

# Pleistocene sea level changes and crocodile population histories on the Isthmus of Panama: A comment on Avila-Cervantes et al. (2020)

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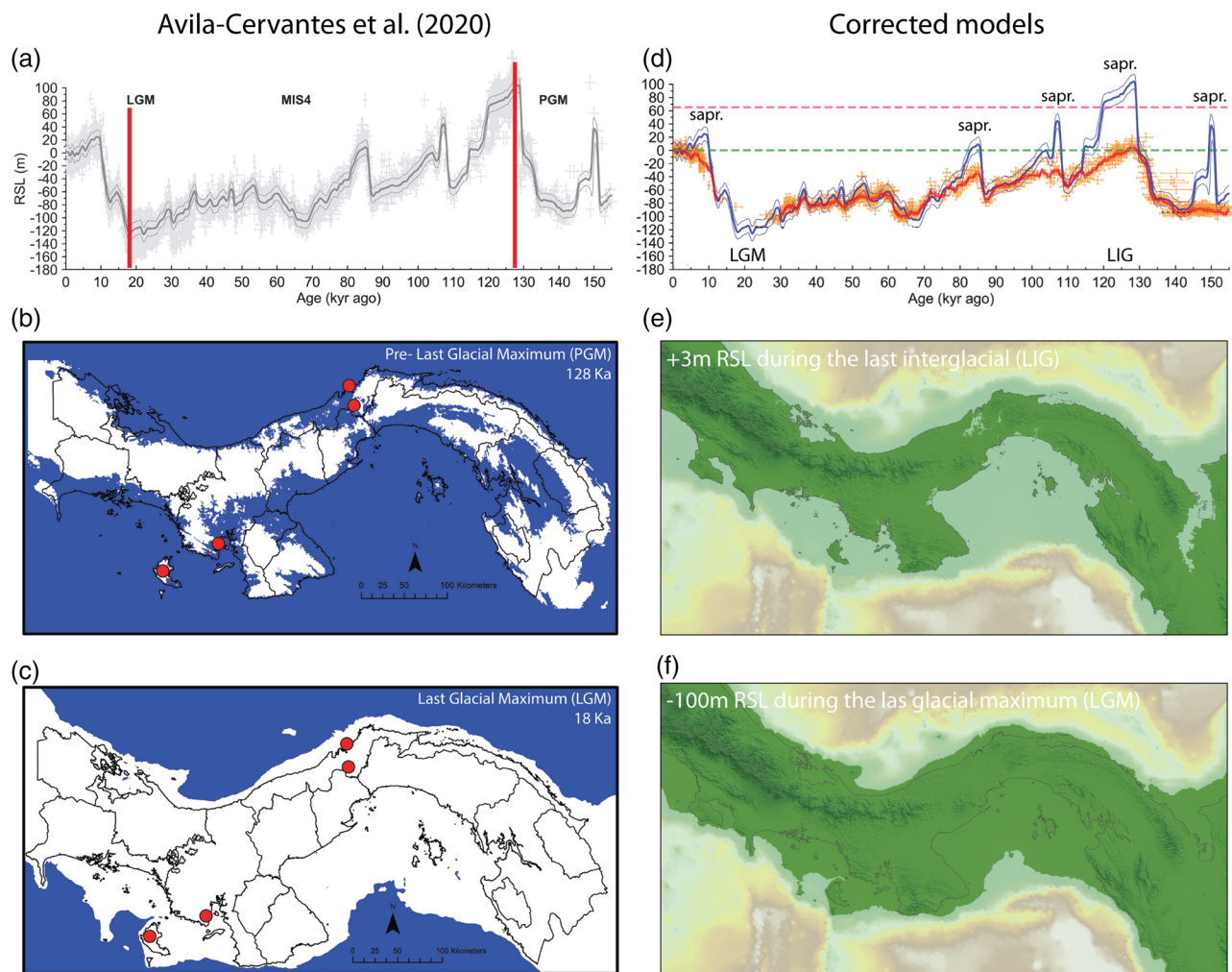
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Avila-Cervantes et al. proposed that glacial-interglacial sea level changes played an important role in the evolutionary and demographic histories of the crocodile *Crocodylus acutus* on the Isthmus of Panama. However, the study used erroneous sea level proxy data that produced flawed paleogeographic reconstructions. We present new paleogeographic reconstructions and review the timing of, and proposed mechanisms behind, the demographic events estimated by Avila-Cervantes et al.. With the data currently available, we find little evidence to support the hypothesis that sea level changes drove population demographic events in crocodiles on the Isthmus. Alternative hypotheses, including changing climate and habitat suitability, are equally valid and should be considered along with well-supported sea level models.

