

dilleran localities. This has not been documented. There is little difference in the diversity of Late Triassic reefal cnidarians and sponges in terranes in central-western Nevada, western Idaho, the Yukon, and southeastern Alaska; and their diversities are similar to those of biotas in the distant Alpine Tethys (3–5). Newton may find low Tethyan affinities among Triassic bivalves, but we disagree with her statement (p. 388) that “Tethyan” species represent only a minor part of the diversity in most Cordilleran terranes.” Most Triassic terranes contain sponges, spongiomorphs, corals, bivalves, ammonites, brachiopods, crinoids and microproblematica, which are 52 to 100% Tethyan (3–6). Among these, a number of species are found to occur only in the western Tethys and in specific Cordilleran terranes. To say that Tethyan species are pantropical because they can also be found in western North America, Peru, south China, Japan, and Siberia is unjustified because such species also occur within suspect terranes. Without knowledge of the geographic location and extent of displacement of these circum-Pacific terranes, we believe one cannot say they support a valid pantropical model. Triassic species of non-Tethyan corals known only from a Siberian terrane and two terranes on opposite sides of the Pacific in Cordilleran North America (4) could be interpreted as the kind of mirror image expected if both originated together in the ancestral Pacific and subsequently were tectonically dislocated to adjacent sides of the Pacific.

Permian biotas do not fit the model. Biotas in tropical areas of Asia and cratonal North America are very distinct, and neoschwagerinid fusulinids and waagenophyllid corals are indicators of Tethys because there was so little dispersal across the Pacific Ocean basin. Only one occurrence of neoschwagerinids is known in cratonal North America, and the few North American occurrences of waagenophyllids are in displaced terranes. Supposed mixtures of Tethyan and North American species in the eastern Klamath and Hayfork terranes are not real, because (i) the eastern Klamath terrane contains highly endemic biotas from a third province with very few Tethyan taxa, and (ii) the Hayfork terrane is a collage of rocks that was not assembled until the Triassic (7), thus providing no evidence of Permian biogeography.

Temporal changes in biogeographic patterns dictated by the longitudinal displacement model can be tested with faunal data from the Wallowa terrane. Well-dated late Triassic reefal biotas show strong Tethyan components, while a Jurassic biota nearly 50 million years younger yields corals and mol-

lusks unrelated to those of Tethys and closely related to those of the craton (8). Such changing temporal patterns suggest tectonic terrane convergence toward North America, resulting in isolation from the Tethys and free larval exchange with cratonal faunas.

There is paleomagnetic evidence of significant amounts of longitudinal (tectonic) movement in many of the Cordilleran terranes. Terrane trajectory paths based on the goodness of fit of paleomagnetic data (9) suggest that for some terranes like Wrangellia that from only the Middle Jurassic to the time of Cretaceous accretion to North America more than 60° of eastward displacement is accountable. Wrangellia is one terrane “most generally accepted as truly exotic to North America” (10).

Without concrete evidence of diversity attenuation across terranes, a pantropical model is difficult to apply to biotic patterns from Cordilleran terranes. On the other hand, the longitudinal displacement idea is testable. Faunal similarity data can be tested (i) against projected relative motions of Pacific terranes derived from paleomagnetic data, (ii) by recognition of species restricted exclusively to the western Tethys and specific terranes, (iii) with endemic patterns within groups of oceanic terranes and mirror-image patterns occurring on adjacent sides of the Pacific, and (iv) by recognizing changing temporal patterns of paleogeographic affinities.

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Response: I thank my colleagues Paul Smith, Gerd Westermann, George Stanley, and Thomas Yancey for their comments. I particularly appreciate Smith and Westermann’s comments and corrections concerning the distribution of the important Jurassic bivalve *Weyla* and Stanley and Yancey’s information concerning their unpublished work on Permian through Jurassic faunas (their references 7 and 8). These two groups present five summaries of the two different models—marine corridors and longitudinal displacement—that have traditionally been used to account for “Tethyan” faunal anomalies in the American Cordillera. It was precisely this disparity in corridor-versus-displacement interpretation of “Tethyan” Cordilleran faunas that prompted me to propose an alternative, steady-state hypothesis of pantropic dispersal, against which these other models can be tested.

