

outlines mark the presence of a prominent throat pouch. The ventral scales have sizes of up to 2.5 mm, polygonal morphologies, and their relief displays no clear overlapping pattern typical for squamate scales. Dorsally the scales are generally smaller, but conspicuous craniocaudal rows of large oval to rectangular scales occur within the meshwork of smaller scales. The reddish preserved skin colouration follows no simple pattern: There is a larger colour patch along the posterior margin of the skull, the ventral neck and anterior trunk display scales with tiny colour spots, and the dorsal rows of larger scales are sometimes marked by thin aligned stripes. Apart from ecological and functional implications the skin fossils of the Madygen Formation yield the rare possibility to acquire data concerning the evolution of integument in basal diapsids of the Triassic.

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The evolution of freshwater stingrays (Myliobatiformes, Potamotrygonidae) revisited

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Extant stingrays (Myliobatiformes) form a monophyletic group characterized *inter alia* by one to several serrated tail spines. The monophyly also is supported by molecular studies. However, despite all progress accomplished in the last years, the phylogenetic relationships among the major lineages of myliobatiforms are still poorly resolved, and there is a lack of consensus regarding composition of some myliobatoid families. Additionally, the evolutionary history of South American Potamotrygonidae, which is the only group of myliobatiforms that adapted completely to freshwater conditions remains ambiguous. This is mainly because of the lack of fossils and because their sister group remains unsettled, with both *Urobatis* and *Himantura* being candidates. Potamotrygonidae includes four living genera, *Heliotrygon*, *Paratrygon*, *Plesiotrygon*, and *Potamotrygon*. The fossil record of freshwater stingrays is very patchy and includes rare isolated bucklers, tubercles, spines, and oral teeth occurring in the Middle Miocene of central Colombia, the Late Miocene of Brazil and the Late Miocene of Argentina. These very patchy

occurrences may indicate a time of origination in the early Neogene, probably related to extrinsic factors such as plate tectonics (uplift of Andes, closure of marine connections). Nevertheless, one must caution the use of rare fossils to reconstruct evolutionary events.

Based on all available information, the origination of Potamotrygonidae generally is assumed to have occurred in the Late Cretaceous or Palaeogene during one of several marine transgressions into the Amazonian Basin. Their common ancestor most likely was trapped in isolated freshwater habitats by subsequent orogenic events during the Palaeocene-Miocene (65–23 Ma). Different hypotheses exist from where stingrays invaded continental habitats. One hypothesis assumes that an ancestral stingray population immigrated from the Pacific into an inland sea. The inland rivers subsequently were blocked in the course of the Andean orogeny in the early Mesozoic. Nevertheless, this hypothesis underestimates the age of the Atlantic Ocean and opening of the proto-Caribbean. Consequently, a marine stingray population could have immigrated from northern South America or along the eastern coast. Evidence for a northern invasion includes the discovery of marine deposits in Ecuador, Colombia, Venezuela, and the Guyanas. The southernmost records of marine fossils are from Peru and Brazil. Additionally, three different evolutionary scenarios are conceivable: (1) change from a marine to euryhaline lifestyle in the ancestor of the clade including *Himantura* + *Potamotrygon* and then a second change to a freshwater lifestyle in the *Potamotrygon* lineage (the *Himantura fluviatilis* complex includes three species, which may be synonymous.); (2) the ancestor of the *Himantura* + *Potamotrygon* clade also was marine and each lineage made an independent change to a euryhaline (*Himantura*) or a freshwater (*Potamotrygon*) lifestyle, respectively; and (3) direct change from a marine to freshwater lifestyle in the ancestor of the *Himantura* + *Potamotrygon* clade, and then a second change to euryhaline lifestyle in the *Himantura* lineage. If *Paratrygon* represents the most basal potamotrygonid, it might have been the first true freshwater member of this group and the onset of their successful radiation. The hypothesis that evolution from a marine to freshwater lifestyle passed through a euryhaline intermediate only is applicable if one assumes a priori that freshwater adaptation occurred from marine through an euryhaline to a freshwater lifestyle, which would be a circular argumentation. Although we can't provide a final conclusion to the problem, we favour the third hypothesis although slightly modified.

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