**KEY WORDS:** Biogeography, paleobiology, population biology.

Avila-Cervantes et al. (2020) used restriction site associated DNA sequencing (RAD-Seq) and demographic models to explore the histories of populations of the American crocodile *Crocodylus acutus* (Cuvier 1807) on either side of the Isthmus of Panama. The authors proposed that some demographic events coincided with sea level extremes at the last interglacial (LIG) and the last glacial maximum (LGM), and concluded that Late Pleistocene sea level changes drove gene flow patterns between trans-isthmian crocodile populations. To support their hypothesis, Avila-Cervantes et al. (2020) presented paleogeographic reconstructions of the Isthmus during the LIG and LGM using a sea level curve derived from Rohling et al. (2017) (Fig. 1). Their reconstructions, however, suffer from significant errors.

The sea level curve of Rohling et al. (2017) was derived from oxygen isotope measurements of planktonic foraminiferal tests from a series of marine sediment cores taken in the eastern Mediterranean covering the last 160,000 years. The ratio of the stable isotopes <sup>18</sup>O and <sup>16</sup>O are reported in delta notation as  $\delta^{18}\text{O}$  and measuring the  $\delta^{18}\text{O}$  of foraminifera tests (skeletons) has become a standard tool for estimating past sea levels. The premise of the approach is that because <sup>16</sup>O is lighter than <sup>18</sup>O, water molecules containing the lighter isotope evaporate more readily from the oceans. Consequently, as ice sheets develop, they sequester <sup>16</sup>O and the oceans become enriched in <sup>18</sup>O. The ratio of the two isotopes ( $\delta^{18}\text{O}$ ) in the seawater is dependent on the amount of ice that is locked into ice sheets and glaciers, and



**Figure 1.** The uncorrected sea level curve of Rohling et al. (2017) from the eastern Mediterranean (a) was used by Avila-Cervantes et al. (2020) to reconstruct the coastlines on the Isthmus of Panama during the LIG (b) leading them to propose the Isthmus was effectively breached at this time. However, their LIG sea level estimate was derived from data affected by anomalous values from sapropel events (sap. in D). Rohling et al. (2017) identified these events and produced, in the same paper, a corrected sea level curve (the red line in D). It is widely accepted that RSL was only slightly higher than it is today at the LIG and our findings tentatively suggest RSL was ca. +3 m around the Isthmus of Panama. Consequently, the form of the Isthmus during the LIG was almost identical to today (e). In addition, Avila-Cervantes et al. (2020) applied an RSL of  $-200$  m in the LGM (c) but typical glacial conditions on the Isthmus were around ca.  $-100$  m (Gowan et al. 2021) (f). Higher-resolution versions of these new paleogeographic models (i.e., E and F) are available in Figure S1, and the full model with sea level animations and a discussion of the caveats of using these types of reconstructions are available in Titcomb and O'Dea (2020). Horizontal dashed green line on D represents modern sea level (0 m), and the pink dashed line represents the maximum eustatic sea level that would be reached if all ice caps, ice sheets, and glaciers melted (ca. +66 m; Davies 2016), even though that was not the case during the LIG.

therefore it is an excellent proxy for sea level. As organisms secrete their calcium carbonate ( $\text{CaCO}_3$ ) skeletons, the  $\delta^{18}\text{O}$  of the seawater is reflected in the  $\delta^{18}\text{O}$  of their shells, giving paleontologists the chance to reconstruct past sea levels by measuring the  $\delta^{18}\text{O}$  in fossil skeletons. Using  $\delta^{18}\text{O}$  in fossil organisms from high-resolution ocean cores to build sea level curves in this way is now standard practice, applied globally and regionally with ever increasing resolution (e.g., Zachos et al. 2001; Miller et al. 2020).