I propose a more general, dispersal-based pantropic model (1) that can provide an effective starting point for paleobiogeographic testing. I suggest that a steady-state model should be tested first and that only where faunal anomalies are quantitatively beyond that expected by dispersal models should other hypotheses, such as corridors and longitudinal displacement, be invoked. The goal of this dispersal-based model is to provide a general, initial model that can be tested before ad hoc explanations of marine corridors or longitudinal displacement are invoked. My article did not suggest that marine corridors cannot exist or that longitudinal translation has not taken place; these can be plausible explanations. Rather, I proposed a new protocol for paleobiogeographic testing that involves explicit, quantitative consideration of dispersal mechanisms before alternatives are invoked. In few previous studies (2) has dispersal been given thorough consideration.

The pantropic model makes only two modest claims for comparison between the modern tropical Pacific and the ancient Pacific basin (sometimes called Panthalassa). First, it asserts that some ancient species likely had teleplanic larvae (3) comparable to those of modern invertebrates. This is a reasonable assertion, if one judges from the numerous studies that have compared the larval shell morphology of living and fossil invertebrates (4). Second, equatorial marine species dispersing by means of teleplanic larvae from the Tethyan seaway into other regions would likely show a gradient of attenuated “Tethyan” diversities comparable to the attenuated diversities of Indo-West Pacific (IWP) species in the central and

eastern Pacific ocean today (5, 6). For western American cratonal sites and for terranes that originated in the eastern proto-Pacific, one would expect to find attenuated “Tethyan” diversities that might be as high as 50% [by comparison with modern, insular faunas of Clipperton Island, for example, (6)], but would ordinarily be somewhat lower (~20% or lower for molluscan taxa) [see discussion in (1)].

The most important—and surprising—element in the pattern of “Tethyan” Cordilleran fossils is the occurrence of “Tethyan” species (usually in minor proportions) in both cratonal and parautochthonous rocks of the Cordillera, as well as in the allochthonous terranes. The existence of such “Tethyan” taxa in a broad range of invertebrate groups in cratonal or craton-related sites provides strong evidence that these organisms did disperse across the vast proto-Pacific ocean basin. This key observation was documented in my article, but is not mentioned in either of the comments. “Tethyan” taxa represented in cratonal and parautochthonous terranes of the Cordillera include (but are not restricted to) scleractinian corals, brachiopods, bivalves, ammonoids, microcrinoids, and conodonts (1, 7, 8). Since publication of my article, evidence of such pantropic distributions has continued to increase (7, 8). There is also evidence from the cratonal Permian Basin of west Texas for one species of neoschwagerinid fusulinids (9), a group widely believed to be a “Tethyan” indicator in the western Cordilleran terranes (10). In view of the cratonal nature of the west Texas Permian basin, Stevens (11) proposed a short-lived, Pangaean marine corridor to explain this neoschwagerinid occurrence. I offer an alternative explanation: the west Texas neoschwagerinid occurrence likely represents a low-diversity occurrence of broadly dispersed “Tethyan” fusulinids on the western North American continent. Ironically, then, one of the two Permian groups used by Stanley and Yancey to support the longitudinal-displacement model may actually provide a nice example of an attenuated, pantropic distribution.

In addition to larval shell morphology and broad geographic ranges, another feature of ancient pantropic taxa is that certain ecological groups may be differentially represented. As an example, among modern IWP bivalves occurring in the eastern Pacific, most are attached species (epibyssate or cemented) or borers (6). It is therefore striking that of the seven bivalve genera from the Wallowa terrane cited in my article (1, p. 387) as having “Tethyan” affinities, all are attached: five show evidence of byssal structures and two are cementers (12). In-

deed, in reviewing the whole discussion of Triassic bivalve genera with “Tethyan” affinities, I found only one—*Palaeonucula*, a burrower—that is an exception (*Palaeonucula* was a broadly distributed genus in Triassic time).

