are terminal deletion derivatives of the *γ238* inversion (*11*).
59. K. D. Donaldson and G. H. Karpen, unpublished results.
60. In cases where partners were marked with the same genetic marker (most of Fig. 2B), disomic animals could not be positively identified in the F_1 generation. Therefore, in each experiment a large number (*30*) of randomly selected ry+ or y+ F_1 progeny (which includes both 1 Dp and 2 Dp animals) were outcrossed to *X^Y, y/0*; ry^{506} males. The 2 Dp F_1 animals used to estimate disjunction frequencies were identified by observation of high transmission rates in the F_2 scoring generation. Nondisjunction rates were calculated as above, except that the nondisjunction class was determined by doubling the number of 0 Dp animals in the F_2 generation. This correction was necessary because the 2 Dp nondisjunction progeny could not be distinguished phenotypically from the 1 Dp class in these crosses. The fact that recovery of the 0 Dp and 2 Dp classes did not differ significantly when both classes could be monitored independently strongly validates the use of this correction. Furthermore, outcrossing the F_2 ry+ progeny from putative *γ1230/γ1230* F_1 animals demonstrated that the F_2 progeny contained equal numbers of 0 Dp and 2 Dp animals (G. H. Karpen *et al.*, data not shown). This result confirmed both the disomic nature of the F_1 parents and the appropriateness of using the 0 Dp class to estimate nondisjunction.
61. Animals with two differentially marked minichromosomes and zero, one, or two copies of the $P(nod^+)$ transgene (*19*) were generated from the cross *y* ; $P(nod^+)$*/SM1, Cy* ; *ry* ; *31E*, y^+ females x *y*/Y ; $P(nod^+)$/ *Sp* ; *ry* ; *J21A*, ry^+ males (or *20A* or *10B*). The *y* ; $P(nod^+)$/*Sp*; *ry* female progeny provided the 2E+1T class, and the 2E+2T females were the *y*; $P(nod^+)$/ $P(nod^+)$; *ry* siblings. The *J21A* monosome siblings (y− ry+) were used for the transmission tests, whereas the *31E/J21A*, *31E/10B*, and *31E/20A* disomes (y+ ry+) were used in the nondisjunction tests. The 2E+0T control ND frequencies were taken from the data in Fig. 2A, because independent analyses demonstrated that the SM1 balancer raises nondisjunction frequencies significantly. For the *J21A* monosome transmission tests, the 2E+0T class used in the transmission assay were produced by the cross *y*; *ry*; *J21A*, ry^+ females x *y*/Y; $P(nod^+)$/ Sp ; *ry* males. All test females were crossed and the results analyzed as described (*56, 57*).
62. T. Murphy contributed significantly to discussions and data analyses, and his efforts are gratefully acknowledged. We also thank K. Cook, R. Kolodner, T. Murphy, and D. Weigel for comments on the manuscript, K. Afshar and R. S. Hawley for the nod^+ transgene stock (placW nod^+-15), J. Simon for the artwork in Fig. 4, and A. Dernburg, J. Sedat, and S. Hawley for communicating results before publication. This research was supported by a grant from the American Cancer Society (DB-1200), which we gratefully acknowledge.

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TECHNICAL COMMENTS

Miocene Deposits in the Amazonian Foreland Basin

In their report, Matti E. Räsänen *et al.* state that there is a tidal origin for the sedimentary sequences they studied in the western Amazon region (*1*). Their interpretation of these sequences in Acre, Brazil, as tidal, on the basis of a relatively small data set, implies the existence of a marine connection between the Caribbean Sea and the southern Atlantic Ocean. Background information and earlier work suggests that this conclusion is not the best explanation of the sediments in Acre. The sedimentary history and paleogeography of this area are more complex than Räsänen *et al.* or S. David Webb, in his Perspective (*2*), suggest.

