History of side-necked turtle diversification revealed

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Fossils of *Pleurodira carapaces*. Credit: Gabriel Ferreira (FFCLRP-USP)

A work authored by a group of paleontologists affiliated to University of São Paulo's Biology Department in Ribeirão Preto, Brazil, published in *Royal Society Open Science*, is the most comprehensive phylogeny of the

Pleurodira suborder of side-necked turtles produced. Pleurodira includes the yellow-spotted Amazon River turtle (Podocnemis unifilis).

The study gathers phylogenetic, biogeographical and morphological data in search of an explanation for the biogeographical history of Pleurodira, especially the discrepancy between their distribution in the fossil record and in the world today. The researchers constructed a new phylogeny of Pleurodira, tracing the group's evolutionary history as broadly as possible in order to reveal unknown patterns of past biogeographical distribution.

The first step in building the phylogeny was a matrix analysis of 245 morphological characters in 101 species. "This matrix of morphological data for Pleurodira included both living and extinct species. The matrix was analyzed using parsimony, and from the analysis, we obtained a new phylogenetic tree for Pleurodira," said Gabriel Ferreira, lead author of the article.

"The phylogenies of pleurodires constructed to date have been partial. Our purpose in undertaking the large phylogenetic analysis was to understand the lineage's evolution during the Mesozoic and Cenozoic Eras," said Langer.

These turtles are called side-necked because they fold the neck horizontally under their shell, tucking it into the space in front of one of their front legs. The dozens of living pleurodire species are restricted to terrestrial and freshwater environments; they do not tolerate contact with salt water.

Side-necked turtles are found mainly in the Southern Hemisphere—South America, sub-Saharan Africa, Indonesia, Australia and New Guinea, the exception being the isolated species inhabiting the Arabian Peninsula. Apart from the Indonesian archipelago, all these regions were once part of Gondwana, the ancient supercontinent that

existed between 250 million and 150 million years ago.

The oldest fossils of pleurodire turtles in North America, Europe and North Africa have been dated to between 105 million and 70 million years ago. In North America and North Africa, they survived until at least 35 million years ago The oldest pleurodire fossil, Atolchelys, was found in Northeast Brazil. Atolchelys lived 125 million years ago during the Lower Cretaceous, when Africa was starting to separate from South America. It belonged to the extinct Bothremydidae family.

The expansion of Pleurodira geographical distribution occurred as Africa and South America were separating completely from the rest of Gondwana, between 105 million and 100 million years ago, when the turtles started spreading to North Africa and Madagascar, and to Europe, North America, the Middle East and India.

If pleurodire species living some 100 million years ago were already restricted to terrestrial and freshwater environments, then the South Atlantic opening must have separated populations and forced them to adapt to different conditions, leading over time to the emergence of new genera and species.

The discovery of many extinct genera in the past decade has revealed gaps in the biogeographical narrative that the traditional theory has proved unable to fill. Differently from today, oceans in the Upper Cretaceous, the Paleogene and the Cenozoic were not an environment exclusively inhabited by suborder Cryptodira. Pleurodires from the extinct Bothremydidae family were also living in salt waters on today's Northeastern Brazilian coast at least 110 million years ago.

At that time, the South Atlantic was not yet fully open. This development occurred later, between 80 million and 66 million years ago, when Bothremydidae inhabited both sides of the Atlantic.

Inaechelys lived on the coast of the Pernambuco State in Northeast Brazil, and on the other side of the still young (and for this very reason narrow), Atlantic Ocean lived the Portuguese Rosasia, as well as Foxemys and Polysternon, found in Spain and France. Another marine genus of Bothremydidae, Bothremys, was more widely distributed, as shown by fossils found in four US states as well as Morocco and Jordan.

The young South Atlantic may not have been a sufficiently formidable barrier to prevent their dispersal to other continents—at least not while the distance between South America and Africa was relatively small, perhaps a few hundred kilometers.

"If the traditional hypothesis was that the current distribution of pleurodires derives from vicariant events linked to continental drift, there was a second hypothesis according to which the group was broadly distributed, and successive extinctions eventually confined its lineages to the areas where they're found today," Ferreira said. "We imagined a third hypothesis: a complex pattern of dispersal from Gondwanan areas explains the broad distribution found in the past."

The new phylogeny leads to the conclusion that Araripemys and Euraxemys were relatives of Pelomedusoides, the ancestral group that gave rise to the families which comprises the Pleurodira suborder—Bothremydidae, Podocnemididae and Pelomedusidae.

Moreover, during the Lower Cretaceous, when Araripemys and Euraxemys were extant, both of the main pleurodire lineages already existed. They were the Pan-Chelidae (the group comprising all Chelidae) and Pan-Pelomedusoides (Bothremydidae, Podocnemididae, Pelomedusidae, and the other extinct families). The new tree suggests that Atolchelys, the oldest known pleurodire (and the oldest member of Bothremydidae, alive in the Lower Cretaceous 125 million years ago in the Brazilian State of Alagoas) shares a common ancestor with

Araripemys and Euraxemys (alive 110 million years ago in what is now Ceará State).

Despite the scarcity of the fossil record for the Lower Cretaceous (half a dozen species are known), the new phylogenetic tree suggests that a large number of lineages of Chelidae and ancestors of Pelomedusoides were already established in the period.

The mass extinction that wiped out the dinosaurs at the end of the Cretaceous apparently did not correspond to a critical period for the pleurodires, involving neither extinction nor diversification. This finding makes sense, as the turtles were the animals that suffered least from the mass extinction among terrestrial vertebrates.

The biogeographical history of Pan-Pelomedusoides, in contrast, is dominated by the occurrence of areas of endemism for each group, with several dispersal events to other areas. The exception is Pelomedusidae, which was always endemic to continental Africa.

Some pelomedusids are currently found in Madagascar, the Arabian Peninsula, the Seychelles and other small islands, but the absence of fossil records other than very scarce and fragmentary remains in continental Africa precludes a more detailed account of the biogeographical history of Pelomedusidae. Given the current data, the researchers believe that Pan-Pelomedusidae were always restricted to the African continent and only recently dispersed transoceanically.

The results also show that the ancestors of Araripemys, Euraxemys and Pan-Podocnemididae originally inhabited Africa, dispersing to South America during the Lower Cretaceous. The ancestors of Podocnemidoidae remained in South America, whereas the ancestors of Bothremydidae returned to Africa.

Bothremydidae diversified significantly in Africa, but several representatives dispersed independently to other areas: at least once to Europe, India, Madagascar and back to South America, and at least three times to North America. The results highlight the strong dispersal capability of Bothremydidae due to their marine habits. They were the most widespread group of side-necked turtles during the Cretaceous and Paleocene, when they started to decline in diversity until their complete extinction approximately 50 million years ago.

The new phylogenetic tree for pleurodires enabled the researchers to detect and differentiate vicariant events, dispersal events and founding events that occurred in the past 125 million years. The previous hypotheses did not satisfactorily explain the distribution of pleurodires over time.

"Our third hypothesis, which assumes a complex pattern of dispersals to North America, Europe and Asia from Gondwanan areas (South America and Africa), is the best explanation of the past and present distribution patterns," Ferreira said.

"Furthermore, we noted that the pleurodire groups with above-normal diversity were precisely those that diversified in different environments—in other words, those that became sea turtles."

More information: Gabriel S. Ferreira et al, Phylogeny, biogeography and diversification patterns of side-necked turtles (Testudines: Pleurodira), *Royal Society Open Science* (2018). DOI: 10.1098/rsos.171773

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