Avila-Cervantes et al. (2020) used the  $\delta^{18}\text{O}$  record presented by Rohling et al. (2017) to estimate sea level changes on the Isthmus of Panama during the late Pleistocene. The data of Rohling et al. (2017), however, was derived from the Eastern Mediterranean and not from Central America. Sea level response to glacial cycles can vary substantially between regions around the globe because of local tectonics, differential thermal expansion, basin morphologies, tidal differences and a number of other

processes such as glacial isostatic adjustment, ocean basin collapse and siphoning; all of which are especially important when comparing sea level responses in equatorial regions and those in higher latitudes (e.g., Khan et al. 2019). In short, sea level estimates made in the enclosed eastern basin of the Mediterranean cannot be applied to the southwestern Caribbean and Tropical Eastern Pacific in the way Avila-Cervantes et al. (2020) did without the risk of introducing significant regional differences.

More problematic, however, is that the  $\delta^{18}\text{O}$  data used by Avila-Cervantes et al. (2020) is heavily influenced by local phenomena known as “sapropel events.” These events occurred when African monsoonal conditions intensified resulting in a significant increase in freshwater run-off into the Mediterranean through the Nile river. These freshwater pulses enriched Eastern Mediterranean seawater with lighter  $^{16}\text{O}$  resulting in striking negative shifts in  $\delta^{18}\text{O}$  recorded in fossil foraminifera (Ryan 1972; Rohling et al. 2015). These negative  $\delta^{18}\text{O}$  excursions are imprinted over the glacial-interglacial pattern of  $\delta^{18}\text{O}$  (Fig. 1, “sapr.”), and the data are therefore unsuitable for sea level reconstruction without an isotopic correction. Rohling et al. (2017) did identify the sapropel events in the original Eastern Mediterranean  $\delta^{18}\text{O}$  record, described their erroneous impact on the interpretations of  $\delta^{18}\text{O}$  measurements to resolve sea level estimates, and subsequently presented a corrected sea level curve.

Unfortunately, however, Avila-Cervantes et al. (2020) took the uncorrected, sapropel-influenced,  $\delta^{18}\text{O}$  data at face value and used it to estimate sea levels on the Caribbean and Pacific sides of the Isthmus of Panama. One of the largest sapropel events coincided with the LIG, which lead Avila-Cervantes et al. (2020) to propose that relative sea level (RSL) on the Isthmus of Panama during the LIG was 100 m higher than today and the seas “nearly completely flooded the isthmus to connect the two coasts.” Indeed, their paleogeographic maps show apparent seaway connections between the Pacific and Caribbean in both the Canal Zone and the Atrato Basin (Fig. 1). This is a significantly overestimated sea level for the LIG and it is universally accepted that global eustatic sea levels during the LIG were only ca. 1–4 m higher than today (Clark et al. 2020).

More local estimates from tectonically stable areas around the Caribbean suggest that RSL in the LIG was between –3 and +5 m (e.g., Muhs et al. 2012; Simms 2021). A 100 km long suite of raised reefs of presumed LIG age in the Guna Yala region of Caribbean Panama offer the only currently available way to estimate RSL during the LIG from the seas around the Isthmus itself (Hendrickson et al. 2011). These reefs are up to 10 m higher than their life position relative to modern sea levels. Uplift rates of the isthmus in the last million years were on average 59 m per million years (O’Dea et al. 2016), which results in an uplift amount of 7 m in the last 125 kyrs since the LIG and provides a crude estimate of RSL of ca. +3 m, corroborating other Caribbean es-