The outcrops studied by Räsänen *et al.* represent a small (areal) part of the Miocene stratigraphic level. The Solimões Formation (also Pebas Formation), to which these sediments belong, crops out in a vast area of Brazilian, Peruvian, and Colombian Amazonia. This formation is up to 980 meters thick and is part of the infill of several sedimentary basins. In the last 20 years, extensive geological studies (*3–10*) have shown that the Solimões Formation was mainly formed in a fluvio-lacustrine system of Andean origin, which was periodically affected by marine ingressions. This fluvio-lacustrine system originated during the Middle Miocene as a result of the uplift of the Eastern Cordillera, and was the ancestor of the present Amazon River. Contrary to what Webb suggests (*2*), "substantial evidence" concerning the marine influence during the Miocene in the area was published (*7–10*) before the Räsänen *et al.* report appeared.

The changes in drainage patterns caused by the genesis of the paleo–Amazon River system and the abortion of the previously existing east-to-west–directed fluvial system had a major influence on the development of the ecosystem, the sedimentary history, and the paleogeography of Amazonia (*8–11*). Subsequently, when establishing a paleogeographic model for the Miocene history of Amazonia, both the fluvial dynamics as well as the tidal influence and marine ingressions should be included. Therefore, Webb's conception of an Amazon seaway as a cause of Amazonian floral and faunal diversity seems limited.

Räsänen *et al.* consider two possible depositional environments for the sediments they studied (p. 388), fluvial or tidal, and conclude that they are tidal. However, in a tropical fluvial environment such as that in which the Solimões Formation was deposited, periodical flooding of the overbank environment causes alternating mud and sand lenticles such as those described (*1*). Moreover, the north- to southeast-directed paleocurrents and the sediment composition of Andean origin coincide with the transport direction and the sediment composition reported for the paleo-Amazon River (*9*). Furthermore, Räsänen *et al.* relate the timing of the presumed seaway to the Late Serravallian, which is Middle Miocene (*12*), and not to Late Miocene, as the title of their report suggests. The base of the Late Miocene [~10.4 Ma (million years ago)] represents the largest drop in sea level in the entire Miocene; thus it is not likely that a marine ingression would occur. Moreover, during the Late Serravallian, the maximum sea level rise was estimated at about 50 m, whereas at the base of the Serravallian (~14.2 Ma), the maximum sea level rise was estimated at 150 m (*13*). If there was a marine ingression it would be thus more understandable if it occurred in this interval. Indeed, there is evidence elsewhere in Amazonia (*8–10*) of a base Serravallian marine ingression, on the basis of the presence of marine fossils and palynomorphs (*14*). In addition to this, the connection between the paleo-Amazon and the Atlantic was well established during the Late Miocene. The clastic sediments on the Guyana shelf and in the Amazon cone are evidence of the Amazon-Atlantic connection (*15–17*). Therefore, a Late Miocene marine connection between the Caribbean and the southern Atlantic at this same time is highly unlikely.

The Late Miocene sediments studied by Räsänen *et al.* are most likely fluvial, not tidal, and were probably deposited by the ancestral Amazon River. There were marine ingressions in Amazonia during the Early and Middle Miocene, but not in the Late Miocene. Moreover, during the Early and Middle Miocene, the connection between Amazonia and the sea had a more modest character than the seaway postulated by Räsänen *et al.* Their model might be applicable to the Cretaceous (for which marine deposits are well known to exist in the eastern Andes and in the foreland basins), but it is not suitable for the Miocene paleogeography.

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The Rio Acre formations studied by Räsänen *et al.* (*1*) are more compatible with a freshwater than with a tidal marine environment.

In addition to the absence of marine mollusks, the fish species Räsänen *et al.* list from the Rio Acre sediments (with the exception of the bullshark *Carcharinus leucas*) are freshwater species typical of modern Amazonian flood plains: Osteoglossidae, freshwater stingrays, three families of freshwater catfishes, and the characoid *Colossoma* (*2*). The latter genus consists of fruit-eating fishes typical of seasonally inundated forests (*3*). *Carcharinus leucas* is euryhaline and is reported from freshwater habitats world-wide, including the upper Amazon (*4*). We know of no exclusively marine fish in the Rio Acre sediments.

