **:**

Leatherback turtle *Dermochelys coriacea*. Photo from SOS Turtles Panama.

Corsochelys + (*Eosphargis* + (*Psephophorus* + *Dermochelys*))

Comments: The family Dermochelyidae is represented today only by the leatherback turtle *Dermochelys*. This is a huge animal with a shell length up to 2 meters in length, 1 to 1.5 m in width, weighing up to 590 kg. As with the Cretaceous protostegids (with which dermochelyds have in the past been grouped), the leatherback turtle takes the reduction of the bony shell to extremes. The costalia dermal plates fused to flattened ribs and the neuralia (dermal plates over vertebrae) are greatly reduced, somewhat like in the soft-shelled trionychid turtles, and no longer fused to build a carapace. Instead of a hard shell and horny plates it bears a mosaic of numerous bony platelets situated in a thick, leathery skin external to the free ribs and vertebrae. The plastron is also greatly reduced, and at least in Tertiary specimens the ventral side shows secondary platelet armour.

Although the fossil record of the Dermochelyidae is poor, the family has a long evolutionary history, with the earliest undisputed dermochelyids occurring in the Late Cretaceous (Campanian) of North America (Parham and Stidham, 1999) and Japan (Hirayama and Hikida, 1998). The Dermochelyidae reached a peak of diversity during the Eocene period with at least six species worldwide (ref). Prominent fossil taxa include *Psephophorus* from the Eocene of Europe and *Eosphargis* from the Paleocene and Eocene genus of Europe and Eastern USA Joyce et al 2004, Jehle, 2006, Wikipedia

The unique morphology of *Dermochelys coriace*a has resulted in many early authors placing it in a monotypic genus (e.g., Dermochelys Blainville, 1816; Sphargis Merrem, 1820), family (e.g., Sphargidae Gray, 1825), or even suborder (e.g., Athecae Cope, 1871; Athecata Lydekker, 1889). Joyce et al 2004

The taxon Pandermochelys is used by Joyce et al 2004 to refer the clade uniting the Dermochelyidae and the Cretaceous marine Protostegidae, with "Dermochelyidae" applied to all marine turtles more closely related to *Dermochelys coriacea* than to *Protostega gigas* (the type species of Protostegidae). Subsequent cladistic analysis including the ancestral protostegid *Santanachelys gaffneyi* shows that the Protostegids are not Cheloniodea at all, but belong to more ancient and primitive lineage of stem-cryptodires or even stem testudines dating back to the late Jurassic (refs), and that the similarities to Dermochelyids are the result of convergence. Joyce et al 2004 p.1001 suggest that a new name Pandermochelys should be used as the stem taxon for Dermochelyidae, but as these two terms seem to be synbonymous we see little reason to prefer the former over the well established Dermochelyidae.

Corsochelys haliniches

Range: Early Campanian Mooreville Chalk Formation of Alabama. A similiar form has been found in the Maastrichtian Ouled Abdoun phosphate basin, Morocco.

Phylogeny: Dermochelyidae **:** Dermochelyinae + *

Comments: Basal dermochelyid and the earliest known crown chelionoidean. As with other early sea-going forms like *Santanachelys* and *Toxochelys,* likely possessed developed, salt-excreting lachrymal glands. A primitrive feature in all three is a carapace with only minimally reduced coastal plates. Like the protostegid *Archelon* and the extant *Dermachelys*, Corsochelys had channels penetrating the subphyseal plate from bone into the cartilage, which means that Corsochelys would have reached their large size quickly through fast skeletal growth, as with the leatherback. (adapted from Wikipedia)

Dermochelyinae : leatherback turtles:

Cosmochelys, Dermochelys, Eosphargis, Psephoporus

Range: Paleocene or Early Eocene to Recent, Cosmopolitan

Phylogeny: Dermochelyidae **:** *Corsochelys* + * **:** + (*Eosphargis* + (*Psephophorus* + *Dermochelys*))

Description: "Carapace broken up into numerous mosaic-like pieces of dermal ossification, wholly unconnected with the vertebrae and ribs. Epidermal shields absent. Skull without descending parietal processes; ternpored region completely roofed, the scpiamosal joining the parietal. Humerus flattened ; limbs paddle-shaped, dateless, the digits of the manus much elongated ; phalanges without condyles" - Zittel, Eastman, et al (1902) pp.197

Adult *Dermochelys coriacea*, Leatherback Sea Turtle, public domain, via wikipedia

Comments: Following the taxonomy of Bishop 2007, Dermochelyinae can be used to refer to higher Dermochelyidae; equivalent to the Dermochelyidae of Zittel, Eastman, et al.

Eosphargis Lydekker 1889

Range: Early Eocene London Clay and Ypresian of Belgium, possibly Paleocene (Thanetian Maryland/Virginia), and Eocene of Eastern USA

Phylogeny: Dermochelyidae **:** *Corsochelys* + ((*Psephophorus* + *Dermochelys*) + *)

Description: Carapace represented by a single median row of broad carinated scutes and a series of marginals on either side. Plastron probably devoid of tesserae. Skull broad and flat..- Zittel, Eastman, et al (1902) pp.197

Comments: Broad and flat shell 1 to 1.5m long, carapace reduced relative to cheloniids, palate as in *Dermochelys*. The Western European species *Eosphargis gigas* (Owen, 1861) has a skull upto 33 cm wide. (Zittel, Eastman, Woodward, et al(1932), p.315, Jehle, 2006)

Image: *Eosphargis breineri* skull cast at the Geological Museum in Copenhagen, photo by FunkMonk, GNU Free Documentation/Creative Commons Attribution, via wikipedia

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Psephophorus H. von Meyer

Range: Eocene to Pliocene of Europe, Late Eocene of Egypt and Alabama, Miocene of Maryland (Zittel, Eastman, Woodward, et al(1932), p.316), Mid Eocene of New Zealand Kohler (1995

Phylogeny: Dermochelyidae **:** *Corsochelys* + (*Eosphargis* + (*Dermochelys* + *))

Description: "Skull shorter, thicker, and relatively larger than in *Dermochelys*; shell completely tessellated, sculptured ; scutes of the larger longitudinal row of the carapace devoid of carinae" - Zittel, Eastman, et al (1902) pp.197, (Zittel, Eastman, Woodward, et al(1932), p.316),.

Comments: Predecessor and most likely ancestor of the extant leatherback turtle.

Dermochelys coriacea (Vandellius, 1761). Leatherback turtle

Dermochelys coriacea, Leatherback Sea Turtle, from: amigosdomarnaescola.com, via Reptilis net

Synonym: *Sphargis*

Range: Recent, Atlantic, Pacific, and Indian Oceans

Phylogeny: Dermochelyidae : *Corsochelys* + (*Eosphargis* + (*Psephophorus* + *))

Description: "Carapace completely, plastron incompletely bony in the adult, the former with seven, the latter with five keels ; plastral elements eight. Recent ; Atlantic, Pacific, and Indian Oceans. In this, the largest and sole surviving member of the family, the separation of the vertebral column from the carapace was deemed by Cope, Dollo, and others a character of sufficient importance to warrant the establishment of a group (Athecae) equal in value to the rest of the Chelonia. Baur has endeavoured to prove that the mosaic-like carapace was an acquired character, and that this and the following family are directly related to the Chelonidae. - Zittel, Eastman, et al (1902) pp.197

Comments: largest living turtle (more), and the only surviving representative of an ancient family. As a highly advanced Dermochelyid, it has a reduced, soft, cartilaginous shell without scutes, , a throat and upper digestive tract lined with spines (to stop swallowed jellyfish from escaping) and an ability to generate some of its body heat from within. (more)

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Fine Fossil Sea Turtle Skull from Cretaceous Morocco

Name: Class Reptilia; Order Chelonia; Suborder Cryptodira; Family: Cheloniidae; Lytoloma elegans

Age: Upper Cretaceous

Size (25.4mm=1 inch): 215 mm long, 175 mm wide, 70 mm tall

Location: Khouribga Plateau, Morocco

Fossil Sea Turtle Skull

Description: This is a skull from the seagoing reptile Lytoloma elegans coming from the Late Cretaceous/Early Paleocene phosphate bed deposits near Khouribga, Morocco. Examples of the relatives of these coastal and marine turtles have been found in deposits of the opening Atlantic coastline of West Africa, the interior of the Sahara, North Africa, and Western Europe. This fine specimen comes from the phosphate mine region of the Khouribga Plateau of Morocco.

