There is a considerable controversy about whether western Amazonia was ever covered by marine waters during the Miocene [23 to 5 Ma (million years ago)]. We investigated the possible occurrence of Miocene marine incursions in the Llanos and Amazonas/Solimões basins, using sedimentological and palynological data from two sediment cores taken in eastern Colombia and northwestern Brazil together with seismic information. We observed two distinct marine intervals in the Llanos Basin, an early Miocene that lasted ~0.9 My (million years) (18.1 to 17.2 Ma) and a middle Miocene that lasted ~3.7 My (16.1 to 12.4 Ma). These two marine intervals are also seen in Amazonas/Solimões Basin (northwestern Amazonia) but were much shorter in duration, ~0.2 My (18.0 to 17.8 Ma) and ~0.4 My (14.1 to 13.7 Ma), respectively. Our results indicate that shallow marine waters covered the region at least twice during the Miocene, but the events were short-lived, rather than a continuous full-marine occupancy of Amazonian landscape over millions of years.

**INTRODUCTION**

The Neogene history of Amazonia is essential for understanding the evolution of the rainforest and associated fauna living in one of the most diverse places on Earth (1). A central question about our understanding of Amazonia remains unsolved: Did continental-scale marine flooding occur in western Amazonia during the Neogene? Miocene marine transgressions in the continental interior would have had a profound effect on the diversification and structuring of both terrestrial and aquatic Neotropical communities (1–6).

To date, about 80% of Amazonian landscape is occupied by terra-firme forest, where flooding is rare, whereas ~20% is characterized by wetlands (annually flooded floodplains with isolated lakes and river-bound oxbows) (7, 8). Flooded and terra-firme forests have distinctive floras that are among the most diverse on the planet (9). However, during the Miocene, the situation in western Amazonia was very different. Widespread occurrence of Miocene sediments indicates that subsidence of western Amazonian basins was active, extensive (1, 10), and probably driven by plate–mantle interaction associated with the rise of the Andes (11). These Miocene sediments, known as the Solimões, Pebas, and Acre formations, are on average 250 to 300 m thick but, in some places, can be more than 1000 m in thickness (12, 13). Many of these sediments have been studied over the years (for a more comprehensive list of publications, see the Supplementary Materials) (14–19). Previous investigations focused primarily on isolated river outcrops, where generally only 5 to 60 m of strata are exposed. Lack of exposure makes it very difficult to study a complete and continuous Miocene sequence.

There are several conflicting interpretations of the Miocene depositional environment in western Amazonia. They include (i) an epi-continental shallow sea that covered the Amazon for millions of years (4, 20); (ii) a large freshwater megalake, either long-lived Neogene [15 My (million years)] or Pleistocene-Holocene (16); (iii) a fluvial-lacustrine system with extensive floodplains and a few marine incursions (17, 21–23); (iv) a high frequency of transgressive-regressive bay-margin successions (18, 24); (v) avulsive fluvial belts in a floodbasin-floodplain environment lacking marine influence (12, 25); (vi) a long-lived [23 to 8 Ma (million years ago)] megalake/wetland system (or “para-marine megalake,” as it is an environment without a modern analog), composed of widespread and semipermanent aquatic ecosystems (26, 27); (vii) a complex series of interconnected megalakes overlying a regional peneplain (14); and (viii) a tidal system (28). All of these interpretations involve discussion of the evidence for marine incursions during the Neogene. Did they occur, and if so, how frequently and for how long?

All recent studies show a biogeographic connection between western Amazonia and the Llanos Basin of Colombia during most of the Miocene (4, 20, 22, 26, 29), yet direct evidence for a marine pathway is lacking. Marine incursion into Amazonia, if any, should have come primarily through the Colombian Llanos (3, 18, 20) and the Venezuelan Barinas/Apure and Eastern basins (fig. S1) (19). We analyzed age, fossil record, geochemistry, and depositional environments on two cores from a nearly horizontal Miocene sequence in the Llanos and Amazonas/Solimões basins, together with seismic information and electric logs, to identify the timing, duration, and frequency of marine floodings during the Miocene in western Amazonia (see Fig. 1, fig. S2, Materials and Methods, and the Supplementary Materials).