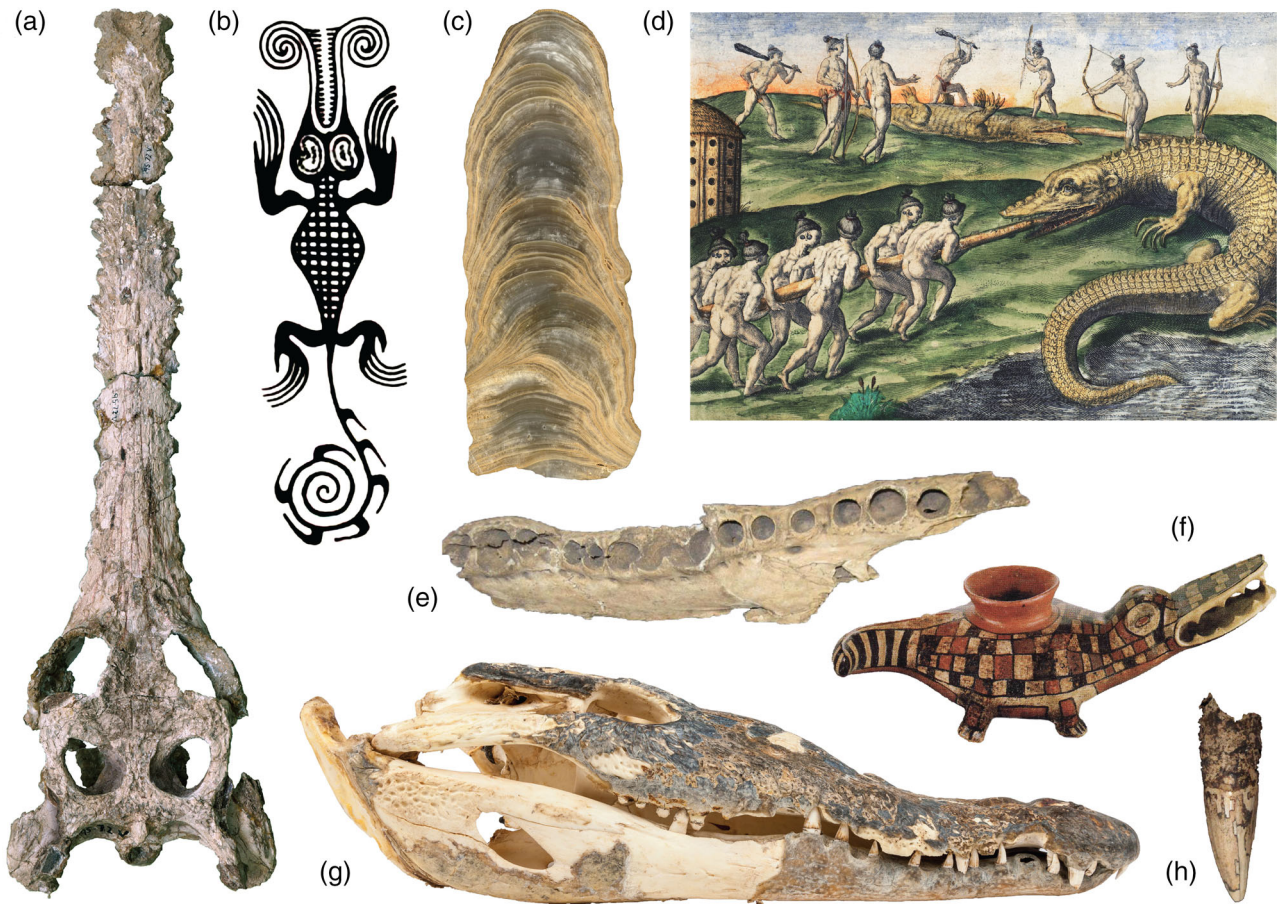
timates. There are no LIG RSL estimates for the Pacific side of the Isthmus and we know of no LIG wave-cut platforms or raised reefs that could be used to estimate RSL. In our new models, we therefore use the Guna Yala estimate of ca. +3 m RSL during the LIG for both sides of the isthmus because it corroborates regional estimates and global averages. We find that during the LIG, the Isthmus was little different in form to today, contrasting sharply with the reconstruction of Avila-Cervantes et al. (2020) that shows the isthmus effectively breached at this time (Fig. 1).