click fossil pictures to enlarge

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Chelonii: Chelydridae

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Pleurodira
         |--Paracryptodira
         `--+--Protostegidae
            `--+==Xinjiangchelyidae
               `--o Centrocryptodira
                  |==Sinemydidae
                  |--Trionychoidea
                  `--+==Macrobaenidae
                     |--+--Chelonioidea
                     |  `--+--Emarginachelys
                     |     |--o Chelydroidea
                     |     |  |--o
Platysternidae
                     |     |  |  |-
-Macrocephalochelys
                     |     |  |  `-
-Platysternon
                     |     |  `--o Chelydridae
                     |     |     |-
-Protochelydra
                     |     |     `-
-Chelydrinae
                     |     `--Kinosternoidea
                     `--Testudinoidea
```

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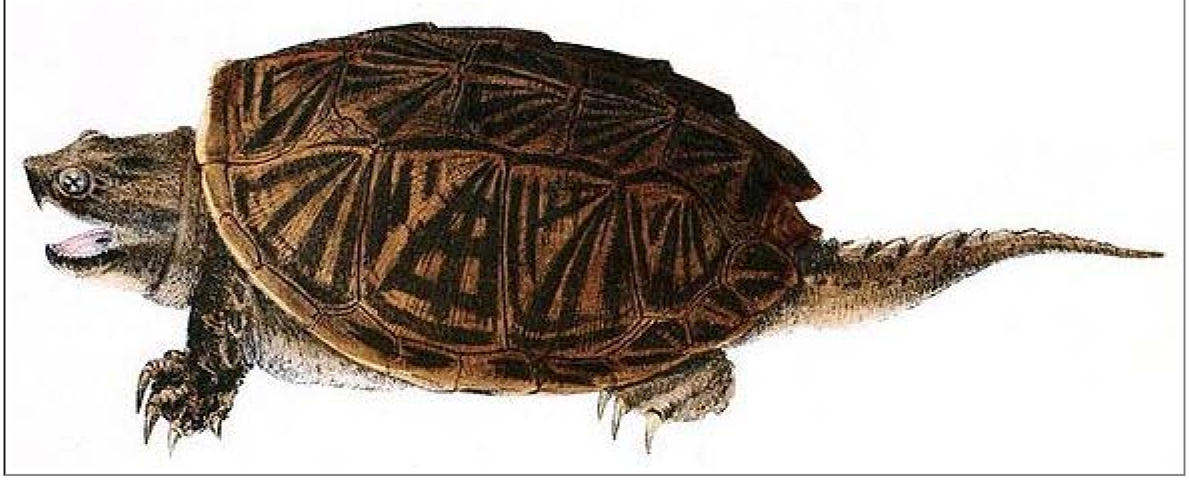
6. *Platysternon*
7. *Protochelydra* X

The Chelydrids or snapping turtles are



Common Snapping Turtle, *Chelydra serpentina*, hand-colored lithograph, John Edwards Holbrook, 1842, *North American herpetology; or, A description of the reptiles inhabiting the United States*, modified from Biodiversity Heritage Library, public domain, via Wikipedia

aquatic ambush predators known today from only two species from North and Central America, although during the Tertiary they were more widespread, ranging across Eurasia. They are distinguished by a lack of advanced characteristics (synapomorphies) which is why in the cladistic studies of Gaffney and co-workers they are placed as the most basal of extant cryptodires. Molecular phylogeny however positions them in a more derived group, along with Chelonioids (sea turtles) and Kinosternoids (mud and musk turtles).

The Asian genus big-headed turtle *Platysternon megacephalum* has been unanimously related to the Chelydridae on morphological cladistic grounds, but equally unanimously excluded on the basis of molecular phylogeny, which places it instead in the tortoises and terrapin crown group (Superfamily Testudinoidea), which makes no morphological sense (there are many similiar morphological nonsensical placements based on molecular phylogeny, e.g. turtles as crown group archosaurs, and insectrs as crown group crustacea). Although we have for the most part followed the current consensus, the premise that molecular sequencing should automatically confer a more reliable phylogenetic signal than morphology is something that has, to the present writer's knowledge, not been empirically tested. Just to be different, we decided to use a morphology-based interpretation. MAK130403

Descriptions

Chelydroidea

Range: Fr the Paleocene

Phylogeny: Chelonioidea-Chelydridae-Kinosternoidea clade **:** Panchelonioidea + (*Emarginachelys* + Kinosternoidea + * **:** Chelydridae + Platysternidae)

Comments: An informal morphology-based taxon, which may be paraphyletic or, if molecular phylogeny is any indication, polyphyletic. The Chelydroids are first known from the Paleocene. *Emarginachelys*, may belong here as well (e.g. Carroll, 1988, p.616), or it may be related to the Kinosternoid, or for that matter to both groups (which would fit with Molecular phylogeny which places the Chelydridae and Kinosternoidea close together) MAK130403

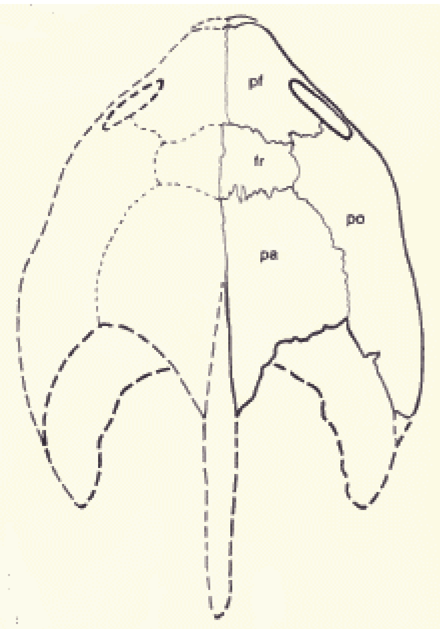
Platysternidae

Range: Paleocene to Recent

Phylogeny: Chelydroidea **:** Chelydridae + * **:** *Macrocephalochelys* + *Platysternon*

Characters: well-developed maxilla-postorbital contact (Gaffney 1975b)

Comments: The family Platysternidae contains only one living species, *Platysternon megacephalum* Gray, 1831, the big-headed turtle of South-East Asia. This species is distinguished from other freshwater turtles by its enormous head that cannot be retracted into the shell, its unusually long tail, and flat carapace (ref). Apart from *Macrocephalochelys*, whose placement here is by no means unambiguous, the only fossil representatives are a few highly fragmentary specimens from the Oligocene and Paleocene of Kazakhstan. (Joyce et al 2004 p.1005). For the controversy regarding the overall phylogenetic placement of this family, see Platysternon: comments. MAK130403



Macrocephalochelys pontica, dorsal view. Restoration from Pidoplichko and Tarashchuk (1960), via Gaffney (1975b) fig 1D, p.165. The partial nature of the specimen is evident from the dotted lines.

Macrocephalochelys pontica Piboplichko and Taraschchuk, 1960

Range: Pliocene of Ukraine

Phylogeny: Platysternidae **:** *Platysternon* + * **:**

Comments: Known from a partial skull, it was it was interpreted as a near relative of *Platysternon* by Piboplichko and Taraschchuk. Chkhikvadze (1971) placed it in the Chelydridae without *Platysternon*, while Gaffney 1975b reaffirmed Piboplichko and Taraschchuk's interpretation, placing the two taxa together in the Subtribe Platysternina. The subtribe ranking is because Gaffney follows Hennig in interpreting Linnaean ranks in terms of phylogenetic branching sequence. Because the two systems are incompatible we have restored the family Platysternidae. MAK130403

Platysternon megacephalum Gray, 1831

Range: Recent

Phylogeny: Platysternidae **:** *Macrocephalochelys* + * **:**

Comments: The Asian big-headed turtle. The phylogenetic placement of this species is highly controversial, and represents a major incongruency between morphology-based cladistics and testudine molecular phylogeny.

Platysternon megacephalum. Photo from the European Freshwater Turtle Breeders Association.

Hennigian morphological studies interpret *Platysternon* as a derived (Gaffney 1975b, Gaffney & Meylan 1988) taxon within the Chelydridae. The recent statistical parsimony cladistic analysis of Joyce 2007 resolves *P. megacephalum* as related to both testudinoids and trionychoids, whereas the still more recent analysis of Anquetin, 2009, which incorporates Joyce's data, instead unambiguously places *Platysternon* as the sister group of panchelydrids (Anquetin, 2009 p.203).

Early molecular sequencing results recovered a sister group relationship between *Platysternon megacephalum* and the Testudinoidea does have some precedent, and this led Joyce et al 2004 to revive the old taxon Cryptoderinea. The Cryptoderinea was named by Vaillant (1894), who united *Platysternon* and Testudinoids based on the unique arrangement of the articular surfaces on their cervical vertebrae. Williams (1950) reached the same conclusion in his comprehensive review of turtle cervical vertebrae. Joyce et al 2004 therefore selected the Cryptoderinea Vaillant, 1894 as the crown clade arising from the last common ancestor of *Platysternon* and the Testudinoidea, with Pancryptoderinea as the stem-group (Joyce et al 2004 p.1004-5).

However greater refinement of molecular sequencing nested *Platysternon* in the crown Testudinoidea as sister taxon to the Emydidae (Barley et al 2010, Thomson & Shaffer 2010, Guillon et al 2012), a placement that makes no morphological sense at all, at least as far as recent taxa go. Interestingly, the problematic fossil testudine *Acherontemys* from the Miocene of North America may have features of both groups, as it was assigned to Chelydridae by Hay and to Emydidae by Hutchison (1992).

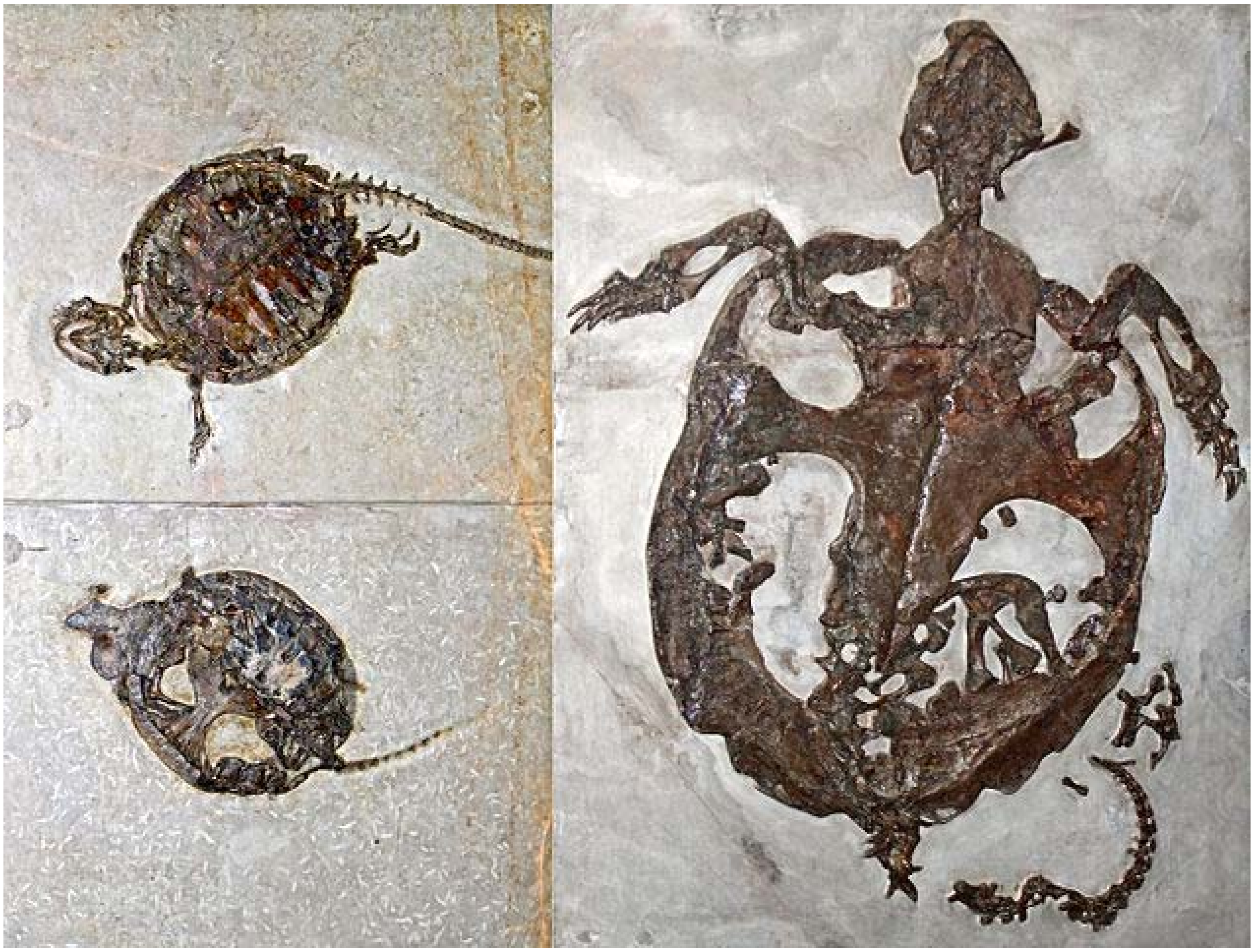
Even so, it seems that the current paradigm requires that whenever there is a lack of agreement between morphological and molecular phylogenies, the latter must automatically be preferred, despite the two being equally robust, and for this reason *Platysternon* (and the monotypal family Platysternidea) are now unanimous placed it in the superfamily Testudinoidea. Without additional methodologies or total evidence it is difficult to go beyond this gridlock. Unfortunately to date there has been no combined approach beyond the early work of Shaffer et al. 1997 and the rather surreal tree of Sterli 2010 (which nests Pleurodires in Crown Cryptodira). Another hypothesis, which would conflict both morphologicak and molecular analyses, is that *Platysternon* is a transitional form between the Chelydridae and the Testudinoidea. For now we have followed Anquetin, 2009. MAK130305

Chelydridae = Panchelydridae Joyce et al. 2004

Range: Fr the Paleocene

Phylogeny: Chelydroidea : Platysternidae + * : *Protochelydra* + Chelydrinae

Characters: medial contact of abdominal scales absent; anal scales overlap medially onto hypoplastra (Anquetin, 2009 p.203)



Chelydropsis murchisoni, Chelydridae; left: juvenile (plate and counter plate), right: adult; Miocene, Öhningen layers, Öhningen, Germany; Staatliches Museum für Naturkunde Karlsruhe, Germany. Photo by H. Zell, GNU Free Documentation/Creative Commons Attribution license; via Wikipedia.

Comments: The American snapping turtles. As with the morphologically very similar but genomically distinct Asian genus *Platysternon*, the phylogenetic position of this group is quite uncertain, although this ambiguity goes for chelonii in general. Hennigian morphologists (e.g. Gaffney et al 1991; Gaffney, 1996) consider the Chelydridae the most primitive extant cryptrodires, computational cladistics (e.g. Joyce 2007, Danilov & Parham, 2008, Anquetin, 2009) makes it the second most basal after the Chelonoidea, and molecular phylogenists (e.g. Krenz et al 2005, Barley et al. 2010) placed in a Kinosternid-Chelydrid-Chelonioid clade, and sometimes within that clade as sister group to the Kinosternids, MAK110922

Protochelydra zangerli

Range: Late Paleocene of North Dakota

Phylogeny: Chelydridae **:** Chelydrinae + *

Characters: "Chelydrid turtles having a relatively larger jugal and greater posterodorsal and cheek emargination than in Chelydrinae; triturating surfaces of skull relatively wide in comparison to most Chelydrinae; posteriorly directed ridge on ventral surface of pterygoid present; plastron cruciform, as in Chelydra and Macroclemys, but apparently lacking median fontanelles." (Gaffney 1975b)

Comments: The earliest known chelydrid. Its carapace is higher domed than the Recent *Chelydra*, perhaps as a defense against chelonivorous (i.e., turtle-eating) crocodilians (Jehle, 2006). Gaffney (1975b) places it in its own subfamily, the Protochelydrinae, MAK130306

A common snapping turtle, *Chelydra serpentina*, photographed at Taum Sauk Mountain State Park. Photo by Dakota L., Creative Commons Attribution license, via Wikipedia

Chelydrinae Chelydra serpentina + Macrochelys temminckii)

Range: Fr the Oligocene

Phylogeny: Chelydridae **:** *Protochelydra* + *

Characters: retention of a central plastral fontanelle in adult individuals Anquetin, 2009 p.203)

Comments: The Chelydridae or snapping turtles of the family are aquatic ambush predators with large heads, thick hooked beak and strong jaws and long scaly tails. There are two extant species: *Chelydra serpentina*, the Common Snapping Turtle, and its larger relative *Macrochelys temminckii*, the Alligator Snapping Turtle, both endemic to the Western Hemisphere (North and Central America). The latter genus is famous for lying in ambush open-mouthed, attracting fish with its moving worm-like tongue until the heavy jaws rapidly close on its prey. Chelydrids are the only group that can retract the head with jaws wide open. They are are slow swimmers, and feed on plants, carrion, or anything that moves. About 20 to 40 spherical eggs are laid. As with many aquatic turtles there is a reduction of the heavy shell; in this case the plastron is connected to the carapace by ligament rather than heavy bone (Refs: Wikipedia Family Chelydridae @ itech.pjc.edu (no longer online)).