There is insufficient sedimentological evidence to safely conclude that the channel lithosomes were deposited in a tidal environment. (i) Räsäsnen *et al.* assert that the coarsening upward sand and the sharp contact with the overlying mud are diagnostic of a tidal environment and rule out the possibility of their deposition during a fluvial flood event. This is not a valid argument. The flow velocity in a fluvial flood event would follow the same general pattern of increase followed by decrease as seen in tidal floods (*5*). The observed features are not uniquely indicative of a tidal environment. (ii) The scatter of palaeocurrent indicators within the units at Rio Acre is compatible with the effects of local channel and floodplain geometry within a meandering fluvial system. (iii) The apparent periodicity in sand-mud couplet thickness variation is unconvincing, given the number of maxima and minima in the data and the arbitrary choice of the starting point for the spring-neap cycles. The thickness variations could equally be a result of seasonal fluvial flood cycles. Also, even within a single flood cycle in the modern Amazon, river levels can oscillate by up to 2 meters over a few days; a phenomenon known locally as the "repiquete" (*6*). (iv) Other features, such as desiccation cracks and bioturbation, are just as likely to occur in a fluvial setting. Mud flats exposed at low water or by "repiquetes" form deep desiccation cracks within a couple of days.

In sum, from a sedimentological viewpoint, a fluvial origin of the deposits seems equally if not more plausible than a marine-tidal origin. The deciding factor, we believe, is that freshwater fish are present while marine fish and mollusks are not. Both the fish fauna and many of the characteristics of the sediments are strongly reminiscent of the "várzea" flood plains of modern Amazonia. Perhaps a more detailed picture of the habitat could be determined through pollen analysis.

We agree with Webb (*7*) that the putative Amazonian sea requires more precise dating. Räsänen *et al.* state that the marine incursion occurs at the latest Serravallian highstand of global sea level shown on the chart by Haq *et al.* (*8*). The chart actually shows a pronounced low point at 10 Ma. The Miocene highstand is shown at approximately 15 Ma (Langhian). These conflicting dates and the still contentious nature of the chart by Haq *et al.* make it necessary to consider other mechanisms. It is possible that flooding of the South American continent to form the Amazonian sea was a result of tectonic mechanisms, such as lithospheric loading by the Andean orogenic wedge, or dynamic topography related to the Andean subduction, or both. More work is required to resolve the temporal and spatial boundaries of the Miocene Amazonian sea.

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Because the Pebasian and Paranan (that is Paranense) seas (Fig. 1) ingressed to large structural basins, the dynamic depositional history of these basins should be compared. Similarities of the basins include direct (though distal) connections with the marine realm, epicontinental settings, and restricted marine conditions in parts of both basins. Differences include that the Pebasian had a restricted connection with the Caribbean and a large watershed and was dominated by an estuarine-influenced setting, whereas the Paranan had a broad connection with the South Atlantic and a smaller watershed and (south of Bolivia) was an epicontinental sea.

The sedimentary features used by Räsänen *et al.* (*1*) to establish estuarine conditions in their study area are rhythmites. Tidal rhythmites are found in a variety of modern low salinity or freshwater settings in contact with coastal waters which, with few exceptions, have tidal ranges of about 3 m (*2*). Under certain conditions, tidal energies can propagate hundreds of kilometers landward into freshwater settings. For this reason rhythmites cannot be used to infer salinity.

Räsänen *et al.* (*1*) list four fish groups from the Solimões Formation as indicators of a marine setting in the southern part of the Pebasian Sea, but a detailed comparative description of these fossils is not referenced, and all other Miocene fish faunas from inland northern South America indicate freshwater habitats (*3*).

Webb (*4*) proposes in his Perspective that some modern fishes and mammals of South American rivers with marine affinities owe their origin to entrapment upon regression of seas. A proximate marine ancestry has long been inferred for several Neotropical fish and mammal species or small clades, but there is no compelling evidence that the ancestors of these groups could not have entered freshwater rivers directly, as related taxa do today around the world. Webb (*4*) lists tilefish among these, but tilefishes (Malacanthidae) are unknown in fresh waters.