Given the complex history of accretion that has characterized the North American Cordillera—particularly the large-scale strike-slip faulting that has tectonically reshuffled the terranes of the western Cordillera—it is unlikely that simple east-west biogeographic gradients will be preserved everywhere along the western Cordillera. However, as I outlined in my article, such a trend has been reported for some California terranes (13), Permian faunas of the Death Valley region lived on the North American margin; the eastern Klamath faunas have North American ties in the early Permian, but “Tethyan” ties in the late Permian; and the western Klamath region (Hayfork terrane) contains limestone masses that yield “Tethyan” fusulinids and waagenophyllid corals. Luken *et al.* conclude, “thus, the faunas suggest that the eastern Klamath Mountains lay between the western Klamaths and North America. . . and that there has been an enormous amount of shortening since then” (13, p. 367). Stanley and Yancey have challenged this interpretation on the grounds that the eastern Klamath terrane does not contain a mixture of North American and “Tethyan” fossils. The published literature on the subject contains some conflicting results: for the eastern Klamath terrane alone, some studies have found North American faunas, others have described mixed North American and “Tethyan” assemblages, and still others have recorded distinctive, endemic taxa (14). Watkins and Wilson have argued that Yancey and Hanger’s model of a spatially isolated eastern Klamath terrane that originated far from North America is not consistent with observed occurrences of *Palaeoaplysina*, which require that there was some faunal exchange with North America during Permian time (15). There is also evidence of temporal variation in the influx of “Tethyan” species in assemblages of the eastern Klamath terrane (13–15).

I agree wholeheartedly with my colleagues that the late Paleozoic–early Mesozoic proto-Pacific ocean was larger than its modern counterpart and that there are considerable uncertainties regarding the patterns of circulation in this enormous ocean. However, I do not agree that this larger size and different configuration rule out pantropic dispersal as an important mechanism. For one thing, as my article noted, there have been no quantitative models yet developed for latest Paleozoic–early Mesozoic

global paleocirculation. A recent, quantitative reappraisal of Cretaceous circulation provided some surprises: predominant circulation in the Tethyan seaway was found to be eastward-, rather than westward-directed (16). Until such modeling is done for earlier intervals, we should not presume that broad equatorial circulation was not possible for the Paleozoic–early Mesozoic ocean; instead, we should look directly for faunal evidence of the extent of dispersal. The cratonal and parautochthonous occurrences of “Tethyan” taxa mentioned above argue strongly for dispersal across this enormous ocean.

Much of the comment by Smith and Westermann concerns the timing of origin of the Hispanic Corridor, the inferred Jurassic seaway that extended from the western Americas to western Tethys. My article dealt only with the problem of pre-Middle Jurassic “Tethyan” occurrences in the Cordillera, and hence much of their discussion is not strictly relevant to my arguments. Since in the Blake–Bahama–Gulf of Mexico region the oldest ocean crust with overlying sediments is of Callovian (latest Middle Jurassic) age (17), there is considerable doubt as to whether during Early Jurassic time a marine connection existed in the Central America–Gulf of Mexico region. The statement by Smith and Westermann that there are Early Jurassic marine sediments on both ends of the corridor therefore seems overoptimistic. Although early Jurassic (Sinemurian?–Pliensbachian) marine strata are known from the Huayococotla Formation in Mexico and were initially interpreted as the beginning of a throughgoing rift in the Gulf of Mexico (18), more recent and extensive regional surveys suggest that “the Huayacocotla does not mark the beginning of continuous marine deposition in the circum-Gulf region” (19, p. 326). These studies consider the Huayococotla and related sediments in Mexico as “pre-opening sediments” (19, p. 328). Thus, the isolated marine basins with Lower Jurassic sediments in Mexico and Morocco evidently do not interconnect. Other Jurassic marine occurrences cited by Smith and Westermann, such as the Venezuela locality, are of Middle Jurassic age (20) and hence were explicitly younger than any of the case studies considered in my article. In summary, there is no substantive sedimentological evidence for a trans-Pangaean marine connection between the eastern Pacific and west Tethys until at least Middle Jurassic time. Even faunal data, as presented in the excellent studies of Hallam (21) and of Damborenea and Manceñido (22), show no indication of interconnection until the late Early Jurassic (Pliensbachian)—again, an age younger than that of the Jurassic “Teth-

yan" faunas I was considering.