There are a number of fossil forms, although no cladistic analysis has been done to determine their phylogeny. *Chelydropsis*, contains several well known Eurasian chelydrid species that existed from the Oligocene to the Pliocene. (refs, Wikipedia). The extant genera *Chelydra* and *Macrochelys* are reported from the Oligocene and Miocene respectively (Carroll, 1988, p.616). On the basis of morphological analysis of features of the skull, Gaffney (1975b) considers *Macrochelys* closer to *Platysternon* than to *Chelydra*, placing the foremer two in Tribe Platysternini andthe latter in Tribe Chelydrini. MAK110922 130306

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Chelonii: Kinosternoidea

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Pleurodira
         |--Paracryptodira
         `--+--Protostegidae
            `--+==Xinjiangchelyidae
               `--o Centrocryptodira
                  |==Sinemydidae
                  |--Trionychoidea
                  `--+--+--Chelonioidea
                     |   `--+--Chelydridae
                     |      |--Emarginachelys
                     |      `--o Kinosternoidea
                     |         |-
-Dermatemydidae
                     |         `--o Kinosternia
                     |            |--Agomphus
                     |            |-
-Hoplochelys
                     |            `--o
Kinosternidae
                     |               |-
-Kinosterninae
                     |               `-
-Staurotypinae
                     `--Testudinoidea
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7. Kinosterninae
8. Kinosternoidea
9. Staurotypinae

Descriptions

Emarginachelys cretacea

Phylogeny: Chelonioidea-Chelydridae-Kinosternoidea clade **:** Panchelonioidea + (Chelydridae + Kinosternoidea + *)

Range: Late Cretaceous of NA (Maastrichtian of Montana)

Comments: Despite being known from good fossil material, this Cretaceous form is difficult to place phylogenetically. It has been included under the Chelydridae (Carroll 1988, p.616), as a sister taxon to the Kinosternoidea (Joyce 2007), and as sister taxon to a clade uniting Kinosternoidea, Trionychoidea, Testudinoidea, with (Kinosternoidea + Trionychoidea + Testudinoidea) + *Emarginachelys* being the sister clade of Chelydridae (Sterli 2010 fig 1). Until something better comes along we are following Joyce's 2007 study and tentatively placing *Emarginachelys* as stem-Kinosternoidea. Another interpretation could be as part of an unresolved trichotomy in the molecular phylogeny clade uniting Chelydridae and Kinosternoidea MAK130306

Kinosternon cruentatum, photograph by Zippo Zimmermann. via CKT

Kinosternoidea

Range: From the Late Cretaceous

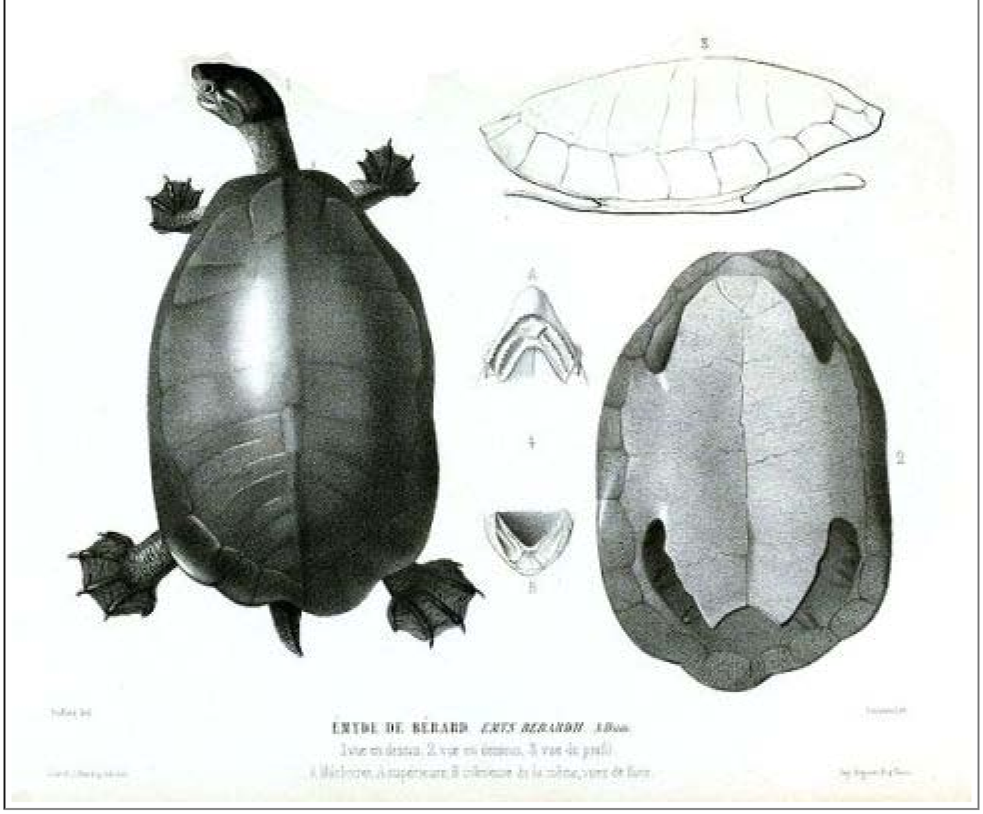
Phylogeny: Chelonioidea-Chelydridae-Kinosternoidea clade **:** Panchelonioidea + (Chelydridae + *Emarginachelys* + * **:** Dermatemydidae + Kinosternia)

Characters: scale set 2 (extragulars) lost from plastron (Hutchison and Bramble, 1981); scale set 4 (pectorals) lost from plastron (Hutchison and Bramble, 1981); no scales on skull roof (Meylan & Gaffney, 1989)

Comments: According to morphological analysis the Kinosternoidea are the sister group to the Trionychoidea. Molecular sequencing however places them with the Chelydridae and Chelonioidea, slightly in closer to the former. There is better consensus regarding the sister group relationship between the Dermatemydids and Kinosternids, which is strong supported by both morphological and molecular data. Corresponds to Kinosternoidae of Gaffney & Meylan 1988 and the Pankinosternoidea of Joyce et al 2004 p.1003). MAK130306

Dermatemydidae *Baptemys*, *Dermatemys* (= Pandermatemys)

Range: Late Cretaceous or Eocene to Recent



Dermatemys mawii, drawing from *Archive du Museum D'Histoire Naturelle*. Tome 6, Public Domain, via Wikipedia

Phylogeny: Kinosternoidea : Kinosternia + *

Characters: commissural ridge on triturating surface; foramen stapedio-temporalis closed; axillary buttresses reach costal bones (Meylan & Gaffney, 1989)

Comments: Represented today only by the now rare and critically endangered Central American river turtle *Dermatemys mawii*. This is a a nocturnal, aquatic species that lives in larger rivers and lakes in Central America, from southern Mexico to northern Honduras. Dermatemys is a fairly large turtle, attaining a maximum size of 65 cm in carapace length, and weight up to 22 kg (Wikipedia). Various fossil forms, including the Adocids (now placed in the Trionychoidae), have been assigned to or related to the Dermatemydidae, with Dermatemydids proper dating back to Cretaceous. The tendency among current, cladistic, workers is to reject earlier taxa based only on plesiomorphic (shared primitive) characters. This is not to say that some of these Cretaceous forms might not be ancestral or stem dermatemydids, only that there status cannot be verified. Some fossil species included in the Dermatemydidae may be placed in the phylogenetic stem of Kinosternoidea. Currently only *Baptemys* from the Eocene of North American is included among the early fossil forms; with the well-known type species *Baptemys wyomingensis* used in cladistic analysis (Joyce et al 2004 p.1003)

Kinosternia

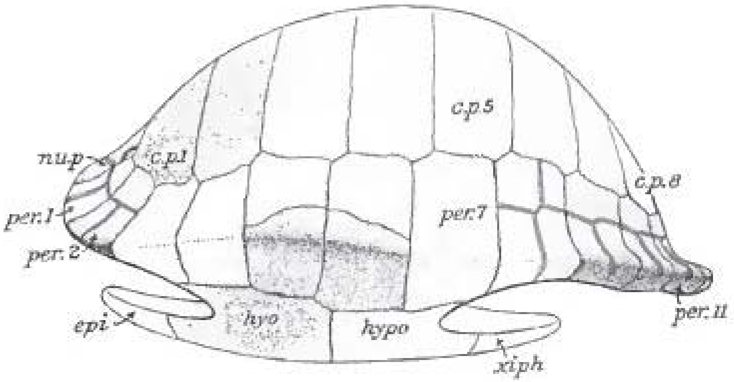
Range: From the Late Cretaceous

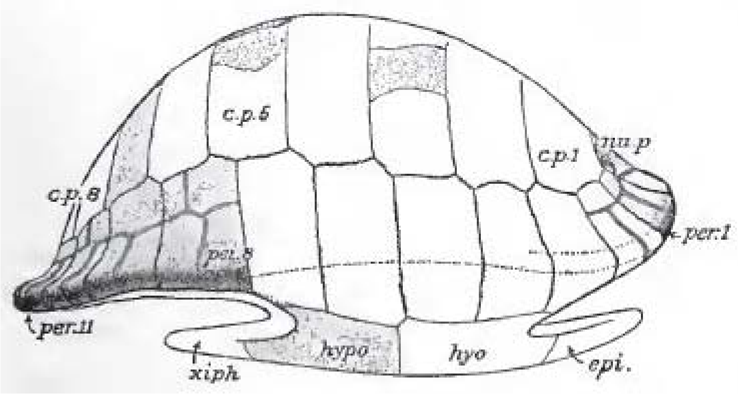
Phylogeny: Kinosternoidea **:** Dermatemydidae + * **:** *Agomphus* + *Hoplochelys* + Kinosternidae)

Characters: no more than three inframarginal scales present on each bridge (occurs also in *Basilemys*) (Meylan & Gaffney, 1989)

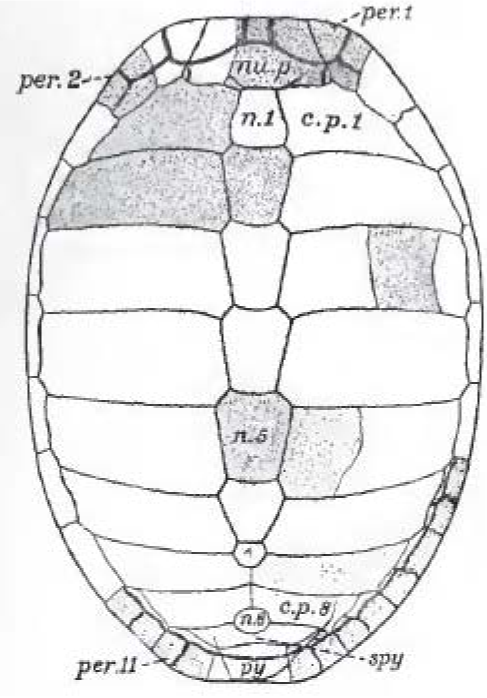
Comments: Includes Kinosternidae and several basal forms (Gaffney and Meylan, 1988; Joyce et al., 2004).

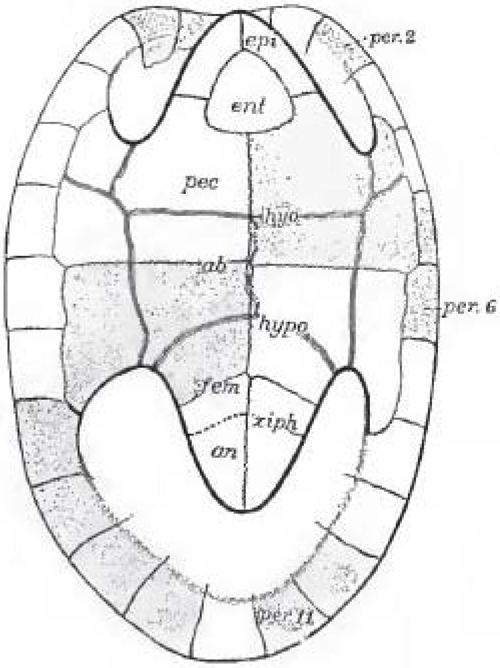
Agomphus tardus Wieland 1905 = *Agomphus turgidus* Cope 1869. Late Cretaceous of New Jersey, The highly domed, tortoise-like form of the carapace shows that this was one of the few land turtles of that time. Carapace of type; length 33 cm, breadth, 23 cm, Above: seen from left side; middle, seen from right side. c.p.1, etc, costal plates; epi,





epiplastron; hyo, hyoplastron; hypo, hypoplastron; nu.p., nuchal plate; per.1, per.2, etc., peripheral bones; xiph, xiphiplastron.. Below, left: Carapace, seen from above, c.p.1, c.p.8, costal plates; n.1, n.8, neural bones; nu.p, nuchal bone; per.1, per.11, peripheral bones; py, pygal; spy. suprapygal. Below, right: Plastron of type, ab, abdominal scute; an, anal scute; epi, epiplastron; ent, entoplastron; fem, femoral scute; hyo, hyoplastron; hypo, hypoplastron; pec, pectoral scute; per.1, per.6, per.12, peripheral bones; Xiph, xiphiplastron. From Hay (1908) p.252-3, figs 315-8; public domain (copyright expired).





Agomphus

Range: Late Cretaceous to Paleocene of North America

Phylogeny: Kinosternia **:** *Hoplochelys* + Kinosternidae + *

Description: Shell thick and heavy. Free borders of the carapace thickened and obtuse. Exposed surfaces of the shell not pitted. Hinder marginal scutes not rising on the costal bones, except slightly in one species. Inframarginal scutes present. The pectoral scutes extending forward to the hinder end of the epiplastrals. Intergulars not known. Nuchal with costiform processes. Rib-heads more strongly developt than in *Adocus*. Hay (1908) p.248.

Comments: Previously included in the Dermatemydidae (Mlynarski 1976, p.63), *Agomphus* is now considered a relative of the mud turtles (Kinosternidae). This was probably a terrestrial genus. It is known only from its fossil shells, which are about 30cm long. Like true tortoises, the shell of *Agomphus* is oval in shape, highly domed and smooth, implying similar habits (Jehle, 2006), Like many reptile and lissamphibian taxa, it crossed the Cretaceous-

Paleocene boundary without harm.

Hoplochelys crassa (Cope 1888)

Range: Paleocene

Phylogeny: Kinosternia **:** *Agomphus* + Kinosternidae + *

Description: Shell thick and solid. Peripherals united to the plastral bones by means of digitations and dentated sutures; with the costals by gomphosis and in addition by simple apposition or sutures. Carapace furnisht above with three carinas. Plastron with anterior lobe immovable and with the posterior lobe narrow. - Hay (1908) p.263,

Comments: Cope assigned this species to the genus *Chelydra*. Hay (1908) erected the new genus *Hoplochelys* and placed it in the Dermatemydidae, where it was still asigned by (Carroll 1988, p.615). Now considered a stem Kinosternid (Joyce et al 2004 p.1003)

Kinosternidae

Range: Late Cretaceous (Campanian) to Recent of North and South America

Phylogeny: Kinosternia **:** *Agomphus* + *Hoplochelys* + * **:** Kinosterninae + Staurotypinae

Characters: (from Gaffney & Meylan 1988): Ten pairs of peripherals; abdominal scales absent; no ribs connecting ninth and tenth vertebrae to eight costal; frontal not reaching orbit; maxilla contacting quadratojugal; ilio-ischial notch in acetabulum; incised anterior musk duct. CKT

Comments: The Kinosternidae of North and South America include the musk turtles, so called because of their production of a foul-smelling substance from glands under the tail when disturbed. CKT Also called mud turtles, they are slow swimmers, with a double-hinged plastron; reduced plastron in musk turtles (rely on jaws for defense) for agility, can climb trees. ref There are 25 living species and 4 extant genera, placed in two subfamilies, the Kinosterninae and Staurotypinae. The oldest known stem-fossil attributed to this group are undescribed remains from the Late Cretaceous (Campanian) of North America. *Baltemys*, from the Eocene, and *Xenochelys* from the Eocene to Oligocene (Carroll 1988, p.615), belong to the crown Kinosternidae. (Joyce et al 2004 p.1003). As both are known from North America it is likely that is the geographic origin of the group MAK130306

Kinosterninae

Range: Eocene to Recent of North and South America

Phylogeny: Kinosternidae **:** Staurotypinae + *

Comments: The oldest fossil forms are *Baltemys staurogastros*, from the Eocene, and *Xenochelys formosa* Hay 1906 from the Oligocene of South Dakota (considered Staurotypinae by Mlynarski 1976, p.68).

Staurotypinae

Range: Recent of North and Central America

Phylogeny: Kinosternidae **:** *Agomphus* + *Hoplochelys* + *

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Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Meiolanoidea
         `--+--Pleurodira
            |--Paracryptodira
            `--+--Protostegidae
               `--+--Angolachelonia
                  `--+==Xinjiangchelyidae
                     `--o Centrocryptodira
                        |==Sinemydidae
                        |--Trionychoidea
                        `--+--+--Chelonioidea
                           |  `--+-
-Chelydridae
                           |      `-
-Kinosternoidea
                           `--o Testudinoidea

|==Lindholmemydidae incl. Mongolemys
                              `--+-Emydidae
                                 `--o
Testudinoidae
                                    |-
-Echmatemys
                                    `--+-
-Geoemydidae
                                       `-
-Testudinidae
```