Avila-Cervantes et al. (2020) invoked the erroneous +100 m estimate of LIG RSL and flooding of the isthmus as a potential cause of their observed oldest genetic signature of separations in trans-isthmian crocodile populations. Gene flow between populations of fully marine species (e.g., reef fish, urchins, and molluscs) ceased ca. 2.8 Ma when shallow interoceanic straits were finally severed by tectonic uplift and volcanic activity (Lessios 2008; O’Dea et al. 2016). *Crocodylus acutus* is a predominantly marine coastal species yet it also inhabits river systems (Balaguera-Reina et al. 2015), has been observed at remarkably high elevations on the Isthmus today (e.g., Lake Yeguada, 650 m above sea level, R. Cooke, Pers. Comm.), and although normally has home ranges less than 1 km (Balaguera-Reina et al. 2016) can migrate hundreds of kilometers (Cherkiss et al. 2014). It is therefore unnecessary to invoke the flooding of the Isthmus to explain post-Pliocene transisthmian gene flow in crocodile populations. This is a topic noted briefly by Avila-Cervantes et al. (2020) who suggest that “the most obvious [scenario] is that the Isthmus is only a semipermeable barrier to a large-bodied amphibious species.” We wholeheartedly agree with this characterization.

The LGM paleogeographic reconstruction presented by Avila-Cervantes et al. (2020) is incorrect. It is widely accepted that eustatic sea levels fell to a maximum of ca. 120 m below modern levels during maximum ice sheet extent (Clark et al. 2009; Gowan et al. 2021). Avila-Cervantes et al. (2020) recognized this in their text, but in their figure 5 they used a LGM RSL of –200 m to reconstruct their coastlines. The most recent estimate of RSL on the Isthmus at the LGM is –100 m (Gowan et al. 2021), and we use this value to produce updated paleogeographic reconstructions during the LGM (Fig. 1).

Avila-Cervantes et al. (2020) concluded that “...divergence times between the Caribbean and Pacific populations are about 20,000 years ago...” and that this “...overlap[s] with the Last Glacial Maximum (LGM)...” The estimated times of separation of Caribbean and Pacific populations reported by Avila-Cervantes et al. (2020) in tables 3 and 4 (i.e., 121.25, 97, 40.75, 38.6, 32.6, and 30.9 ka) all predate, by many thousands of years, the LGM which occurred at 26–20ka (Clark et al. 2009). Estimated times of secondary contact reported in their table 4 (i.e., 25.9, 24.3, 20.7, 19.6 and 19.5 ka) are more coincident with





**Figure 2.** A variety of records can help understand the ecological and evolutionary histories of crocodiles and their interactions with humans. (a) Miocene *Aktiogavialis caribesi* (Salas-Gismondi et al. 2019) (courtesy R. Salas-Gismondi). (b) *C. acutus* design on vessel, redrawn from Sánchez and Cooke (1998). (c) Speleothem from Bastimentos, Panama that records precipitation conditions over millennia (Winter et al. 2020) (courtesy M. Lachniet). (d) Native Americans killing crocodiles by ramming a pole down its throat, turning it over, beating it with clubs, and shooting it with arrows. Engraving by Theodor de Bry, 1591 (courtesy Wikimedia). (e) *C. acutus* maxilla from a ca. 955 years BP midden, Caribbean Panama (Wake et al. 2013) (courtesy T. Wake). (f) Pre-European contact crocodilian figural vessel from Panama (courtesy A. Lara). (g) Museum specimen of *C. acutus* skull (courtesy K. Grace/Florida Museum). (h) *C. acutus* tooth from ca. 1100 years BP midden, Guatemala (courtesy A. Sharpe) (Sharpe et al. 2020).

the LGM. However, later in their study, Avila-Cervantes et al. (2020) present another secondary contact estimate by incorporating “heterogeneous migration models into  $\delta a\delta i$ ”—an approach which Avila-Cervantes et al. (2020) considered more accurate. This later secondary contact was estimated at 19.6–5.7 ka, which postdates the LGM. In short, there is little temporal correspondence between demographic and sea level events.