**RESULTS**

**Marine intervals**

A total of 933 palynomorph types and 54,141 individuals were counted and identified from the cores Saltarin and 105-AM (tables S1 and S2). Saltarin has two stratigraphic intervals composed of laminated, greenish mudstones that contain a high proportion of marine palynomorphs (MPs) (see Fig. 1, figs. S3 and S4, and the Supplementary Materials). The lower interval spans 645.6 to 617.6 m (MP mean = 24.3%; table S3), and the second interval spans 548 to 408.4 m (MP mean = 39.6%; table S3). The high MP percentages in those intervals contrast with a significantly lower proportion of MPs in interbedded intervals (interval...
Fig. 1. Core correlation and marine intervals in the Llanos and Amazonas/Solimões basins. (A) Location of seismic lines, wells, and outcrops used in this study in the Llanos Basin of Colombia and in the Amazonas/Solimões Basin near the Colombia-Brazil boundary. (B) Correlation of the stratigraphic units drilled in the Saltarin and 105-AM wells using age control established by palynology and sequence stratigraphy analysis. The depositional environment interpretation and the abundance of MPs identify the two intervals of marine incursions, the early Miocene incursion (EMI) and the middle Miocene incursion (MMI), in each well and indicate thicker deposition of marine deposits in the Llanos Basin. Biostratigraphic zones follow those in the study of Jaramillo et al. (56). MD, meters depth. (C) Macrofossils found in the Saltarin well: (1) tooth of a Carcharhiniformes shark (fig. S6) and (2) mantis shrimp (fig. S7). These fossils are further evidence of the marine incursion that covered the Llanos Basin. See the Supplementary Materials for a detailed description and identification of these fossils. Depositional environments were grouped into three broad categories: (i) Continental environment that represents accumulation in fluvial channels and adjacent floodplains by subaerial exposure; (ii) Marginal environment that represents accumulation on deltaic plains; low-energy wetlands with swamps, ponds, and channels; and shallow freshwater lacustrine systems; and (iii) Marine environment that represents shallow marine water. Notice that the Marine environment of 105-AM is shallower and less saline than the marine intervals in Saltarin.
are strictly marine stomatopods that dwell in burrows in soft, muddy to sandy sediments of tropical and subtropical low intertidal to shallow subtidal habitats (Saltarin, 2017; Horniella lunarensis). The mean proportion of MPs across the section (mean = 3.9%) and similar among the five stratigraphic intervals (table S3). The variation of lithological associations in both marine intervals of 105-AM, the short periods of subaerial exposure to develop paleosols in the lower marine interval, and the lower proportion of MPs in both intervals compared to those in Saltarin indicate that the Marine environment of 105-AM is shallower and less saline than the marine intervals in Saltarin (Fig. 1 and table S3).

Both marine intervals in Saltarin produce two well-defined subtabular, parallel seismic intervals that can be traced throughout the entire Llanos Basin, indicating their widespread extension. These two intervals were deformed near the Vaupés Arch during the late Miocene (Zell et al. 2015). Although this arch separates the Llanos Basin from the Amazonas/Solimões Basins, seismic data suggest that during the early and middle Miocene, the arch was not active and both marine incursions extended farther to the south, reaching the Amazonas/Solimões Basin (see Fig. 2, figs. S9 and S10, and the Supplementary Materials).

The biostatigraphic and sequence stratigraphic analyses of Saltarin (see the Supplementary Materials) indicate that the core spans the early to the late Miocene, biostatigraphic zone T-12 Horniella lunarensis to zone T-17 Cyathocidites annulatus, 18.5 to 5.5 Ma (see Fig. 1, fig. S11, and the Supplementary Materials). The lower marine interval (645.6 to 617.6 m) extends from zones T-12 to T-13, ~18.1 to 17.2 Ma, respectively, early Miocene, lasting ~0.9 My (Figs. 1 and 2 and fig. S4). The upper marine interval (548 to 408.4 m) extends from zones T13 to T16, 16.1 to 12.4 Ma, respectively, middle Miocene, spanning ~3.7 My (Fig. 1 and fig. S4).