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2. Emydidae
3. Geoemydidae
4. Lindholmemydidae X
5. *Mongolemys* X
6. Testudinoidae
7. Testudinoidea

The Testudinoidea are the largest living group of testudines, and include a variety of both semi-aquatic and fully terrestrial types. Evolving from semi-aquatic ancestors during the late Cretaceous, the true tortoises are among the few groups of testudines that adopted a fully terrestrial lifestyle. By the early Cenozoic they were common in North America, Europe, Asia, and Africa. For some reason, they didn't make it to South America or Australia, where Pleurodires and Meiolaniids predominated instead. Like the Meiolaniids, they evolved a number of distinct island dwelling forms.

Descriptions

Testudinoidea = Pantestudinoidea of Joyce et al 2004

Range: Cretaceous to Recent

Phylogeny: Centrocryptodira or Durocryptodira **:** Sinemydidae + ((Macrobaenidae + Chelonioidea-Chelydridae-Kinosternoidea clade) + * **:** *Mongolemys* + (Emydidae + Testudinoidae))

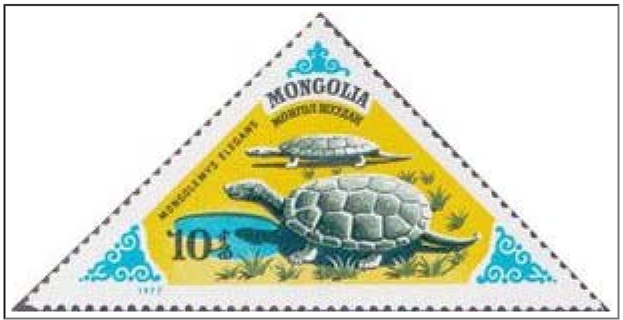
Characters: "Skull without parieto-squamosal arch, and squamosal separated from postorbitofrontal,with a fortune it palatinum between the palatine and maxilla. Articular fenestrae in the sixth and seventh cervical vertebrae not plane, and two of the cervicals biconvex. Nuchal without well-developed costiform processes ; series of inframarginals incomplete." - Zittel, Eastman, et al (1932) p. 202

Comments: The superfamily Testudinoidea is the most speciose of the testudines, including the true tortoises and most fresh-water and semi-aquatic turtles

Included here are three major crown clades, Testudinidae, Emydidae, and Bataguridae, along with a number of fossil taxa from the Cretaceous of Asia, such as *Lindholmemys* and *Mongolemys* (Joyce et al 2004 p.1005), which are placed in the paraphyletic family Lindholmemydidae. Two other poorly known Asian Cretaceous families, the Haichemydidae and the Sinochelyidae, may or may not belong here.

Molecular sequencing unambiguously nests the Asian genus big-headed turtle *Platysternon megacephalum* within crown Testudinoidea. Morphological cladistic analysis, equally unambiguously places it in or near the Chelydridae. There being no resolution for this disagreement between equally robust but conflicting phylogenetic hypotheses, we have for now retained *Platysternon* among the chelydrids

Although molecular dating indicates a Latest Cretaceous age (Campanian-Maastrichtian) (ref) or 95.0 Mya Lourenço et al 2012 for the radiation of modern testudinoids, the latter date being coeval with the larger Durocryptodire radiation event, this dating may not be reliable (consider the overestimation ofd age with placental mammals), as no fossils are known earlier than the Late Palaeocene, and the group only became well established by the early Eocene, where it is represented by the geoemydids *Paleoemys* and *Merovemys* and the testudinids *Hadrianus* and *Achilemys*. Conversely, the divergence of higher testudinoid clades may be found within the paraphyletic Lindholmemydidae, in which case inframarginal scutes, a character that distingusihes Lindholmemydids from modern testudinoids, were reduced or lost independently in extant families (Lourenço et al 2012 p.502) MAK130307



Commemorative stamp featuring *Mongolemys elegans*

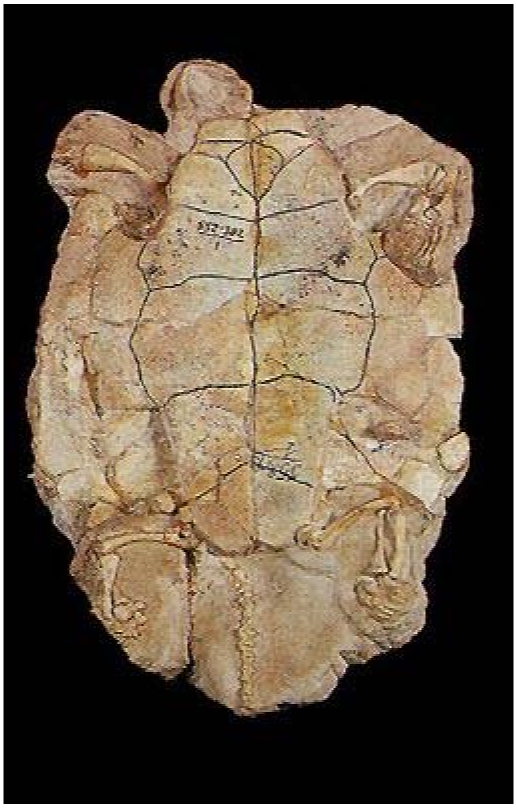
Mongolemys elegans Khosatzky and Mlynarski, 1971

Horizon: Nemegt Formation, Latest Cretaceous (Early Maastrichtian) of Mongolia

Phylogeny: **:** + *

Comments: *Mongolemys elegans* It is the best known of the Lindholmemydidae, a diverse and almost certainly paraphyletic assemblage of otherwise poorly known Mid Cretaceous to Paleocene stem-testudinoids. Known from abundant specimens at all stages of growth from Latest Cretaceous pond deposits from Mongolia, bone histology shows similar patterns of thickness and bone tissue type as freshwater turtles. (Cadena et al 2013). It was originally initially assigned to Dermatemydidae by Khosatzky and Mlynarski (1971) based on similarities of this fossil to Central American river turtle *Dermatemys mawii*, but these are more plesiomorphic features and the result of convergences due to shared lifestyle. Morphological computational analysis unambiguosly places *M. elegans* as a stem testudinoid (Cadena et al 2013).

The Lindholmemydidae represent a paraphyletic assemblage, either of stem forms or early representatives of extant groups (Lourenço et al 2012) or both. They are defined by the presence of inframarginal scutes, a feature lost in modern Testudinoidea Genera such as *Lindholmemys* and *Mongolemys* have been placed within 'Testudinoidea' primarily because of the development of an ossified bridge connecting the plastron with the carapace (Joyce et al 2004 p.1005).



Mongolemys elegans skeleton and carapace, from The Russian Dinosaur Exposition, original url. Also at Mathematical com

Lindholmemydids first appears in the mid Cretaceous. *Mongolemys occidentalis* from the Late Albian or early Cenomanian of Uzbekistan was reassigned to the separate genus *Khodzhakulemys*, and represents the oldest well-known testudinoid occurence, and so can be used for constraining the age of the divergence of testudinoids and chelonioids. Lourenço et al 2012. *Tsaotanemys* is tentatively from the ?Albian of China so it can be considered a similar age. Purported stem testudinoid material has been been reported from the Early Cretaceous Kuwajima formation (Barremian-Aptian) of Japan (Hirayama, 2000), but this was not described in detail, and as no diagnostic characters were listed it is not possible to assess this claim cladistically.

Other Lindholmemydids include *Paragravemys* from the Cenomanian-early Turonian of Mongolia, *Lindholmemys* from the Turonian to early Campanian of Middle Asia and Kazakhstan, *Hongilemys* from the Turonian-Campanian of Mongolia, *Gravemys* from the Maastrichtian of Mongolia (a contemporary of *Mongolemys*), and Amuremys from the Maastrichtian of the Amur River (Russia-China border), and *Hokouchelys* and *Elkemys* from the Paleocene of China. (Cadena et al 2013).

Elkemys australis is similar to *Gravemys barsboldi*. Those two species and *Hokouchelys chenshuensis* from the Paleocene of China differ from other lindholmemydids and testudinoids in their unique inframarginal pattern (four or five pairs of wide inframarginal scutes which strongly extend on to peripherals), and may form a clade or grade of basal testudinoids. Other characters (large anal notch and relatively narrow vertebrals 2 and 3) are shared by some geoemydids and testudinids and may indicate closer relations of the three mentioned genera to these groups. (Danilov et al 2012 p.21)

New material also reveals a previously unrecognized cranial similarity between *M. elegans* and geoemydid testudinoids: contact between the quadrate and the parietal, which are well exposed dorsally at the roof of the otic chamber and encapsulate the foramen stapedius temporalis. In other testudinoids, the prootic bone generally prevents contact between the parietal and quadrate at the dorsal roof of the otic chamber, which implies this feature may be convergently acquired. (Cadena et al 2013 p.21) MAK130303

Emydidae Rafinesque, 1815 : terrapins, and box, pond and river turtles,

Range: Paleocene to Recent

Phylogeny: Testudinoidea : Testudinoidae + *

Characters: (from Gaffney & Meylan 1988): Batagurine process absent, no pterygoid-basioccipital contact; angular usually reaching Meckel's cartilage; double articulation of fifth and sixth cervical; chromosome number 2n = 50. (via CKT)


The European pond turtle *Emys orbicularis*, one of the few emydids found outside the Americas. Photo by Nicola Maraspini. (via CKT)

Comments: The Emydidae are a diverse group, which together with Eurasian terrapins make up the largest group of extant chelonians. They include mostly aquatic tortoises, although some are semi-aquatic or terrestrial. All are omnivores. The feet usually have webbing between toes and claws. All of the 12 genera and 46 extant species are found today in the western hemisphere, with the exception of *Emys orbicularis* in Europe and western Asia. The family includes the red-eared slider *Trachemys scripta* which has, thanks to the pet trade, reversed the grim fate facing many extant testudine species by becoming an invasive species in many parts of the world. (CKT, Study notes)

Both morphololological-cladistic (Gaffney & Meylan 1988) and molecular studies (Iverson et al 2007, Thomson & Shaffer 2010, Guillon et al 2012) divide this family into two main clades, the Emydinae (with the genera *Clemmys*, *Emys*, *Terrapene*, and according to molecular sequencing *Glyptemys*) and Deirochelyinae (with the genra *Chrysemys*, *Deirochelys*, *Graptemys*, *Malaclemmys*, *Pseudemys*, and *Trachemys*).