Räsänen *et al.* (*1*) correlate and credit the Pebasian transgression "with the latest Serravallian high global sea stand ~10 Ma" (*1*, p. 389) on the basis of a report by Haq *et al.* (*5*). Webb (*4*), using associated fossil land mammals, suggests an age of about 12 Ma for both the Pebasian and Paranan transgressions, which he correlates with an earlier part of the Serravallian highstand. However, a tectonic, not eustatic, event created the conditions that permitted both transgressions. Beginning about 11 Ma, the Quechua tectosedimentary episode initiated along the Central Andes (*6, 7*). Resumption of nearly perpendicular movement of the Pacific plate against the western edge of the South American plate produced crustal shortening, hence uplift, and resulted in tectonic loading in the cordillera and subsidence (enhanced by sediment loading) in the foreland basin. Because of a lagtime before erosion could provide enough sediment to compensate subsidence in the foreland basin, its axial groove, which ran adjacent and parallel to the thrust front, subsided without being completely filled by alluvial deposits (*7*). This subsidence permitted the ingression of marine waters by their infilling of the underfilled axial groove which was, at least at times and in places, tens of meters below sea level. A marine highstand for the latest Serravallian (*8*) would have augmented this tectonically induced transgressive event.

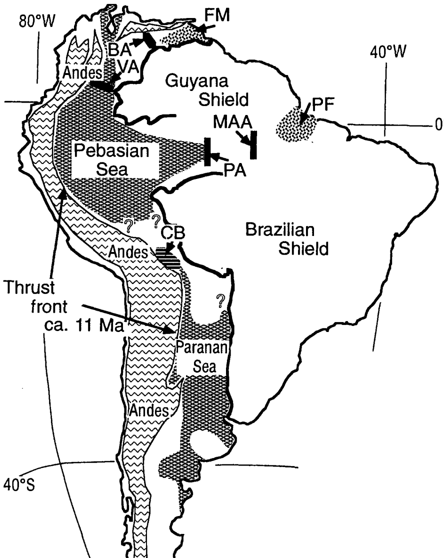

Fig. 1. Distribution of Pebasian and Paranan seas (data in *11*). BA, El Baul arch; CB, Chapare Buttress; FM, Freites formation; MAA, Monte Alegre arch; PA, Purus arch; PF, Pirabas formation; and VA, Vaupes arch. These seas are not continuous across southwestern Amazonia, there are no mid-lower Amazonian or Orinoco seaways, and geologic structures are shown that monitor the location of these late Middle Miocene seas: the Andean thrust front, edges of shields, and arches.

The sediments of the Paranan and Pebasian seas were the first units to be deposited in relation to this tectosedimentary episode which continued until about 5 Ma (*6*). Coeval with and tracking the regression, these sediments are transitionally overlain by continental units containing Chasicoan (~11 to 9 Ma) and Huayquerian (~9 to 6 Ma) Land Mammal Age faunas (*6*). The basins were bounded to the west by the Quechua thrust front, and to the east by the Guyana and Brazilian Shields and associated structural arches (Fig. 1). As the Andes were built from west to east (*6*), the western edge of the Paranan and Pebasian basins were deformed and uplifted by subsequent thrust deformation.

We know of no geologic evidence for interconnection of marine or large freshwater bodies between the Pebasian and Paranan seas, of the Pebasian Sea with the present mouth of the Amazon, or with the present mouth of the Orinoco (Fig. 1). Webb's (*4*) "species pump" model, based on the recognition of three portals of a hypothetical "Amazon Sea" that divided the continent into three land masses, is uncorroborated by geotectonic data (*9*).

The tectonic episode beginning at about 11 Ma had a major impact on shaping the modern drainage systems. Earlier tectonic episodes documented in the Central Andes (initiated at ~73, ~59, ~43, and ~27 Ma) monitored earlier phases of Andean foreland evolution (*6, 10*). With each episode, the axis of the Andean foreland was progressively propagated eastward. Initiation of the episode at about 73 Ma permitted two marine-influenced transgressions into the Andean foreland (*10*), and within these basins can be envisioned the earliest record of what today we call the Amazon, Orinoco, and Parana drainage systems. These earlier tectonic episodes also must have affected the development of trans- and cis-Andean drainage systems. Models for the evolutionary diversification of the Neotropical continental biota must, therefore, take into account multiple occurrences of vicariance or coalescence.

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Response: The comments about our report (*1*) include criticism and comments on three main points: The interpretation of the genesis of the sediments, the value of the fish fossils in the sediments as evidence for a marine connection, and the question of the age of the sediments.

