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Response: Development of the mouse small intestine is often viewed in terms of the cytodifferentiation of its endoderm that occurs in late fetal life, or the formation of its crypt-villus units, which is completed during the first three postnatal weeks. Umesaki *et al.* emphasize the importance of having a broader vision of gut development. We agree. A "trialogue" between the intestinal microbiota, the self-renewing intestinal epithelium, and the diffuse gut-associated lymphoid tissue (GALT) is probably critical in forming and maintaining this dynamic ecosystem. Studies by Umesaki *et al.* provide strong evidence that a component of the normal microbiota can influence the composition of the diffuse GALT. Colonization with the *B. thetaiotaomicron*–type strain, VPI-5482, is associated with similar composition changes. For example, an influx of IgA^+ B cells occurs after exposure to this organism.

One should consider the diffuse GALT's composition, but also its spatial complexity, which has been hard to characterize because markers are difficult to detect with conventional immunohistochemical methods. More sensitive techniques (*1*) have allowed us to examine these features in mice that contain a normal (conventional) microbiota. For example, $\alpha\beta$ T cells populate the intraepithelial and lamina propria compartments in crypts and villi, while $\gamma\delta$ T cells are limited to the villus epithelium. T_H1 and T_H2 cells appear predominantly in the lamina propria of the villus (*2*).

Like the diffuse GALT, components of the microbiota are arranged asymmetrically along crypt-villus units: SFB attach to epithelial cells located in the upper two-thirds of the villus. Histochemical stains of unperfused small intestines obtained from specified pathogen-free conventional mice suggest that crypts are not colonized by this or other bacterial species. The asymmetric distribution of the microbiota may serve to organize components of the diffuse GALT. Conversely, the diffuse GALT may influence the spatial organization of the microbiota.

The diffuse GALT also communicates with the intestinal epithelium: Mice that lack $\gamma\delta$ T cells have fewer crypt epithelial cells and slower epithelial cell migration up the villus (*3*). Contaminating adult GF mice with SFB or VPI-5482 reveal another component of this trialogue: communication between the microbiota and the gut epithelium. VPI-5482, which was originally recovered from a human, signals the epithelium to induce and sustain α1,2 fucosyltransferase gene transcription and production of fucosylated glycoproteins and glycolipids. This is not a nonspecific response of the epithelium to bacterial colonization. Monocontamination of GF NMRI mice with two other anaerobes that normally colonize the mouse and human intestine, *Peptostreptococcus micros* and *Bifidobacterium infantis*, produces no detectable effect on fucosylated glycoconjugate production (*4*).

Unlike SFB, signaling occurs without direct bacterial attachment to enterocytes (*5*). Signaling depends on the ability of the organism to use fucose as a carbon source (*5*). We recently found that the *B. thetaiotaomicron* genome contains a locus analogous to the *Escherichia coli* fucose utilization regulon (*6*). A Tn4351 insertion renders the Fu-4 strain of *B. thetaiotaomicron* unable to use fucose and unable to signal enterocytes to produce fucosylated glycoconjugates. The site of insertion is the open reading frame of one of the genes within this locus (*7*). Monocontamination of GF mice with isogenic strains of *B. thetaiotaomicron* that contain engineered disruptions of each gene in the regulon should provide clues about the nature of the signal that emanates from this metabolic pathway.

To induce and sustain fucosylated glycoconjugate production in enterocytes, VPI-5482 must reach a critical population density (*5*). This requirement may reflect secretion of a soluble bacterial factor that produces a concentration-dependent response in the epithelium. Or there may be a density-dependent change in the metabolic properties of the bacteria that affects production of a signaling molecule—a process known as "quorum sensing" (*8*). In the mammalian gut, where there is a highly complex society of microorganisms, secreted signaling molecules may allow communication between (and within) bacterial species. Multiple species may cooperate to generate a concerted signal that establishes a mutually beneficial niche. Such density-dependent signaling systems may also interfere with one another if a similar set of molecules is used by different species to modulate distinct metabolic pathways. This type of interference could allow the microbiota to prevent the encroachment of pathogens. If such encroachment occurs, the response of the host may depend on the relative locations of the pathogen, components of the diffuse GALT, and members of various intestinal epithelial lineages—factors that likely are influenced by the trialogue.

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Determining the Early History of El Niño

Daniel H. Sandweiss *et al.* (*1*) reiterate arguments advanced a decade ago (*2*) that climatic and oceanic changes 5000 years before present (B.P.) resulted in the onset of El Niño/Southern Oscillation (ENSO) events along the coast of Peru. A major argument used to support this conclusion is the occurrence of southwardly displaced tropical molluscan assemblages in natural deposits and shell middens older than 5000 years B.P. along the coast of northern Peru. One of the best examples of such a thermally anomalous molluscan assemblage (TAMA) is found in the paleo-lagoon at Santa (9°S). A detailed geological and paleoecological study (*4*) showed that the presence of the Santa TAMA was the result of changes in coastal morphology, not climate. Contrary to the contention of Sandweiss *et al.* (*1*, p. 1532, and notes 22 and 23), DeVries and Wells (*4*) showed that the Santa TAMA developed in a warm, narrow embayment open to the ocean and coexisted with temperate species then occupying more open coastal environments. More evidence for the Santa setting was provided by extensive geochronological and geochemical studies (*5*, *6*), which also revealed that dated *Trachycardium procerum* shells (5500 to 6100 years B.P.) from the Santa paleolagoon registered growth anomalies and isotopic signatures (^{18}O, ^{13}C) of ecological stress comparable to those of modern shells that survived the 1983 ENSO event at the same latitude. In such shells, shifts in ^{18}O contents of abnormal growth rings indicate short-term temperature rises as great as 7°C to 8°C (*6*).