A number of fossil forms have been associated with the group. They were most varied during the Paleocene in Asia, and it is likely this continent their probable site of origin. Late Paleocene emydids from Asia include *Anhuichelys*, *Hokouchelys* and *Pseudochrysemys*. In North America at this time they are known from a single unnamed large headed genus (known informally as "Emydid C") that appears in the Middle Paleocene and is the most common turtle of this region in the Late Paleocene. This jaws of this species have simple triturating surfaces, which suggest a mixed diet Jehle, 2006. To date, none of these early fossil forms have been integrated into a cladistic analysis (Joyce et al 2004 p.1006). Perhaps a more unambiguous fisrt record of oldest crown emydid is "*Chrysemys*" *antiqua* from the Latest Eocene Chadronian of South Dakota (Hutchison, 1996, via Lourenço et al 2012 p.505

There were also a number of other forms of uncertain phylogenetic position, such as for example *Broilia*, from the Oligocene of France, which was assigned to Emydidae by Carroll (1988). This large genus, with a 75cm long shell, had cartillaginous attachments connecting the plastron to the carapace, providing a very flexible link on both sides. These animals had somewhat domed shells which implies a semi or fully terrestrial lifestyle. ref

Indian pond turtles *Melanochelys trijuga* (subfamily Geoemydinae), photographed by Manoj Sindagi.

Testudinoidae

Synonym: Testuguria

Range: Fr the Late Palaeocene

Phylogeny: Testudinoidea **:** Emydidae + * **:** *Echmatemys* + (Batagurinae + (Geoemydinae + Testudinidae))

Characters: (from Gaffney & Meylan 1988): (Including *Echmatemys*) Axillary and inguinal musk duct foramina enclosed within peripheral plates or between peripherals and plastral buttresses. (Excluding Echmatemys) Sixth marginal scute often reaching third pleural scute; postorbital-squamosal contact absent. (CKT)

Comments: Testudinoidae, not to be confused with Testudinoidea, is a proposed clade uniting the land tortoises of the Testudinidae with the Asian pond turtles of the 'Bataguridae'. Although it is agreed that the Testudinidae and Bataguridae/Geoemydidae share a close phylogenetic relationship he monophyly of this clade is unsettled, as proposed synapomorphies are also found in other testudinates, and are not universal within testudinoidaens. (Gaffney & Meylan 1988). (CKT). They may be sister taxa (Gaffney 1979) or the batagurids may be paraphyletic with regard to testudinids (Hirayama 1984; Gaffney & Meylan 1988). Molecular phylogeny however unambiguously distinguishes the Testudinoidae from the Emydidae + Platysternidae (ref, ref, ref Lourenço et al 2012).

Echmatemys Hay 1906

Range: Eocene of North America and West Asia

Phylogeny: Testudinoidae **:** (Batagurinae + (Geoemydinae + Testudinidae)) + *

Comments: A stem Batagurid known from several species, its exact phylogenetic position is unclear (Joyce et al 2004 p.1006). It is tentatively placed here as a stem Testudinoid. A medium-sized testudine with a shell 30 to 45 cm long, depending on the species (Mlynarski 1976, p.88), MAK130306

Geoemydidae Theobald, 1868 **:** Asian river turtles, Asian leaf turtles, Asian box turtles and roofed turtles


Female Chinese striped-neck turtle *Ocadia sinensis*, photographed by Tim McCormack.

Synonym: Batagurina Gray 1869, Bataguridae Gray 1870; Panbataguridae Joyce et al 2004

Range: Early Eocene to Recent

Phylogeny: Testudinoidae **:** + *

Characters: (from Gaffney & Meylan 1988): Fissura ethmoidalis oval and broad; frontals sometimes excluded from orbital rim by prefrontal-postorbital contact; foramen palatinum posterius small, excluded from pterygoid. - CKT

Comments: The Geoemydidae, or Bataguridae as they are also called (the two names being used sysnonymously in different scientific papers, although Geoemydidae has priority) include the Asian river, leaf, roofed or Asian box turtles. There are 24 extant genera and 62 extant species, making up a significant proportion of the species of extant turtles. The demands of the food and pet trade has meant that many species are now endangered, some critically.

According to cladistic studies (Gaffney & Meylan 1988), the family Geoemydidae or Bataguridae is paraphyletic assemblage that gave rise to, and hence according to cladistic formalism includes, the Testudinidae. See dendrogram by CKT here and here. But according to molecular studies this is an unambiguously monophyletic group. Several subfamilies have been posited, such as Batagurinae and Geoemydinae, but they seem to have neither cladistic nor molecular support.

Determining the molecular phylogeny of the geoemydid turtles is difficult due to their propensity to hybridize, even between unrelated genera such as Sacalia and Cuora. Regardless of whether or not this is the case in wild populations, human husbandry and transport in the food and pet trades, and hence opportunity for genetic contamination through escape and hybridization, complicate efforts to understand the evolution of this group, and identify valid species (Iverson et al 2007 p.94)

A number of primitive fossil forms have been interpreted as stem taxa but the phylogenetic relationships of most of these relative to the extant species remain unclear. (Joyce et al 2004 p.1006). *Paleoemys* and *Merovemys* from the Early Ypresian of France mark the oldest known occurrences of crown Geoemydidae (Lourenço et al 2012 p.505)

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Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Meiolanoidea
         `--+--Pleurodira
            |--Paracryptodira
            `--+--Protostegidae
               `--+--Angolachelonia
                  `--+==Xinjiangchelyidae
                     `--o Centrocryptodira
                        |==Sinemydidae
                        |--Trionychoidea
                        `--+--+--Chelonioidea
                           |   `--+-
-Chelydridae
                           |      `-
-Kinosternoidea
                           `--o Testudinoidea

