



## AMAZONIAN PALAEOENVIRONMENTS AND THE CROCODYLIAN AND TURTLE FOSSIL FAUNA DURING THE NEOGENE

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Environmental reconstructions basing on tectonic, sedimentary, palynological and macrofossil studies of the Neogene of northern South America point to a change from a lake and wetland environment in the Early-Middle Miocene (mainly represented by the Honda Group, in Colombia, and Pebas Formation, in Ecuador, Peru, Colombia and western Brazil) to an early Late Miocene fluvio-tidal wetland system (represented by the Upper Solimões Formation of western Brazil) into the modern riverine system in Late Miocene. The turtle and crocodile record is consistent with this view, supporting a marine-influenced environment only in coastal areas, as represented by the Late Miocene Urumaco Formation in Venezuela. The turtle record include mainly pleurodirans, and all extant genera (*Chelus* and *Podocnemis*) represented by fossil species in northern South America have been collected in freshwater deposits. The scarce cryptodiran reported are included in the riverine Trionychidae (Honda Group and Castillo Formation, Venezuela) and terrestrial Testudinidae (Honda Group and Petaca Formation, Bolivia). The majority of the extant podocnemidids shows no preference for a specific freshwater environment and could occur in several habitats, such as rivers and lagoons. The unique direct evidence of marine adaptations in a pelomedusoid pleurodires, based on the discovery of a nesting site with eggs, was attributed to *Bairdemys venezuelensis*, in sediments of the middle member of the Urumaco Formation. Regarding the crocodile record, a lower diversity of gavialoids characterizes the Lower-Middle Miocene of northern South America, with only one species in the Upper Oligocene-Lower Miocene Castillo Formation in Venezuela (*Siquesiquisuchus venezuelensis*) and one in the Middle Miocene Honda Group and in correlated Peruvian sediments (*Gryposuchus colombianus*). However, we do have three genera and at least four species in the Late Miocene Urumaco and Solimões Formations (*Ikanogavialis gameroi*, *Hesperogavialis cruxenti*, *Gryposuchus jessei* and *Gryposuchus croizati*). The considerably greater number of specimens in these two deposits compared with the scarcity of gavialoid remains in the older formations also suggests larger gavialoid populations during the Late Miocene. Another genus, *Piscogavialis*, lived in Peru during the Pliocene. Interestingly, the Neogene of southern South America does not share this greater gavialoid diversity, with only one species (*Gryposuchus neogaeus*) known from the Upper Miocene Ituzaingó Formation of Argentina. Today, gharials inhabit deep, fast-flowing rivers, preferentially occupying calmer areas within these rivers, such as sandbanks, and do not occur in lagoons or swamps. Environmental changes occurring in northern South America during the Late Miocene led to a system dominated by large tidally influenced river systems and probably increased gavialoid diversity as opposed to contemporaneous southern faunas, where a similar environment was present but not as extensively developed. The intolerance of the extant gharial to prolonged saltwater exposure is also concordant with a freshwater habit for the closely related South American gavialoids. It also emphasizes the freshwater nature of the Solimões Formation and Honda Group and other deposits from which they were found. The caimanine record also seems concordant with a change from wetlands to river-dominated systems in the Late Miocene. *Melanosuchus* and possibly *Paleosuchus* are represented respectively in the Urumaco Formation and Honda Group and are typical crocodylians of the modern Amazon River system. *Caiman* is represented today in this system by *C. crocodilus*, and marginally by *C. yacare* at the southwestern limit of the Amazon River system; *C. latirostris* is absent from the Brazilian Amazon, and occurs in the Amazonian drainage only in Bolivia, where it is extremely rare. The distribution of *C. latirostris* is concentrated in the Prata, Paraná and São Francisco river systems and along the Brazilian coast. This species also inhabits estuaries, but only ones with abundant freshwater sources,

due to its inability to perform osmoregulation. In southern regions where the species occurs sympatrically with *Caiman yacare*, *C. latirostris* prefers slow-moving waters with dense vegetation (swamps and lagoons), but when there is no overlapping range, this species can occupy a wider variety of habitat types. *Caiman latirostris* is reported in the Middle Miocene Honda Group, where wetlands composed the landscape, and from the Upper Miocene Itzaingó Formation, but not from the Upper Miocene Solimões Formation, in spite of intensive collection efforts. This suggests that the northern extinction of this species in South America can be related to the change from a lacustrine to a river-dominated floodplain system in Amazonia. The alleged occurrence of *C. latirostris* in the Upper Miocene Urumaco Formation does not contradict this hypothesis, due to the coastal habits presented by extant *C. latirostris*. This view, however, leads to the question of why gavialoids do not live today in the Amazonian rainforest. Except for *Charactosuchus*, all extinct reptilian groups from northern South America share a large to giant body size (including all gavialoids, nettosuchids, *Purussaurus*, some sebecids and turtles as *Stupendemys*). The impoverishment of the opened habitats and food supplies possibly coincided with a major change from wetland systems to riverine systems in the late Late Miocene and may also have been exacerbated by Pliocene global cooling, which could have been especially critical for large animals, due to the demise of ecosystem productivity. Such animals were mostly top-predators with a large body size and, even as poikilotherms, must have required greater energy and space requirements.