Graphic correlation of 105-AM indicates that the core spans the early to the late Miocene, biostatigraphic zone T-12 Horniella lunarensis to zone T-16 Fenestrites spinosus, 18.8 to 10.7 Ma (see Fig. 1, fig. S12, and the Supplementary Materials). The lower marine interval (293.4 to 284 m) lies within zone T-12, 18.0 to 17.8 Ma, early Miocene, lasting ~0.2 My (Figs. 1 and 2). The upper marine interval (101.4 to 96.7 m) lies within zone T-15, 14.1 to 13.7 Ma, middle Miocene, lasting ~0.4 My (Figs. 1 and 2 and fig. S4).

**DISCUSSION**

Hoorn et al. (1) described three major phases in Amazonia: (i) 24 to 16 Ma, lacustrine conditions alternating with episodes of fluvial drainage and marginal marine influence; (ii) 16 to 10.5 Ma, maximum extent of lacustrine conditions with a marginal marine influence; and (iii) 10.5 to 7 Ma, complex environment of deltaic, estuarine, and fluvial environments. Our results indicate that both the Llanos and Amazonas/Solimões basins of western Amazonia experienced two distinct marine transgressions (Figs. 1 and 2 and fig. S4). In the Llanos Basin, the first marine transgression completely covered the basin during the early Miocene and lasted ~0.9 My (18.1 to 17.2 Ma). This transgression event is also registered in the Amazonas/Solimões Basin in northwestern Amazonia, but its duration was much shorter there, lasting only ~0.2 My (18.0 to 17.8 Ma) (Figs. 1 and 2 and fig. S4). The second transgression in the Llanos Basin occurred during the middle Miocene and lasted ~3.7 My (16.1 to 12.4 Ma). This transgression event continued toward the Amazonas/Solimões Basin in northwestern Amazonia, but there, it lasted a much shorter time, only ~0.4 My (14.1 to 13.7 Ma) (Figs. 1 and 2 and fig. S4). All evidence indicates that marine incursions transformed fluvio-lacustrine landscapes into a gently sloping marine environment, being shallower and with lower salinities in 105-AM than in Saltarin. In both marine intervals, the onset of the transgression occurred earlier in the Llanos Basin or at the same time in the Amazonas/Solimões Basin and lasted longer in the former (Figs. 1 and 2 and fig. S4). This geographic pattern would be expected if transgression progressed from the Caribbean into western Amazonia, as many have suggested (3, 18–20). Our data suggest that the Llanos Basin transformed into a fluvial basin around 11.5 Ma, as Saltarin indicates, a condition that still prevails today (Figs. 1 and 2, figs. S3 and S4, and the Supplementary Materials). Therefore, any possible late Miocene incursion into western Amazonia (3) would have been derived from pathways other than the Llanos, like the Amazon trunk valley. Correlation of these two events with strata in Putumayo, Napo, Pastaza/Maraño, Acre, Ucayali, and Madre de Dios basins (fig. S1) remains uncertain and is beyond the scope of the present analysis.
**Fig. 2.** Paleogeographic reconstruction of the two marine incursions in the study. (A to I) The reconstruction is based on the stratigraphic correlation shown in Fig. 1 and on the stratigraphic analysis of nine wells in the Llanos Basin and one well and nine outcrops in the Amazonas/Solimões Basin (see the Supplementary Materials for descriptions of sections and a movie based on the construction of 30 paleogeographic maps). Marine ingressions occurred earlier in the Llanos Basin than in the Solimões Basin. The two basins were separated during the late Miocene (G, H, and I) by the uplift of the Vaupés Arch. Notice that marine intervals are shallower and less saline toward the 105-AM region.
The thin nature of both marine intervals in 105-AM (9.3 and 4.5 m) could explain the large discrepancy in interpretations about possible marine incursions in Amazonia (see the Supplementary Materials for an extensive list of references). Better understanding of the Neogene of western Amazonia will require a high-resolution study of multiple sediment cores spanning the entire Neogene sequence throughout the many basins that compose western Amazonia (35). Nevertheless, it is evident that Amazonian landscape has had major changes over the past ~20 Ma. We need to understand those changes across the vast Amazonian landscape, because they must have had a profound effect on the evolution and biogeographic distribution of its ancient and extant biota as well as on the modern and ancient climate of the continent.