|==Lindholmemydidae
                              `--+-Emydidae
                                 `--+-
-Geoemydidae
                                    `--o
Testudinidae
                                       |-
-Hadrianus
                                       `--+--o
Xerobatinae
                                          |  |-
-Manouria
                                          |  `-
-+--Stylemys
                                          |
`--+--Gopherus
                                          |
`--Hesperotestudo
                                          `--o
Testudininae
                                             |-
-Testudinini
                                             `-
-Megalochelyini
```

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3. *Hesperotestudo* X
4. *Manouria*
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6. *Stylemys* X

7. Testudinidae
8. Testudininae
9. Testudinini
10. Xerobatinae

Tortoise Resurrection

By Christopher Taylor

> In a subsequent portion of this narrative I shall have frequent occasion to mention this species of tortoise. It is found principally, as most of my readers may know, in the group of islands known as the Gallipagos... They are frequently found of an enormous size... They can exist without food for an almost incredible length of time, instances having been known wher they have been thrown into the hold of a vessel and lain two years without nourishment of any kind - being as fat, and, in every respect, in as good order at the expiration of that time as when they were first put in... They are excellent and highly nutritious food, and have, no doubt, been the means of preserving the lives of thousands of seamen employed in the whale-fishery and other pursuits in the Pacific.

--Edgar Allen Poe, The Narrative of Arthur Gordon Pym of Nantucket

For sailors in tropical oceans before the invention of refrigeration, keeping supplies of food was a serious issue. It was a permanent challenge to keep supplies fresh and edible, and indeed, much of the time stores failed at both. Under such conditions, the giant tortoises of the Galapagos islands and the Mascarenes and other islands in the Indian Ocean would have been seen as nothing short of miraculous. Tortoises could be captured easily and kept in the hold of a boat for extended periods without feeding, only slaughtered when they were actually required for eating. As a result, ships that were in a position to do so often took on tortoises in large number, and Charles Darwin apparently recorded single vessels taking up to 700 individuals at a time. By modern standards the idea of seven hundred starving tortoises crammed into a single hull seems unthinkably cruel, but doubtless the sailors who otherwise faced another six months of decomposing ship's biscuit saw things differently.

Unfortunately, such intense harvesting took an inevitable toll. Tortoise numbers declined rapidly, and many went extinct. Honneger (1981) lists three extinct species of tortoise from the Galapagos (including *Geochelone abingdoni* from Pinta island, which only survived in the form of a single captive male) and at least six extinctions from the Seychelles and Mascarenes. Extinct populations on the Galapagos islands of Rabida and Santa Fe may have represented further undescribed species.

Geochelone becki, the Volcano Wolf tortoise. Photo by Joe Flanagan.

However, a paper published in the Proceedings of the National Academy of Sciences adds a remarkable coda to the history of one of the "extinct" species, the Floreana tortoise *Geochelone elephantopus*. Using DNA extracted from museum specimens collected on Floreana before the population disappeared, Poulakakis et al. (2008) have demonstrated that *G. elephantopus* may not be quite as extinct as previously thought. Instead, anomalous genetic haplotypes previously identified in some living individuals of Geochelone becki, a species found on the Volcano Wolf at the northern end of Isabela, the largest island in the Galapagos, indicate descent from *G. elephantopus*. These individuals would appear to be descendants of past hybridisations between native Volcano Wolf tortoises and introduced Floreana tortoises.

Such a situation is quite believable. As a result of the widespread transport of tortoises for food, many tortoises ended up on islands to which they were not native*. Tortoises were regularly imported to Réunion in the Mascarenes after the native population became extinct. Living populations of giant tortoises on the Granitic Islands of the Seychelles probably descend from imports from Aldabra rather than representing the species originally found there (Honegger, 1981). According to Poulakakis et al. (2008), some 40% of the Volcano Wolf tortoises tested showed evidence of Floreana ancestry, so the genetic legacy of *Geochelone elephantopus* is alive and well, at least in hybrid form.

*Potentially a serious issue for taxonomy, as researchers cannot assume that species names based on inadequate type material necessarily represent the species native to the island the type was collected on. Honegger (1981), for instance, cast doubt on whether Geochelone gouffei, known from a single specimen found on Farquhar Island in the Seychelles, actually originated there.

This still leaves a significant problem - most conservation policies do not cope well with hybrids. A number of species worldwide, such as the black stilt (*Himantopus novaezelandiae*) in New Zealand, are regarded as endangered because of the risk of hybridisation with related species. The red wolf (*Canis rufus*) and the Florida panther (*Puma concolor coryi*) represent two 'endangered' taxa in the United States for which the suggestion that their histories could have been compromised by hybridisation led to the suggestion that they should be abandoned as worthwhile conservation targets. However, the disappearance or decline of a species in its pure form due to hybridisation with another species is a different proposition from its decline due to replacement by that species. The genetic legacy of the declining species may still persist. Overemphasis on species "purity" may actually hinder the conservation of endangered taxa, especially if natural hybrid zones with related taxa exist in the first place (Allendorf et al., 2001). If there are no purebred Florida panthers, should that mean that there is no place for panthers in Florida?

CKT081009

Descriptions


Pair of male gopher tortoises *Gopherus polyphemus* duking it out, photographed by Daniel Parker. - (via CKT)

Testudinidae True Tortoises

Range: Paleocene to recent, cosmopolitan except Australasia

Phylogeny: Testudinoidae : *Echmatemys* + (Batagurinae + (Geoemydinae + * : *Hadrianus* + (Xerobatinae + Testudininae)

Characters: (from Gaffney & Meylan 1988): Two or fewer phalanges in manus and pes; only four digits in pes; quadrate usually enclosing stapes; axillary and inguinal glands absent; slightly wide fissura ethmoidalis; cloacal bursae absent; coracoid blade wide; foramen nervi trigemini with maxillary aperture; trochanters of femur coalesced. (CKT), loss of the longitudinal ridges on the palatines (Gerlach 2001)

Further description: "Skull with open temporal fossae; quadrate closed behind. Shell completely ossified even in the young, more or less ovoid, and covered with epidermal shields. Plastron suturally united with the marginals; an entoplastron present. Sternal bridge long, sternal chambers very slightly developed ; anterior and posterior extremities of hyo- and hypo-plastron little extended inwards; marginals of bridge mth median processes interlocking with rib ends. Skull with open temporal fossae ; quadrate closed behind. Pubic and ischiadic symphyses firmly connected with each other. Limbs with free digits, which are short and moderately elongate ; terminal claws four or five. Second and third digit of pes never with more thou two phalanges. Tertiary and Recent." - Zittel, Eastman, et al (1932) p. 203

Comments: The Testudinidae or Tortoises are the only extant group of entirely terrestrial Testudines, having descended from aquatic and semi-aquatic forms, completing a cycle that began in the Triassic with terrestrial ancestors such as *Proganochelys* and *Proterochersis*. Although the transitional anatomical changes are not well known, the flat shells of aquatic forms were replaced by the physiologically important high domed shell which allow for greater lung capacity. Their stance also changed, and the true tortoises became fully functional digitigrades (the toe walkers), like terrestrial ungulate mammals, with elephant-like legs and feet and stubby unwebbed toes. Although the number of scutes remained constant, shell ornamentation and shape vary greatly. Also in contrast to aquatic forms, they are almost all herbivorous (study notes, ref, ref). Tortoises are generally reclusive animals, which tend to be diurnal with tendencies to be crepuscular depending on the ambient temperatures (Wikipedia).


The presumably stem Testudinid *Ergilemys insolitus* Matthew and Granger, 1923, Carapace, Late Eocene, Ergilin Dzo, Gobi Desert, south-eastern Mongolia, from The Russian Dinosaur Exposition, original url. Also at Mathematical com

The heavily armoured shell of some species, and the tendency of others to live in burrows, this clade has an excellent fossil record. The oldest tortoise fossils are known from the late Palaeocene of Mongolia. An Asian origin for the Testudinidae is also supported by biogeographic analysis based on molecular phylogeny (Le et al 2006). True tortoises do not appear in North America before the early Eocene, at which time they are represented by *Hadrianus*. A phylogenetic analysis is, however, necessary to assess if these taxa are situated within or outside of crown clade Testudinidae. Their colonization of the North American continent occurred during a sudden warming period in the earliest Eocene, when mild climates enabled many kinds of mammals to migrate between the northern continents via landbridges at high latitudes (Jehle, 2006). By the mid to late Eocene, tortoises were also known from Europe and North Africa. These hardy animals adapted to a range of environments, from forests to deserts. *Stylemys* is a common form in the Tertiary of North America (Joyce et al 2004 p.1005, ref). Despite a near-cosmopolitan distribution, mostly from the tropics and subtropics, although they never made it to Australasia, where their ecological niche was filled instead by Meiolaniids. Many endemic species, including giant forms, evolved on islands, although in the past giant forms also occurred on the mainland; the late Eocene *Geochelone ammon* was an early form from Egypt with a shell about a meter in length (Mlynarski, 1976, p.105). There are currently 12 genera and 43 extant species of testudinids,

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The basal testudinid, *Achilemys cassouleti* Claude & Tong 2004, Early Eocene (Ypresian) of France. Photo by Ghedoghedo, GNU Free Documentation/Creative Commons Attribution license, via Wikipedia

Hadrianus Cope 1872

Range: Early Eocene of North America and Spain

Phylogeny: Testudinidae **:** (Xerobatinae + Testudininae) + *

Characters: shell with narrow vertebral shields, neural bones usually hexagonal, extremities of costals of uniform length, undivided caudal shield (Zittel, Eastman, et al (1932) p.313)

Comments: Together with *Achilemys* from the Ypresian of France (*right*) (also known from the Middle Eocene Bridgerian age of Wyoming) , *Hadrianus corsonii* (Leidy 1871) is the oldest well-known true tortoise. It may be related to the extant genus *Manouria* (Ehret 2004 p.9), or similarities may simply be due to an absense of derived features. The genus may have evolved in the subtropics of Asia and subsequently migrated to North America and Europe. (via Wikipedia). Similar or related forms reached large size. "*Geochelone*" *abailensis* (Ckhikvadze, 1970) from the Middle Eocene of Kazachistan, had a plastron length of 90 cm, while "*Geochelone*" *eocaenica* (Hummel, 1935) from the Eocene of East Germany, had a plastron length of 1.2 meters. (Mlynarski 1976 p.101). During the Oligocene and Miocene these large basal forms were replaced by comparably sized testudines. MAK130307

Xerobatinae Agassiz, L. 1857.

Range:

Phylogeny: Testudinidae **:** *Hadrianus* + (Testudininae + * **:** *Manouria* + (*Stylemys* + (*Gopherus* + *Hesperotestudo*)))

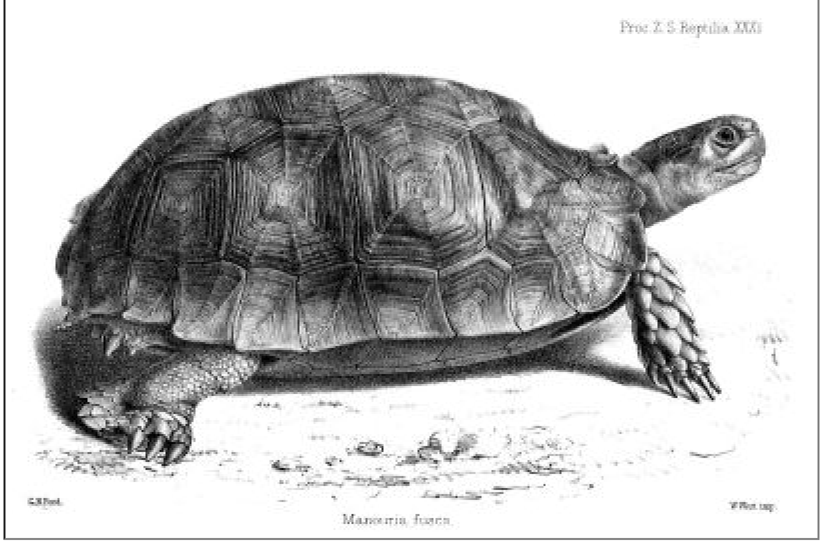
Characters:

Comments: Both morphological and molecular studies recognise this subfamily, but where disagreement arises is regarding primitive represnettaives such as the extant *Manouria* and the Tertiary *Stylemys*. Morphological cladistic studies (Gaffney & Meylan 1988, Meylan & Sterrer 2000, Gerlach 2001) unambiguously show the Asian species *Manouria* to be the most basal of the extant Testudinidae, lacking any of the synapomorphies of more derived species. Both also agree that *Stylemys* is a more advanced form. According to Gaffney & Meylan 1988 *Stylemys* is a basal member of the subfamily Xerobatinae (best represented by the North American genus *Gopherus*), wheras analysis by Meylan & Sterrer 2000 recover it as a stem testudinid that predates the Xerobatine-Testudinine split. Wheras, obviously, the genome of a fossil form like *Stylemys* cannot be tested (although some molecular material may remain in large fossil bones, for example *Tyrannosaurus* has been confirmed as closer to chickens than crocodiles (ref)), initial molecular sequencing of the family Testudinidae recovered an unexpected sister relationship between *Manouria* and *Gopherus* (Le et al 2006). This result was confirmed by later studies on the molecular phylogeny of the testudines as a whole (Thomson & Shaffer 2010, Guillon et al 2012), which would place it in the family Xerobatinae (or Gopherinae, depending on your choice of nomenclature).

Stylemys nebrascensis, photo © Prof. R. Springhorn.

Since both explanations cannot be correct, and lacking any combined approach papers to reference, we are faced once again with the choice of which methodology recovers the more reliable phylogenetic signal. If molecular sequencing is more reliable, either *Manouria* has lost all its advanced features and reverted to an ancestral condition sometime in its evolutionary history, or perhaps more likely the same derived characteristics developed convergently among both in other Xerobatines and the Testudinines. In this latter scenario, *Stylemys* would be a transitional form between *Manouria* and the higher Xerobatine. This may not be so unlikely, in view of the hypothesis of Trionychoidea and Kinosternoidea as only very distantly related but as convergent clades. Wheras if parsimony-based cladistic morphology is more reliable, that means the genomic sequences are convergent. MAK130305

Manouria



Manouria emys, from Proceedings of the Zoological Society of London 1860, public domain, via Wikipedia

Range:

Phylogeny: Xerobatinae **:** (*Stylemys* + (*Gopherus* + *Hesperotestudo*)) + *

Characters:

Comments: Either the most basal living tortoise genus, or the sister taxon of the American gopher tortoise. See Xerobatinae for this morphology vs molecules controversy. This genus has two extant species, the smaller Impressed Tortoise (*Manouria impressa*) and the larger Asian forest tortoise (*Manouria emys*), which lives in mountain areas of forest in Southeast Asia in Burma, southern China, Thailand, Laos, Vietnam, Cambodia and Malaysia. Both are endangered, although *M. emys* is able to breed in captivity. It is the largest tortoise in mainland Asia; a large adult of the northern subspecies, *M.e. phayrei*, reaches 25 kg in the wild and much more than that in captivity. Even larger was *Manouria sondaari* - an extinct giant land tortoise from Luzon Island, Philippines. (Wikipedia) MAK130305

Stylemys Leidy 1851

Stylemys nebrascensis shell at the Museum für Naturkunde, Berlin. Photo by FunkMonk, Creative Commons Attribution-Share Alike 3.0 via Wikipedia.

Range: Late Eocene to Miocene of Europe, Asia and North America

Phylogeny: Xerobatinae **:** *Manouria* + ((*Gopherus* + *Hesperotestudo*) + *)

Characters: neural bones hexagonal, with short anterolateral surfaces, nuchal not emarginate, caudal shield undivided (Zittel, Eastman, et al (1932) p.313)

Comments: *Stylemys* (meaning "pillar mouse") is the first fossil tortoise genus found in the United States (Wikipedia). It is either a primitive member of the subfamily Xerobatinae (Gaffney & Meylan 1988), or a stem testudinid that predates the Xerobatine-Testudinine split (Meylan & Sterrer 2000). Fossils of this genus, especially the type species *Stylemys nebrascensis*, are very common in the Late Eocene and Oligocene Badlands of Nebraska, South Dakota, and Wyoming, the site of many fossil mammal genera, and it is obvious that these reptiles must have inhabited the ancient landscapes in large numbers. This widespread genus lived in temperate to subtropical areas of North America, Europe, and Asia (for example *Stylemys karakolensis* is known from the early Tertiary of Turkistan) (Zittel, Eastman, et al 1932 p.313). Fifteen fossil species are listed. The jaw muscles are more primitive than today's tortoises, and the animals would have been herbivorous. While *Stylemys* species did exhibit the same neck structure as modern tortoises, the forelimbs were unsuitable for burrowing, setting them apart from modern genera. (Wikipedia) MAK130301

Gopherus gopher tortoises.

Range: Oligocene to Recent of North America

Florida Gopher Tortoise (*Gopherus polyphemus*), Green Swamp, Florida. Author Creative Commons Attribution 3.0, via Wikipedia

Phylogeny: Xerobatinae **:** *Manouria* + (*Stylemys* + (*Hesperotestudo* + *))

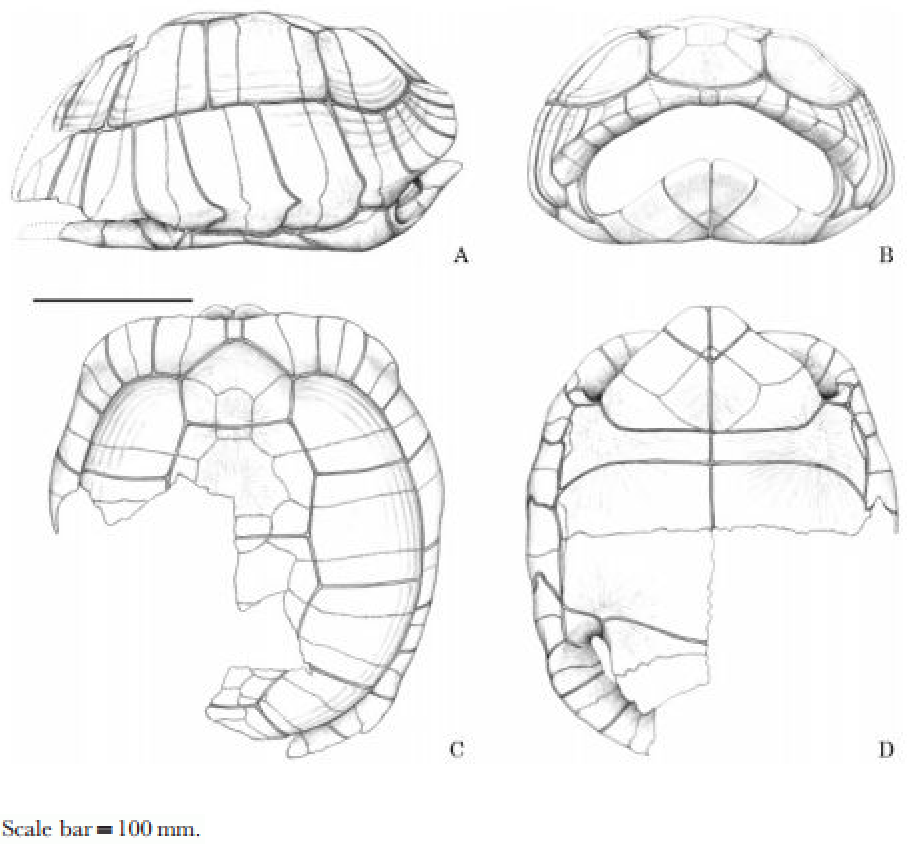
Comments: Desert living, burrowing tortoises. Gopher tortoises are so named because of their ability to dig large, deep burrows; these can be up to 12 m in length and 3 m deep. The burrows are used by a variety of other species, including mammals, other reptiles, amphibians, and birds (Wikipedia). *Gopherus laticunae* (Cope 1873) is known from the Oligocene of Colorado, and had a plastron length of about 30 cm. The giant Late Pleistocene *Gopherus hexagonatus* (Cope 1893) had a plastron length of about 64 cm (Mlynarski, 1976, pp.106-7). There are five extant species that range across the southern United States from California's Mojave Desert across to Florida, and in parts of northern Mexico, and which have a shell of 20-50 cm in length, depending on the species. (Wikipedia). *Xerobates* is a related genus. MAK130301

Hesperotestudo Williams, 1950

Range: Pleistocene of southeastern North America and Bermuda

Phylogeny: Xerobatinae **:** *Manouria* + (*Stylemys* + (*Gopherus* + *))

Comments: Hesperotestudo is a giant Pleistocene tortoise that lived amongst the megafauna of Pleistocene North America. Three species are known, a giant species, *Hesperotestudo crassicutata*, that grew as big as modern day Galapagos Island tortoises, a small species, *Hesperotestudo incisa*, intermediate in size between *H. crassicutata* and the gopher tortoise *Gopherus polyphemus* which was a contemporary found in the same area, and which is still extant, and a large island species, *Hesperotestudo bermudae*



Hesperotestudo bermudae, shell of holotype in A, lateral; B, anterior; C, dorsal; and D, ventral view, from Meylan & Sterrer 2000 fig 1.

Originally considered to be aligned to the giant Indo-Pacific island tortoises (Geochelone), cladistic analysis shows it was actually closely related to the North American tortoises (*Gopherus*) and hence belongs in the family Xerobatinae. Discovery of the island species *Hesperotestudo bermudae* provides a fifth instance of a testudinid dispersing over open ocean to an oceanic island, which shows that members of this family are well suited to over-water dispersal. (Meylan & Sterrer 2000). It is noteworthy that the unrelated Australasian Pleistocene horned tortoises also included a number of island-living species

The presence of such a large animal, *Hesperotestudo crassicutata*, which is sensitive to cold, shows that there were no frosts in southern North America during this time. Although it might be argued that these giant tortoises could burrow like its much smaller relative the gopher tortoise, it is hard to see how this could be possible with an animal about three to five times the linear dimensions. MAK130305

Radiated tortoises *Asterochelys radiata* photographed in Madagascar by czwg.

Testudininae

Range: Late Eocene to Recent

Phylogeny: Testudinidae : *Hadrianus* + (Xerobatinae + * : Testudinini + Megalochelyini)

Characters: (from Gaffney & Meylan 1988): Process of surangular interdigitates with dentary, lower jaw relatively gracile; mental glands absent; medial centrale large, separating distal end of radius from contact with medial proximal carpals. (CKT)

Comments: The Testudininae contains the land tortoises most closely related to the type genus, *Testudo*, with many species having been referred in the past to either that genus or *Geochelone*. Among the most famous members of the group are the giant tortoises of the Galapagos and Seychelles islands. (CKT). This group dates back at least to the Late Eocene; *Cheirogaster maurini* from the Late Eocene of France, and "*Geochelone*" *ammon* and the Late Eocene or Early Oligocene of Egypt are the eraliest known forms, both characterized by a developed epiplastral lip, a unique synapomorphy of the group (Lourenço et al 2012 p.506). Biogeographic analysis based on molecular phylogeny indicate Africa as the ancestral continental area for the Testudininae (all extant testudinids except *Manouria* and *Gopherus*) (Le et al 2006). MAK130307

Testudinini

Phylogeny: Testudininae : Megalochelyini + *

Comments: One of the major groups of testudines discovered through molecular phylogeny (Le et al 2006, Thomson & Shaffer 2010, Guillon et al 2012), which divides the testudinines into two major clades: *Indotestudo*, *Malacochersus*, and *Testudo*; and a diverse assemblage including *Aldabrachelys*, *Chersina*, *Geochelone*, *Homopus*, *Kinixys*, *Psammobates*, and *Pyxis*. MAK130307

Western Hermann's Tortoise (*Testudo hermanni hermanni*). *Testudo hermanni* ranged from the Pleistocene to Recent of Southern Europe (Mlynarski 1976 p.97). Photograph by Bizarria (*Wikipedia*)

Megalochelyini Giant tortoises and their relatives

Phylogeny: Testudininae **:** Testudinini + *

Comments: Less apparent morphologically, but discovered via molecular phylogeny (Le et al 2006, Thomson & Shaffer 2010, Guillon et al 2012), this large and diverse assemblage including *Aldabrachelys*, *Chersina*, *Geochelone*, *Homopus*, *Kinixys*, *Psammobates*, and *Pyxis*. Very impressive are the giant tortoises, such as *Geochelone*, found on on the remote oceanic islands of the Galapagos and the Seychelles. The largest species, such as the giant Galápagos tortoise *Geochelone nigra*, can reach 1.5m in length. When first found their carapaces reminding Spanish explorers of a kind of saddle they called a 'galápago', hence the name of the Galapagos islands. Since the archipelago is volcanic in origin and has never been connected to the mainland, they must have reached the islands by rafting, transported by currents that pass up the coast of Chile and Peru before circulating westward (ref). Such Island colonisation has occurred frequently, not only among different testudine lineages but also both in the case of the Australasian meiolaniids and the Caribbean Xerobatine tortoise *Hesperotestudo bermudae* during the Pleistocene

Both morphology (e.g. Gerlach 2001) and molecular phylogeny (e.g. Le et al 2006) agree that the genus *Geochelone* as currently defined is polyphyletic, having arisen a number of times from smaller ancestors, presumably through island gigantism. In the past however giant tortoises existed on all continents, beginning with "*Geochelone*" *ammon* from the Late Eocene or Early Oligocene of Egypt, was a respectably-sized form with a plastron a meter in length. *G. richardi* (Bergounioux, 1958) from the Oligocene of Catalonia was about the same size. There is no guarantee these early forms belonged in the Megalochelyini crown or even stem group, as to date no comprehensive cladistic analysis has been preformed on these fossil forms. *Geochelone grandidieri* (Vallant, 1885) from the Pleistocene to Holocene (subfossil) of Madagascar, had a plastron about 2 meters long . *G. robusta* (Laith-Adams, 1877) from the Pleistocene of Malata was the same size. (Mlynarski 1976 pp.102-106). The largest of all tortoises, the Plio-Pleistocene *Colossochelys atlas* (Falconer & Cautley, 1844), also known as *Testudo atlas* and *Geochelone atlas* was the size of a Volkswagen Beetle. It had a shell length of about 2.1 to 2.5 meters, and an approximate total height of 1.8 meters. Although some weight estimates go as high as 3 to 4 tonnes, a weight of around a tonne is probably more realistic (Paul and Leahy, 1994). In appearance it probably resembled a giant Galápagos tortoise. . During the dry glacial periods it ranged from western India and Pakistan (possibly even as far west as southern and eastern Europe) as far east as Sulawesi and Timor in Indonesia. (Wikipedia). MAK130307


Colossochelys atlas. Photo: Claire Houck , wikipedia

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Chelonii: Classification

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Meiolanoidea
         `--+--Pleurodira
            |--Paracryptodira
            `--+--Protostegidae
               `--+==Xinjiangchelyidae
                  `--+==Sinemydidae
                     |--Trionychoidea
                     `--+--+--Chelonioidea
                        |  |--Chelydridae
                        |  `--Kinosternoidea
                        `--Testudinoidea
```

