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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 "dialogue" 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 dialogue: communication between the microbiota and the gut epithelium. VPI-5482, which was originally recovered from a human, signals the epithelium to induce and sustain α 1,2 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 dialogue.

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X 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 ther-

mally 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 throughout the late Quaternary. In conjunction with the molluscan 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 alter-