**MATERIALS AND METHODS**

**Location of study sites and seismic lines**

The first core, Saltarin, is located in the Llanos Basin in eastern Colombia (4.612°N and 70.495°W; 671 m thick) (see Fig. 1, figs. S2 and S3, table S5, and the Supplementary Materials). The second core, 105-AM, is located in the Amazonas/Solimões Basin in northwestern Brazil (4.25°S and 69.93°W; 405 m thick) (see Fig. 1, figs. S2 and S8, table S5, and the Supplementary Materials). We analyzed the sedimentology of both cores together with two-dimensional (2D) seismic lines, the electric logs of 14 wells located between Saltarin and 105-AM, and previously published information on 15 outcrops (17, 22, 36) and one core (see Fig. 2, figs. S2 and S13, tables S5 and S6, and the Supplementary Materials) (21). A total of 1148 km of 2D seismic lines were selected to correlate the two intervals of marine incursions in the Llanos Basin with the intervals of marine incursions in the Amazonas/Solimões Basin (EMI and MMI) (fig. S2 and table S6). Seismic lines selected in the distal Llanos Basin cover the area between the Saltarin well and the northernmost expression of the Vaupés Arch in the subsurface (fig. S13). These seismic lines were analyzed in conjunction with the electric logs of nine wells (fig. S9). In the Amazonas/Solimões Basin, a few seismic lines along major rivers in Colombia and a published seismic line in Brazil (37) allowed us to compare seismic facies between the two basins (figs. S2 and S14); however, there are no wells near those seismic lines that would permit a better integration of seismic facies with stratigraphic units (fig. S10). A total of nine isolated outcrops of Miocene units along river margins, as well as two cores in the Solimões Basin, are the only reference for identification of the uppermost stratigraphic level (fig. S2 and table S5). Analysis was restricted to the Llanos and Amazonas/Solimões basins (fig. S1).

**Sedimentology and sequence stratigraphy**

The cores Saltarin and 105-AM were described at a scale of 1:50 for identification of grain-sized trends, sedimentary structures, clast composition, thickness of lamination, bioturbation patterns, and macrofossil identification, all of which are used to identify individual lithofacies. The association of lithofacies within a vertical and conformable succession supports the interpretation of depositional environment, following the criteria of James and Dalrymple (38) and Miall (39). Sequence stratigraphy analysis follows the criteria described by Catuneanu et al. (40) for the definition of dominant stacking patterns of deposition (aggradation, progradation, and retrogradation) and bounding surfaces (sequence boundaries and maximum flooding surfaces) that could be used for regional correlation. For fluvial strata, we used the terms “low accommodation” and “high accommodation” system tracts (40). For homogeneous fine-grained strata accumulated in shallow waters, we used a combination of lithofacies and biostratigraphy data to identify the stratigraphic surfaces of correlation. All sedimentological, biostratigraphic, and stratigraphic data are stored and displayed using the SDAR software (41). We grouped depositional settings into three major depositional environments: Continental, Marginal, and Marine. (i) The Continental environment includes interbeds of massive to cross-bedded sandstones and conglomeratic sandstones with a sharp lower contact and light-colored mudstones that can contain sideritic spherulites and nodules. These lithofacies represent accumulation in fluvial channels and adjacent floodplains, with evidence of paleosol development by subaerial exposure. (ii) The Marginal environment includes greenish to gray, laminated, bioturbated, and locally fossil-rich mudstones coarsening up to very fine grained to medium-grained sandstones with coal interbeds. The association of these lithofacies represents accumulation on deltaic plains; low-energy wetlands with swamps, ponds, and channels; and shallow freshwater lacustrine systems. (iii) The Marine environment includes planar-laminated and massive fine-grained lithofacies with high proportions of MP. In 105-AM, marine lithofacies also include organic matter (peat) and fossil fragments. The content of both MP (dinoflagellates, marine acritarchs, and foraminifera linings) and macrofossils in those lithofacies supports the marine environment interpretation, yet salinities may have been in part very low, ranging from >5 to up to 30 practical salinity units (36).