Contents

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      Subclass Anapsida
             Order Chelonii Brogniart 1800 (Testudinata Oppel 1811,  Testudines Batsch 1788,
Chelonia of Romer etc)
                    Suborder "Odontochelydia"
                                                       Family †Odontochelyidae Li et al., 2008
(monotypal - †Odontochelys)
                    Suborder †Proganochelydia, Romer, 1966
                                                       Family †Proganochelyidae Baur 1888
(Proganochelys, Chinlechelys Joyce et al. 2008)
                                                       Family †Australochelyidae Gaffney & Kitching,
1994 (Australochelys and Palaeochersis - paraphyletic)
                                                       Family †Proterochersidae Nopcsa, 1928
(monotypal - Proterochersis, convergent with Pleurodira)
                    Suborder Cryptodira Cope, 1868 (= Cryptodiramorpha Lee 1995)
                           Infraorder unspecified
                                                       Family †Kayentachelyidae (Kayentachelys
Gaffney et al. 1987 monotypic family)
                                                       Family †Indochelyidae Datta et al. 2000
(Indochelys - monotypic family)
                                                       Family †Solemydidae (may be Ceratocryptodira)
                                                       Family †Kallokibotiidae Nopcsa 1923  (may be
Ceratocryptodira)
                                                       Family unspecified - †Condorchelys Sterli,
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2008, Eileanchelys
Infraorder †Ceratocryptodira Bour & Dubois 1986
Superfamily †Meiolaniodea Gaffney
Family †Meiolaniidae Lydekker, 1887 (horned turtles)
Family †Mongolochelyidae Sukhanov and Pozdnjakov (Mongolochelys - monotypal)
Family †Chelycarapookidae Warren 1969 (Chelycarapookus - monotypal)
Families unspecified - †Chubutemys Gaffney et al. 2007, Otwayemys Gaffney et al. 1998
Infraorder †Paracryptodira Gaffney, 1975 (= Amphichelydia Lydekker 1889) (semi-aquatic, terrapin-like)
Superfamily †Pleurosternoidea Hay, 1930 (= Basicryptodira Bour & Dubois 1986)
Family †Pleurosternidae Cope, 1868
Family †Glyptopsidae Marsh, 1890 (may or may not be synonymous with Pleurosternidae)
Superfamily †Baenoidea Williams, 1950
Incertae sedis †Arundelemys, †Compsemys
Family †Baenidae Cope 1882
Subfamily †Neurankylidae Lambe, 1902 - here used for paraphyletic Neurankylus lineage of Lyson & Joyce 2009

includes monotypal †Trinithchelyinae Gaffeny, 1972
Subfamily: †Hayemydinae Gaffney, 1972 (monotypal - Hayemys)
Subfamily †Palatobaeninae Gaffney, 1972 - here used for Plesiobaena-Palatobaena lineage of Lyson & Joyce 2009
Subfamily †Eubaeninae Gaffney, 1972 - here used for Eubaena-Stygiochelys lineage of Lyson & Joyce 2009
Infraorder Eucryptodira Gaffney 1975 (incl. Pancryptodira Joyce et al. 2004)
Parvorder unspecified
Superfamily †Plesiochelyoidea (paraphyletic, stem eucryptodires, all freshwater aquatic or marginal marine)
Family †Eurysternidae Dollo, 1886
Family †Thalassemydidae Zittel 1889 (monotypal - Thalassemys Rütimeyer, 1859)
Family †Plesiochelyidae Rütimeyer, 1873 (Plesiochelys Rütimeyer, 1873, Hylaeochelys Lydekker, 1889, Portlandemys Gaffney 1975)
Family †Protostegidae Cope, 1872 (small to gigantic Cretaceous marine turtles, cosmop., convergent with Dermochelyidae)
incertae sedis: †Santanachelys Hirayama, 1998, †Notochelone Owen, 1882, etc
Subfamily †Desmatochelyinae Williston, 1894 (monotypal - Desmatochelys - Late Cretaceous of N Am)
Subfamily †Chelospharginae Zanger 1953 (paraphyletic grade of small primitive types - Late Cretaceous of N Am,

if includes Rhinochelys Seeley 1869 then also European distribution)
Subfamily †Protosteginae Zangerl, 1953 (large to giant advanced forms - Late Cretaceous of N Am)
Clade †Angolachelonia Mateus et al. 2009 (= family "Angolocheloniidae"?)
Superfamily unspecified - (eucryptodires of Xinjiangchelyid grade, generally semi-aquatic, terrapin-like)
Family †Xinjiangchelyidae (paraphyletic ancestral forms, Mid Jurassic to Early Cretaceous of Asia)
incertae sedis: Chengyuchelys, Brodiechelys, Larachelus, etc
Parvaorder Centrocryptodira Gaffney and Meylan 1988 ((including Polycryptodira Gaffney and Meylan 1988)
Superfamily unspecified, paraphyletic or polyphyletic (testudines of Macrobaenid-Sinemydid grade, semi-aquatic, terrapin-like)
Family †Sinemydidae Yeh 1963 (primitive forms - Late Jurassic to Paleogene)
Family †Macrobaenidae Sukhanov 1964 (Judithemys & Macrobaena - advanced stem or crown centrocryptodires)
incertae sedis: †Hangaiemys, †Hoyasemys Perez-Garcia et al. 2012, †Wuguia Matzke et al. 2004
Superfamily Trionychoidea Fitzinger, 1826 (sensu Trionychoidae = Pantrionychia Joyce et al. 2004)
Epifamily †Adocoidae Cope, 1870 - shell sculpture in the form of pits, separated by ridges. Late Jurassic - Oligocene of Asia & North America.
Family †Adocidae Cope, 1870
Subfamily †Adocinae Cope, 1870
Subfamily †Shachemydinae Khosatzky in Nessov & Khosatzk y , 1977 - Ferganemys & Shachemys - Cretaceous of Asia
Family †Nanhsiungchelyidae Yeh, 1966 - shell sculpture in the form of large pits with high crests - Cretaceous of Asia and North America.
Epifamily Trionychoidae (softshell turtles and their ancestors Late Hurasisc to Recent)
Family Trionychidae Fitzinger, 1826 (softshell turtles)
Family Carettochelyidae Boulenger, 1887 (pignose turtles)