Other TAMAs, as well as isolated tropical mollusks, have been found in Peru from lower and upper Pleistocene deposits south of Lomas (15°S) and at Ilo (18°S) (*7–10*), and in northern Chile from middle Pleistocene deposits in Antofagasta Bay and La Serena (*11*). In all these cases, tropical TAMA species coexisted with open ocean temperate species. These fossil occurrences are comparable to modern extralimital occurrences of tropical mollusk species in ecologically suitable localities of central and southern Peru (*8*) and northern Chile (*12*) immediately after recent ENSO events.

Temperate mollusks obtained from transgressive intertidal lags off the north-central coast of Peru (*3*) and from numerous fossiliferous deposits of the coast of Peru and northern Chile (*9–11*) demonstrate the similarity of early Holocene and modern nearshore molluscan assemblages. The prevalence of cold-water mollusks and absence of tropical mollusks from these coasts throughout the Holocene and Pleistocene does not support the conclusion of Sandweiss *et al.* (*1*) that the Peruvian littoral was bathed by warmer waters prior to 5000 years B.P. What is probably the most interesting and novel implication of these TAMAs is that ENSO-related disturbances of nearshore conditions appear to have played a major role in larval dispersal and southward displacement of tropical species.

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The following data are inconsistent with the idea of Sandweiss *et al.* (*1*) that dramatic climatic change in Peru resulted from a global current reorganization between 5000 and 7000 years B.P.

1) *Terrestrial environment.* (i) River valleys crossing the Peruvian Desert are filled with 10 to 20 m of overbank flood sediments identical to those deposited by historic ENSO (*2*). Aridic soils separate the flood sheets. Basal flood sediments of Rio Reque (6.5°S) date to 8500 radiocarbon years B.P. (*3*) and older interbedded flood sediments, eolian sediments, and aridic soils (>40,000 radiocarbon years B.P.) are present at 9.5°S (*4*). (ii) Quaternary soils north of 12°S contain thick accumulations of eolian clay and silt that result from deep wetting during rainfall. These same soils have mineral weathering rates among the lowest known, a result of extremely low annual precipitation. Contrary to the assertion of Sandweiss *et al.* (*1*), this paradox cannot be explained by increasing mean annual rainfall. The best explanation involves long-term hyperaridity with episodic and intense precipitation (*5*). (iii) Thick sequences of ancient dune sediments exposed in early Holocene seacliffs north of 12°S indicate that dry conditions prevailed before the erosion of the seacliff at about 6500 years B.P. (*4*, *6*). (iv) Remarkable preservation of early Holocene human burials and fragile plant remains in archaeological middens could not have occurred if annual precipitation had been much higher than the modern mean (*7*).

2) *Coastal geomorphology.* An alternative explanation for the presence of temperate fauna is that they survived in warm lagoons that were dependent on paleogeography and sea-level change stabilization (*6*, *8*). The archaeological sites with tropical fauna (*1*) are all located on shorelines around protected embayments that formed at the mouths of flooded valleys between 5000 and 7000 years B.P. (*4*). Adjacent to both the Almejas and Ostra sites, but closer to the tidal outlets of the lagoons, are contemporaneous or earlier sites with a mixed temperate high-energy and tropical low-energy fauna (*4*). These sites were abandoned as coastal sedimentation rate outpaced sea-level rise and the lagoons filled.

3) *Climatic change?* Along the Peruvian coast, geomorphologic, sedimentary, and soil evidence indicate a hyperarid climate and catastrophic flooding for at least the past 40,000 years and perhaps much longer. Thus, El Niño as manifest today appears to have been a characteristic of the Peruvian climate thoughout the late Quaternary. In conjunction with the molluskan and geochemical evidence for cold open ocean conditions (*9*), we conclude that the best explanation for the tropical species found in archaeological middens was the exploitation of an environmental resource that was a result of sea-level change, not climatic change.

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Response: More research is required to evaluate the hypothesis of a 5000 years B.P. onset of ENSO, and we welcome comments on our work (*1*). DeVries *et al.* and Wells and Noller, however, do not address alternatives to the totality of evidence for a 5000 years B.P. onset of ENSO.

We have proposed warmer conditions only north of 10°S and for a limited period during the mid-Holocene (8000 to 5000 years B.P.). Data from northern Chile (that is, south of 18°S) and from other time periods cited by DeVries *et al.* are irrelevant.

