A Revised Global Biogeography of Turtles

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Background. Over the course of the last decades, much effort has gone into unraveling the biogeographic history of turtles, but while much progress has been achieved in resolving post-Jurassic dispersal events, traditional phylogenetic hypotheses have yielded incongruous results in regards to the early history of the group.

Methods. We re-evaluate the fossil record of turtles in context of recent phylogenetic analyses and fossil finds, including the extensive record of fragmentary but diagnostic remains. However, given that near-coastal and marine turtles readily disperse across aquatic barriers, a broad set of neritic to pelagic groups were disregarded from consideration. Given that significant disagreement still exists among current phylogenetic hypotheses, much effort was placed in tracing unambiguously monophyletic groups through the fossil record. We nevertheless employed molecular backbone constraints, given that the molecular phylogenies are more consistent with the fossil record than current, morphological phylogenies.

Results. Among derived, aquatic turtles, we recognize four clades that can be traced back to four discrete biogeographic centers: Paracryptodira in North America and Europe, Pan-Cryptodira in Asia, Pan-Pelomedusoides in northern Gondwanan landmasses and Pan-Chelidae in southern Gondwanan landmasses. This pattern is partially mirrored by three clades of primarily terrestrial, basal turtles: Solemydidae in North American and Europe, Sichuanchelyidae in Asia, and Meiolaniformes *sensu stricto* in southern Gondwanan landmasses. Although the exact interrelationships of these clades remain unclear, most can be traced back to the Middle Jurassic.

Discussion. The conclusion that the two primary lineages of pleurodires and paracryptodires can be traced back to mutually exclusive land masses is not novel, but the realization that the early history of pan-cryptodires is restricted to Asia has not been realized previously, because traditional phylogenies implied an early, global presence of pan-cryptodires. The timing of the origin of the three primary clades of derived turtles (i.e., Pan-Pleurodira, Pan-Cryptodira, and

Paracryptodira) correlates with the opening of the central Atlantic and the formation of the Turgai Strait in the Middle Jurassic, somewhat later than predicted by molecular calibration studies. The primary diversity of extant turtles therefore appears to have been driven by vicariance. A similar hypothesis could also be formulated for the three clades of basal turtles that survive at least into the Late Cretaceous, but given that their combined monophyly remains uncertain, it is unclear if their diversity was also driven by vicariance, or if they emulate a vicariance-like pattern. Although most groups remained within their primary geographic range throughout their evolutionary history, the dominant vicariance signal was thoroughly obfuscated by rich dispersal from littoral to marine turtles and crown cryptodires.