Avila-Cervantes et al. (2020) put forward the hypothesis that the LGM sea level lowstand would have reduced suitable crocodile habitat and isolated populations, and this could have caused populations to separate at this time. To explore this hypothesis, it would be necessary to estimate the geographical extent of suitable crocodile habitat and combine it with reconstructions of past ecosystem states. A cursory analysis of our paleogeographic maps (Titcomb and O’Dea 2020) demonstrates that

the aerial extent of the low elevation coastal zone has been highly dynamic through the late Pleistocene and Holocene. Interestingly, the timing of expansion and contraction of the low elevation coastal zones was asynchronous on the two coasts of the Isthmus because of the dramatically different shapes of the shelves. The maximum extent of the low elevation coastal zone seems to have peaked around the LGM (or shortly after) on the Pacific side and at the LIG on the Caribbean side. More detailed modeling is required, but doing so could help resolve the extent of potentially suitable crocodile habitat at times in the past and provide quantitative data with which to test potential driving mechanisms behind observed population contractions and secondary contacts.

Regional shifts in precipitation associated with glacial-interglacial cycles are another driver of crocodile biogeography

and dispersal that we suggest should be considered as potentially important. In her reviews of multiple proxies, Piperno (2006, 2007) estimated that the lower Isthmian region was around 30–50% drier during the LGM than today. Rainfall is critical for the success of saline-intolerant *C. acutus* hatchlings which, unlike adults, have low survival in droughts (Mazzotti 1999). This is reflected in the distribution of modern *C. acutus* across areas of high rainfall. The drier conditions during glacial periods may therefore have resulted in a *reduction* in optimal conditions for *C. acutus*, and consequently impacted population sizes and dispersal abilities.

We present these hypotheses not as definitive explanations but as equally valid potential drivers that must be considered in conjunction with sea level. Climate and precipitation on the Isthmus changed dramatically over the late Pleistocene and Holocene (Lachniet et al. 2004; Piperno 2007) and almost certainly played important roles in past distributions given what we know about the modes of life and life histories of *C. acutus* (Mazzotti 1999; Rossi et al. 2020). Incorporating paleoclimate data into demographic models should therefore be enriching. Likewise, because of the marine shelf topographies, the past extent of suitable crocodile habitat on either side of the isthmus followed unique dynamics through the Late Pleistocene and Holocene. Better models that incorporate records of habitat types from archaeological and paleoecological records would be beneficial for understanding historical processes in a wide range of terrestrial and coastal taxa.

In summary, we find significant errors with the sea level estimates and paleogeographic reconstructions of Avila-Cervantes et al. (2020). To prevent these errors propagating into future studies, we present new paleogeographic reconstructions which more faithfully describe the extent of sea level change on the Isthmus in the Late Pleistocene. We also find that contrary to Avila-Cervantes et al. (2020), their estimated timings of demographic events do not appear to coincide with sea level events. With our new models and a review of timings we therefore find little evidence that sea level was an important driver of the estimated demographic events presented by Avila-Cervantes et al. (2020). We do not claim that sea level changes were not important for historical crocodile gene flow and divergences. Instead, we find value in exploring other potential drivers, such as past habitat extent and paleoclimates, alongside robust data on past sea levels. A wealth of fossil, prehistoric and historical records of *C. acutus* and paleoclimatic data are available that could be used in concert with genetic data to broaden our understanding of the historical biogeography and evolution of *C. acutus* (Fig. 2).

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA ARCHIVING

The data that support this study are openly available on Figshare at: <https://doi.org/10.25573/data.11919276>.

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