Average weathering rates in north Peruvian soils over the Quaternary (approximately the last 2 million years) have little to do with the hypothesized 3000-year interval of seasonal rainfall. The supposed evidence for intense episodic rainfall could be from periods when ENSO was active, and this may have occurred frequently during the Quaternary. Neither sediments older than 40,000 years nor Early Holocene dunes are relevant to an hypothesis about the period 8000 to 5000 years B.P.

Concerning the evidence for more than 40,000 years of hyperaridity and catastrophic flooding on the Peruvian coast: We have suggested an interlude of several thousand years for annual rainfall only north of 10°S, and the data referred to by Wells and Noller (*2*) are not fine-grained enough to distinguish such an interlude against the background of prior and subsequent aridity. Also, as we noted (*1*), the Talara Tar Seep fauna indicate that seasonal rainfall occurred at 14,000 years B.P.

The flood deposits referred to by Wells and Noller are either undated, or are dated after 5000 years B.P. or, in the case of the previously unpublished data, earlier than 8000 years B.P. Also, flood deposits need not imply ENSO events, as all rivers flood regardless of climate regime. In 1990 (*3*) DeVries and Wells did not argue that the Santa Lagoon was open to the ocean; they stated on page 18, "Beach Ridge II-A [the oldest subaerial ridge] . . . formed an unbroken barrier to the exchange of water between the Pacific Ocean and the low ground behind [this ridge]. The Santa lagoon formed in the protected low area behind this ridge."

Concerning the geomorphic setting of the pre–5000 year B.P. sites with tropical fauna, the studies by Wells (*4*, *5*) are confined to the Ostra case, where her reconstruction of the "former lagoon" depends on the presence of a hypothetical subaerial beach ridge that no longer exists—even though she postulates its presence at a time of higher than present sea level. Furthermore, the coexistence of exclusively warm-temperature and warm-tropical molluscan fauna north of 10°S and prior to 5000 years B.P. has not been demonstrated through direct or associated absolute dates in sites adjacent to either Almejas or Ostra.

DeVries and Wells' evidence for coexistence of uniquely warm-temperate and warm-tropical molluscan species at Santa rests on the co-occurrence of a rock-dwelling, warm-temperate gastropod and a sand-dwelling, warm-tropical/warm-temperate razor clam (*3*, *5*); these two species are unlikely to have lived together, and all ^{14}C dates on identified shell reported by DeVries and Wells are on species found in warm-tropical waters today. Thus, the association is unlikely biologically and unsupported chronologically; the warm-temperature gastropod was most likely deposited after 5000 years B.P. All pre–5000 year B.P. ^{14}C dates on mollusks identified by species from sites and locales north of 10°S are on warm-tropical or warm-tropical/warm-temperate species, and pre–5000 year B.P. ^{14}C dates on charcoal from sites in this area are associated with similar assemblages. (*1*). Assemblages from pre–5000 year B.P. sites south of 10°S do not contain warm-tropical fauna, even those such as Paloma (*6*) that are as close to valleys as Siches or Ostra (Quebrada Chorrillos is far from any valley, and the valley nearest Siches is perennially dry).

It is possible that El Niño events occurred at other times in the past and could account for isolated warm-tropical species south of their modern distribution—we pointed to one late Holocene, archaeological case from Peru (*1*, p. 1531). The occurrences of warm-tropical organisms at Santa and the other sites we have discussed are significant because they are not isolated and do not co-occur with exclusively cold-adapted species.

The isotopic signature in *Trachycardium* shells from Santa (*7*) could be a result of annual coincidence of fresh water influx from seasonal rain and seasonally high summer sea surface temperatures (SSTs) predicted under our reconstruction of pre–5000 year B.P. climate in northern coastal Peru. *Trachycardium procerum* is a species adapted today to a wide temperature range but reaches greater size in cooler regions (the Santa individuals are small in size); summer conditions warmer than present may have caused enough stress to produce growth anomalies.

Several recent studies support our hypothesis. Michael Gagan (*8*) and his colleagues have analyzed pre–5000 year B.P. corals from the Great Barrier Reef in Australia and failed to find an ENSO signal; Diaz and Graham (*9*) have shown that SSTs are linked to tropospheric air temperatures in a way that connects the Peru coastal SSTs to the Huascaran ice core, which, as we noted, shows higher temperatures from 8600 to 5200 years B.P. (*10*). Abbott *et al.* (*11*, p. 179) confirm earlier studies indicating "a prolonged mid-Holocene dry phase" that would be consistent with permanent ENSO conditions, although they date the appearance of modern conditions more recently than other records suggest for the onset of ENSO.

In the archaeological record from coastal Peru there is a notable *lack* of preservation of noncarbonized soft organics in early northern sites. These materials are preserved only in sites older than 5000 years B.P. south of 10°S and in more northerly sites dating after 5000 years B.P.—preservation begins at the time that warm-temperate mollusks begin to dominate the record, suggesting greater precipitation in the north before 5000 years B.P.

Under the model proposed by Wells *et al.*, one would expect to find sites with abundant warm-temperate mollusks dating earlier than 5000 years B.P. and located north of 10°S. None have yet been found.

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