**Marine intervals**

All the analyses, unless noted, were performed using R for Statistical Computing (42). All comparisons are the result of two-sided t tests to evaluate the equality of means in two unpaired samples. P value is reported for each test at the appropriate point in the text, along with degrees of freedom (df) calculated using the Welch modification to account for different variances in the groups being compared. We measured the proportion of terrestrial palynomorphs (pollen and spores), MP (dinoflagellates, marine acritarchs, and foraminifera linings), and freshwater indicators (Pediastrum and Botryococcus) in 233 samples, which included 138 samples from Saltarin (1 sample every ~4.7 m) and 95 samples from 105-AM (1 sample every ~3 m). We also measured the BIT index of 18 samples from Saltarin to quantify the input of marine-dwelling Thaumarchaeota versus soil bacteria. Two marine macrofossils found in Saltarin were described and identified. Pollen samples were prepared following standard palynological techniques of digesting sediments in mineral acids (HF and HCl), alkaline treatment in KOH, heavy liquid separation using ZnBr2, and sieving (43). We used panning rather than centrifugation to avoid breaking apart fragile palynomorphs (for example, foramin linings). Samples were processed at the laboratory of Paleoflora, Bucaramanga, Colombia. At least 300 palynomorph grains were counted per sample when possible. Palynomorphs were grouped into three broad categories: terrestrial palynomorphs (pollen and spores), MP (dinoflagellates, marine acritarchs, and foraminifera linings), and freshwater algae indicators (Pediastrum and Botryococcus). These groups have been used extensively to distinguish continental, marine, and large-lake sequences (43–48). The proportion of the sum of MP's and freshwater algae indicators (lacustrine) relative to the total sum of each sample was calculated. Samples with counts lower than 100 grains were excluded from the analysis. The BIT index is a proxy for the input of soil and riverine organic matter in marine environments [see the study of Schouten et al. (30) and references therein]. We measured the BIT index of 18 samples from Saltarin to quantify the input of
marine-dwelling Thaumarchaeota versus soil bacteria following the standard technique of Schouten et al. (49) (see the Supplementary Materials).

**Paleogeographic reconstruction**

The construction of 30 paleogeographic maps illustrates the extension of Continental, Marginal, and Marine environments from ~18.4 to ~10.5 Ma. The source of the dating is discussed in the next section. This quantified and age-controlled reconstruction of the temporal and spatial change of depositional environments and illustration of the extension of marine incursions was carried out in the open-source software GPlates (see file S1) (50). This software uses the state-of-the-art global plate reconstruction models, although accumulation occurs in a minor deformed segment of the Andean foreland and intracratonic basins. We used the global coastline and plate movement of South American craton of GPlates (51) as the base information to load our geological data (wells, outcrop localities, and seismic lines) and the interpretation of (i) boundaries among nondeposition, Continental, Marginal, and Marine environments; (ii) location of northern Andes deformation front [modified from Reyes-Harker et al. (52)]; (iii) interpreted location of depositional boundary along the Guiana Shield; and (iv) location of intrabasinal uplifts. Paleogeographic reconstructions of the marine intervals over the Marginal and Continental environments used (i) lithological associations of strata bounded by stratigraphic surfaces of correlations in the two analyzed wells (Saltarin and 105-AM), which have detailed age control; (ii) lithological control on the nine wells in the Llanos Basin, two wells with palynological report of marine influence (53), and one well in the Solimões Basin; (iii) palynological control and sedimentological analysis on nine outcrops of the Colombian Amazonas published in the literature; (iv) location of the northern Andes deformation front for middle and late Miocene (52); (v) provenance analysis from Hoorn (22) and Salamanca Villegas et al. (19) for the Amazonas outcrop sections, as well as from Bayona et al. (54) for the Saltarin well; (vi) location of internal uplifts in the Llanos Basin based on seismic information, as well as location of regional structural highs, such as the Vaupés Arch, Baúl High, and Macarena Range (see section S4.1); and (vii) present extent of Miocene strata on the Guiana Shield.

