

## A new large scale global morphological phylogeny of turtles

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**Background.** We developed a new global turtle matrix using morphological characters to test the age of the turtle crown and to assess the origin and phylogeny of various controversial clades along the turtle stem and within Pan-Cryptodira.

**Methods.** We significantly increased both character and taxon sampling relative to earlier global matrices with special emphasis on Jurassic and Cretaceous stem-cryptodires. Further improvements included the complete, observation-based re-scoring of all previously sampled taxa and the reduction of subjective character assignments with the help of consensus-building between the members of our working group for each scoring.

**Results.** We confirm the previous conclusion that the turtle crown has an extensive phylogenetic stem and that the age of the crown is approximately Middle Jurassic in age. The addition of new fossils allows reinterpreting purported Laurasian meiolaniforms as part of a paraphyletic grade of Mesozoic Laurasian basal turtles, including Solemydidae, Sichuanchelyidae, and *Kallokibotion bajazidi*. A paraphyletic Cryptodira with a deeply nested Pleurodira (as signaled by some recent morphological and molecular analyses) is not recovered when only stem-pleurodires are included in the analysis. This demonstrates conclusively that the false signal is caused by marked morphological convergences between crown cryptodires and pleurodires. We find little or no support for the chelydrid affinities of *Platysternon megacephalum* which had previously been inferred by morphological analyses, in conspicuous contrast with molecular results. Similarly, little support remains for a Trionychia-Kinosternoidea clade, which had been consistently recovered in earlier morphological studies, again in contrast with molecular phylogenies. Contrary to previous hypotheses, our analysis advocates sea turtle monophyly and argue for a diverse Cretaceous stem, including bizarre, giant forms belonging to the extinct clade Protostegidae. Derived

members of Protostegidae nevertheless show remarkable similarities with dermochelyids as a result of parallel evolution.

**Discussion.** Despite increased taxon and character sampling, we are still unable to fully replicate the molecular phylogeny of turtles. This is especially frustrating because the stratigraphic distribution of fossil turtles is more consistent with molecular results. The likely reason for this disparity comes from the high degree of homoplasy in turtles, notable gaps in the fossil record, and the rapid and early diversification of extant turtle lineages soon after the appearance of the turtle crown. The latter is also suggested by the overall good support at the end of the branches and low resolution at the nodes connecting their stem. Future fossil discoveries, particularly from the Jurassic of Gondwana, as well as South and Southeast Asia, will likely help resolve these issues. In the meantime, we support employing the consensual molecular scaffold for global morphological analyses of turtles.

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