Paxton *et al.* and Hoorn point out that the reported sand-mud couplets with the upward coarsening sand could also be formed during fluvial flood events. The upward coarsening and the lower sharp (often deformed) surfaces of the mud layers (interpreted to be deposited during flood-tide) are a common feature in the studied sequences. Even if an increase in the current in the late phase of a fluvial flood event is possible, the subaquatic deposition of the mud follows immediately when the current finally wanes. This process will cause gradual contacts to be more common in a fluvial environment. If the mud layers were formed in the late phases of fluvial flood events (repiquete), we would also expect the presence of desiccation cracks to be more common. The runoff channel [figure 3A in our report (*1*)] indicates that the upper part of the section has probably been subaerially exposed. If the runoff channel had been in a fluvial regime, there would have been enough time for desiccation cracks to form in the mud layers; instead, soft sediment deformation is commonly found.

We agree with Paxton *et al.* that the periodicity of the thickness of the sand-mud couplets is not regular. However, the estimated points of time for the neap tides decrease the amount of sedimentation even during the times of anomalously high sedimentation that can result from local sedimentary conditions or anomalous weather conditions (*2*).

Paxton *et al.* and Hoorn point out that our paleocurrent directions are compatible with the local channel and floodplain geometry in the area. The documented sand-mud couplet sediments are similar neither to the sediments of the modern river system nor to the Quaternary alluvial terraces in the area. They also propose that many of our sedimentary characteristics are reminiscent of the varzea environment of modern Amazonia. According to our field experience in Peruvian, Bolivian, and Brazilian Amazonia, sandwave and dune deposition dominate in the channels, and ripples are occasionally present only in upper parts of point bars. In fact, some modern tidally influenced fluvial systems show processes through which the formation and rhythmicity of the sand-mud couplets may be understood (*2*).

We also used other evidence to interpret the tidally influenced origin of these sediments (sand-mud couplets with the mud-douplet and the interchannel facies with well sorted sand layers) for which the commentators give no alternative explanation. Of the sand in the detailed studied sand-mud couplets ($n \sim 300$) in the channel lithosomes, 90% were ripple drifted sands. The remaining 10% were parallel laminated, cross laminated (dunes), or massive. At Acre, this relation seems to be valid for the approximately 20 locations where channel lithosomes were recognized [arrows in figure 5 in (*1*)]. This indicates how widely and uniformly this type of deposition was present at Acre, as would be expected in a tidally influenced environment rather than in a fluvial regime of the modern varzea type.

Paxton *et al.* mention that all the fish taxa we cite are typical of modern Amazonian flood plains. As we stated (*1*), the fish taxa were found 500 km north of our research area (not at Acre), where foraminifera, ostracods, and mollusks indicate an episodic brackish environment and marine influence together with fluvial and fluviolacustrine conditions (*3*). Paxton *et al.* are correct that only Carcharinus (of the taxa we mention) is euryhaline, while the other groups may have both marine and freshwater species. As Marshall and Lundberg also point out, we must wait for more detailed species determinations to be sure about their indicative value. It is possible that the shark teeth reported from Acre (*4*) are from animals that had migrated far away from the sea, as is known from modern environments. Considering the restricted amount of paleontological collection work performed at Acre, this is, however, unlikely. The common presence of the species in the paleoenvironment is a more likely explanation.

Our dating of the sediments is based on paleontological data and is thus relative and open to discussion. Although elements from adjacent Land Mammal Ages exist, the most likely correlation was with the Huayquerian Land Mammal Age. Webb suggests in his Perspective (*5*) an older possible Chacicoan age for the sediments. Also, if a connection with the Caribbean during the Late Miocene is unlikely, as Hoorn argues, this may indicate that the sediments at Acre are slightly older than Huayquerian. If this is the case, our original correlation with the latest Serravallian high global sea levels may be valid and place the event in Middle Miocene, as Hoorn correctly points out. However, as Paxton *et al.* and Marshall and Lundberg propose, there need not be a correlation with high world sea level. The Andean tectonic loading on the Brazilian craton margin, resulting in subsidence in the Amazonian Foreland Basin, must be taken into consideration when the evolution of the Pebasian and Paranan transgressions are discussed. The landscape evolution may well have followed the hypothesis of Marshall and Lundberg.

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