**Chronology of cores**

Dating and correlation of the two cores were done using sequence stratigraphy together with graphic correlation (55) of palynological data using a biostratigraphic zonation for the region that is calibrated with magnetostratigraphy, carbon isotopes, and foraminifera (56). We also measured the organic carbon stable isotope value in 118 samples from Saltarin and 71 samples from 105-AM and analyzed the mollusk fauna found in 105-AM to calibrate age determinations. Isolated outcrops reported in the literature were also used to establish the extent of any possible marine event. We used graphic correlation to analyze the palynological information. Graphic correlation (55, 57, 58) has been extensively used over the past decades in multiple studies (56, 59–61). It does not make the a priori assumption that first and last appearance data in a section record speciation and extinction events. It combines the information of multiple sections to find the true stratigraphic range of a taxon; therefore, the use of an "index" fossil is not necessary because the whole assemblage is being compared. The graphic correlation analysis was done using GraphCor (62), and it was applied to the records of both Saltarin and 105-AM. We used the standard composite section of Jaramillo et al. (56). Three rounds of correlation were performed until the line of correlation (LOC) for each section became stable. Derived from both LOCs of this first step, a LOC between Saltarin and 105-AM was produced. Sequence stratigraphic events were added to this LOC to improve the correlation between the data provided by biostratigraphy (Fig. 1). The modified LOC of Saltarin versus 105-AM was then extrapolated to the LOC of both sections versus the composite. The new LOC lines were reevaluated using the biostratigraphic data. This process was repeated for several rounds until the LOCs of both Saltarin versus composite, 105-AM versus composite, and Saltarin versus 105-AM were stable.

To transfer the stratigraphic position of each sample in the two well cores from meters to geologic time, we assumed a linear sedimentation rate between the points in the LOC. It is reasonable to assume linearity because the composite does not have major stratigraphic breaks. The calibration of Jaramillo et al. (56) was used, and the R (42) code used for the process can be found in file S2. The geological time scale follows Gradstein et al. (63) and Hilgen et al. (64). It is important to stress that ages provided in this research are relative, and the precision goes as far as the calibration points for the zonation. Ages between calibration points are derived from linear interpolation. Therefore, we do not argue that our ages are precisely calibrated with the geological time record, but they indicate a relative age compared to sediments above and below. These ages represent a hypothesis, and it is based on the best information we have at the moment; they could change as more calibration points are added to the zonation or if a calibration point is shifted or the LOC of each section is modified. Our ages are fully replicable, as we provide the LOC, the full zonation, and the calibration points. Stable carbon isotopes were used to support the age determinations produced by the graphic correlation analysis. Stable carbon isotope values of bulk organic matter (δ13C) were measured via flash combustion at 1020°C in a Costech elemental analyzer fitted to a Thermo Finnigan DELTAplus XL isotope ratio mass spectrometer (Department of Geological Sciences, University of Florida). Carbonate present in the samples was removed by digestion using 1.0 N HCl. Analytical precision and accuracy were determined by repeated analysis of the USGS40 standard. Overall uncertainty was better than 0.08‰. Organic carbon content (total organic carbon) was determined on the basis of measurement of total carbon by combustion using a Carlo Erba elemental analyzer minus total inorganic carbon measured by acidification using the AutoMate Prep Device coupled to the UIC 5011 CO2 Coulometer.

**SUPPLEMENTARY MATERIALS**

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/5/e1601693/DC1

section S1. General information
section S2. Sedimentology and sequence stratigraphy analyses
section S3. Marine intervals
section S4. Basin-wide correlations
section S5. Chronology of cores
section S6. Sites from the literature used in this study
section S7. Other published sites beyond the boundaries of this study

fig. S1. Map of northwestern South America showing the sedimentary basins discussed in the text and the structural features that divide them.
fig. S2. Location of the nine wells in the Llanos Basin, two wells in the Amazonas/Solimões Basin, and 13 seismic lines used for this study (geographic coordinates in tables S5 and S6).
fig. S3. Sedimentological and sequence stratigraphic interpretation of the Saltarin well (see details of interpretation in table S7).
fig. S4. Graphic correlation of Saltarin versus 105-AM using geological time as scale in both axes, rather than stratigraphic thickness.
fig. S5. Photomicrographs of selected dinoflagellate cysts and acritarchs.
fig. S6. Carcharhiniformes gen. et sp. indet. tooth from the core Saltarin, Carbonera C2 Formation, early Miocene, 630.08 m, specimen MUN STRI-40967.
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