- Superfamily Chelonioidea Baur 1893 (= Panchelonioidea Joyce et al. 2004) (sea turtles - Cretaceous to recent)
  - Family unspecified - Genus †Chitracephalus Dollo 1884 (small, semi-aquatic)
  - Iincertae sedis
    - Subfamily †Allopleuroninae (Large sea turtles, Late Cretaceous of Europe, convergent with Protostegids and Dermatemydids)
  - Family †Toxochelyidae Baur 1895
    - Subfamily †Toxochelyinae (medium to large near shore marine types - Late Cretaceous of N Am)
    - Subfamily †Lophochelyinae (Late Cretaceous - may be Toxochelyids or Cheloniids)
  - Family Cheloniidae Oppel, 1811 (sea turtles)
  - incertae sedis: †Mexichelys, †Euclastes, †Gigantatypus - late Cretaceous
    - Subfamily †Eocheloniinae (ancestral types, Paleocene to Miocene)
    - Subfamily: Cheloniinae (recent and related sea turtles - Miocene to Recent, Cosmop.)
      - Tribe: Chelonini (Green sea turtles and their relatives; incl. Syllominae)
      - Tribe: Carettini (Loggerheads and their relatives)
  - Family Dermochelyidae Fitzinger, 1843 (leatherback sea turtles - Late Cretaceous to Recent)
- Superfamily Chelydroidea Baur 1893
  - Family Chelydridae Gray, 1831 (snapping turtles)
  - Family Platysternidae Gray, 1869 (big-headed turtle) (= Platysternoidea Baur 1893)
- Kinosternoidea Holroyd and Hutchison 2002
  - Family Dermatemydidae Gray, 1870 (river turtles)
  - Family Kinosternidae Agassiz, 1857 (mud turtles)
    - Subfamily:
    - Subfamily:
- Superfamily Testudinoidea Gray 1825
  - Family †Haichemydidae Sukhanov and Narmandakh 2006
  - Family †Lindholmemydidae Chkhikvadze, 1970
  - Family †Sinochelyidae Chkhikvadze, 1970 (incl. Peishanemydidae Nesov)
  - Family Emydidae Rafinesque, 1815 (pond, box, and water turtles)
  - Family Geoemydidae Theobald, 1868 ((Asian river turtles, Asian leaf turtles, Asian box turtles, and roofed turtles)
  - Family Testudinidae Batsch, 1788 (true tortoises - Late Paleocene to Recent)
    - incertae sedis: †Achilemys Hay, 1908, †Hadrianus Cope, 1872, etc
    - Subfamily: Xerobatinae Gaffney & Maylan, 1988 (desert and burrowing tortoises, Late Eocene to Recent)
    - Subfamily: Testudinidae (most tortoises, Paleogene to Recent)
      - Tribe: Testudinini - typical tortoises
      - Tribe: Megalochelyini - average to giant tortoises

Suborder Pleurodira Cope, 1864 (3 families) (incl. Eupleurodira Gaffney and Meylan 1988)

- Superfamilies unspecified
  - Family †Platychelyidae Bräm, 1965 (= Platychelira Gaffney et al. 2006)
  - Family †Dortokidae de Lapparent de Broin and Murelaga 1999
  - Family †Propleuridae Cope 1872
  - Family †Eusarkiidae Bergounioux 1952
  - Family Notoemydidae de Broin and de la Fuente 1993
  - Family †Araripemydidae
  - Family Chelidae Gray, 1825 (Austro-American sideneck turtles)
- Superfamily Pelomedusoidea (incl Pelomedusoides (Broin 1988))
  - Family †Bothremydidae (incl Bothremydinura Gaffney et al. 2006)
  - Family Pelomedusidae Cope, 1868 (African sideneck turtles)
  - Family Podocnemididae Cope, 1868 (Madagascan big-headed and American sideneck river turtles)

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Chelonii: Dendrogram

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Meiolanoidea
         `--+--Pleurodira
            |--Paracryptodira
            `--+--Protostegidae
               `--+==Xinjiangchelyidae
                  `--+==Sinemydidae
                     |--Trionychoidea
                     `--+--+--Chelonioidea
                         |  |--Chelydridae
                         |  `--Kinosternoidea
                         `--Testudinoidea
```

Contents

```
                    `--Polycryptodira MH

ANAPSIDA ?  WP, MH
|
o CHELONII ToL
|--Odontochelys
`--o Testudinata
   |--Proganochelys ToL
   `--+--Chinlechelys
   `--o <>Casichelydia
      |--Palaeochersis
      |--Australochelys
      `--+--Proterochersis
         `--o Cryptodira MH
            |--Kayentachelys •X ToL
            `--+--Condorchelys
               |--Eileanchelys
               `--+--Solemydidae
```

```
  |--o Meiolanoidea (Joyce 2007;  Anquetin, 2009)
  |  |--Chubutemys
  |  |--Naomichelys
  |  |--Chelycarapookus
  |  `--+--+--Mongolochelys
  |     |   `?--Otwayemys (if statistical morphology)
  |     `--o Meiolaniidae
  |        |--Niolamia
  |        `--+--Ninjemys
  |           `--Meiolania
  `--+--Kallokibotion
     |?-- Hispaniachelys
     `--o Testudines crown group
        |--o Pleurodira ToL, MH
        |  |--Proterochersis •X ToL
        |  `--o Eupleurodira
        |     |--Chelidae MH, ToL
        |     `--o Pelomedusoidea
        |        |--o Podocnemoidae
        |        |  |--Bothremyidae •XToL, MH
        |        |  `--Podocnemidae MH
        |        `--Pelomedusidae MH, ToL
        |--o Paracryptodira
        |  |--Compsemys
        |  |--+-Dorsetochelys
        |  |  `--o Pleurosternidae
        |  |     |--Pleurosternon
        |  |     `--Glyptops
        |  `--+--Arundelemys
        |     `--o Baenidae
        |        |--Neurankylus
        |        `--o Baenodda
        |           |--o Plesiobaena-Palatobaena lineage
        |           |  |--Plesiobaena
        |           |  `--Palatobaena
        |           `--o Eubaena-Stygiochelys lineage
        |              |--+--Boremys
        |              |  `--Eubaena
        |              `--+--Stygiochelys
        |                 `--+--Baena
        |                    `--Chisternon
        `--o Eucryptodira

`--+--o Paracryptodira
   |--o Pleurodira (Joyce 2007)
   `--o Eucryptodira
      |--+--Thalassemyidae
      |  `--Protostegidae
      `--+--Plesiochelyidae
         `--+--Angolachelonia
            `--+--Xinjiangchelyidae
               `--+--o Pleurodira (Anquetin, 2009)
                  `--o Centrocryptodira
                     |--Meiolaniidae (Gaffney, 1996)
                     `--+==Sinemydidae
                              `--+?--Trionychoidea (molecular + stratigraphy)
                           |== Macrobaenidae
                           `--Durocryptodira
```

`--o Eucryptodira |--Thalassemyidae |--Protostegidae `--+--Plesiochelyidae `--+--o Angolachelonia | |--*Solnhofia* | `--+--*Sandownia* | `--*Angolachelys* `--+==Xinjiangchelyidae `--o Centrocryptodira |--Pleurodira `--o Eucryptodira ? |--Thalassemyidae | |--Protostegidae | |--Plesiochelyidae | `--+--o Angolachelonia | | |--*Solnhofia* | | `--+--*Sandownia* | | `--*Angolachelys* `---- ?--+--Chengyuchelyidae | |--*Chengyuchelys* | `--Xinjiangchelyidae `--o Centrocryptodira |?--Meiolaniidae (hennigian morphology) `--o Cryptodira crown group (molecular) |?--Trionychoidea (molecular + stratigraphy) `--o Durocryptodira (molecular + stratigraphy) |==Sinemydidae `--o Cryptodira crown group (morphology) |--Chelonioidea `--+--Chelydridae |--+?--Trionychoidea (morphology) | `--Kinosternoidea `--Testudinoidea `--o Centrocryptodira |---------------? (if molecular + stratigraphy) | `,--o Trionychoidae | | |--*Basilochelys* | | `--+--o Adocusia (stratigraphy implies paraphyly) | | | |--*Yehguia* | | | `--+--o Adocidae | | | | |-- *Adocus* | | | | `-- Shachemydinae | | | |--o Nanhsiungchelyidae | | | |--*Kharakhutulia* | | | `--+--*Hanbogdemys* | | | |--o "Nanhsiungchelyini" | | | | |--*Anomalochelys* | | | | `--*Nanhsiungchelys* | | | |--*Zangerlia* | | | `--*Basilemys* | | `--+--*Peltochelys* | | `--+--Crown group Trionychoidae | | |--*Kizylkumemys* | | `--+--Carettochelyidae | | `--o Trionychidae | | |--+--Plastomeninae | | | `--Cyclanorbinae | | `--Trionychinae |--+--o Trionychoidea | |--*Basilochelys* | `--+--o Adocusia | | |--*Yehguia* | | `--+--o Adocidae | | | |-- *Adocus* | | | `-- Shachemydinae | | `--o Nanhsiungchelyidae | | |--*Kharakhutulia* | | `--+--*Hanbogdemys* | | |--o "Nanhsiungchelyinae" | | | |--*Anomalochelys* | | | `--*Nanhsiungchelys* | | |--*Zangerlia* | | `--*Basilemys* | `--+--*Peltochelys* | `--o Trionychia | |--Carettochelyidae | `--o Trionychidae | |--+--Plastomeninae | | `--Cyclanorbinae | `--Trionychinae o Chelonioidea |--*Chitracephalus* `--+--*Mesodermochelys* `--+--Toxochelyidae `--+--Chelonioidea |--+--*Euclastes* | |--*Puppigerus* | `--Cheloniidae `--Dermochelyidae `--+--+--Chelonioidea | `--+--Chelydridae | |--*Emarginachelys* | `--o Kinosternoidea | |--Dermatemydidae | `--o Kinosternia | |--*Agomphus* | |--*Hoplochelys* | `--o Kinosternidae | |--Kinosterninae | `--Staurotypinae `--Testudinoidea `--o

Centrocryptodira |--Trionychoidea |--+--*Hoyasemys* | `--Sinemydidae |?--*Osteopygis* `--+--*Kirgizemys* `--+--o Macrobaenidae | |--*Judithemys* | `--*Macrobaena* |--o Chelonioidea-Chelydridae-Kinosternoidea Clade `--+--Angolachelonia `--o Xinjiangchelyid - Crown Cryptodire clade |--*Chengyuchelys* |--*Larachelus* |==Xinjiangchelyidae `--o Centrocryptodira |==Sinemydidae (in part) |--Trionychoidea |--+--Chelonioidea | `--+--*Emarginachelys* | |--o Chelydroidea | | |--o Platysternidae | | | |--*Macrocephalochelys* | | | `--*Platysternon* | | `--o Chelydridae | | |--*Protochelydra* | | `--Chelydrinae | `--Kinosternoidea `--Testudinoidea `--+--+--Chelonioidea | `--+--Chelydridae | `--Kinosternoidea |--Trionychoidea `--+--+--Chelonioidea | `--+--Chelydridae | `--Kinosternoidea `--o Testudinoidea |==Lindholmemydidae incl. *Mongolemys* `--+-Emydidae `--o Testudinoidae |--*Echmatemys* `--+--Geoemydidae `--Testudinidae `--o Testudinidae |--*Hadrianus* `--+--o Xerobatinae | |--*Manouria* | `--+--*Stylemys* | `--+--*Gopherus* | `--*Hesperotestudo* `--o Testudininae |--Testudinini `--Megalochelyini

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Chelonii: References

Abbreviated Dendrogram

```
ANAPSIDA ?
|
o CHELONII
|--Odontochelys
`--+--Proganochelys
   `--+--Proterochersis
      `--+--Pleurodira
         |--Paracryptodira
         `--o Eucryptodira
            |--Protostegidae
            `--+--Angolachelonia
               `--+--Xinjiangchelyidae
                  `--+==Sinemydidae
                     |--Trionychoidea
                     `--+--+--Chelonioidea
                        |  |--Chelydridae
                        |  `--Kinosternoidea
                        `--Testudinoidea
```

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