Stanley and Yancey misrepresent the available evidence on the "Tethyan" frequencies in Triassic terrane assemblages. Although it is true that Stanley and his co-workers find high "Tethyan" frequencies among Late Triassic scleractinian corals in Cordilleran terranes, cratonal North American scleractinians of this age are poorly known; hence, it is not likely that "North American affinities" would be the result of investigations on Cordilleran Triassic corals. In contrast, for invertebrate taxa for which there is abundant North American cratonal representation (for example, mollusks and brachiopods), relative "Tethyan" frequencies are much lower, and a mixed North American-"Tethyan" signal is more often observed. Stanley and Yancey do not correctly portray the "Tethyan" frequencies in bivalves from Cordilleran terranes. My article and previous papers (1, 9, 23) have clearly shown that for bivalves, which are represented in craton-bound, parautochthonous, and allochthonous terranes, "Tethyan" frequencies are low (18 to 19% for early Norian; possibly as low as 10% for late Norian). Stanley and Yancey also err in stating that brachiopods show overwhelming (52 to 100%) affinities in the Cordilleran terranes. Although little has been published on Triassic Cordilleran brachiopods, and Stanley and Yancey cite no brachiopod systematics papers in support of their statement, Ager (24) has shown that the brachiopod *Halorella* occurs both in the Tethyan seaway and in several localities in Oregon and Nevada; of these two species (*H. amphitoma* and *H. cf. H. ancilla*), *H. amphitoma* has a broad distribution within Tethys and has been found in the Alps, in the Pamir region of the U.S.S.R., and on the island of Seram, as well as in the Cordilleran sites. The distribution of *H. cf. H. ancilla* was not discussed in detail by Ager. Even more significantly, a new database on Cordilleran Late Triassic cyrtinoid spiriferinaceans (8) indicates that only two of nine species (22%) of these articulate brachiopods occur in the Tethyan seaway; both of these *Zugmayerella* species are broadly distributed tropical species, which indicates a pantropic distribution.

A recurring problem for the longitudinal displacement model has been to design adequate and convincing scientific tests of the model. I have suggested a protocol for such testing (1, p. 390), but Stanley and Yancey have not presented these sorts of tests. They state that temporal variation in the frequency of "Tethyan" components provides a yardstick for longitudinal displacement of terranes. In fact, although spatial proximity may sometimes govern such patterns, cli-

matic variation can also cause the expansion and contraction of longitudinal distribution of equatorial species. A short-term example of this is provided by recent documentation of multiple species of IWP organisms invading the eastern Pacific as a result of El Niño events (25). Longer term climatic variations affecting geographic ranges of Tethyan seaway species have been documented by Piccoli *et al.* (26) and were also reviewed in my article. Since climate clearly exerts a major control on the expansion and contraction of distributions of equatorial organisms, variation in frequency of "Tethyan" species does not provide a simple index for longitudinal terrane motions.

Stanley and Yancey, in suggesting that paleomagnetic evidence can locate terranes with respect to longitudinal position, do not correctly portray the implications of recent paleomagnetic models for terrane motion presented by Debiche *et al.* (27). These models were designed "in order to establish the southern and western limits to possible points of origin of terranes within the proto-Pacific ocean (27, p. 1); they therefore provide trajectories from the most distant points of origin for terranes within the basin, given known interactions of oceanic plates over the last 180 million years. These models do not provide unique positions for any individual terrane; for most case studies, the authors provided several possible trajectories. There is the further constraint, not mentioned by Stanley and Yancey, that for the eastern Pacific, only the Kula, Farallon, and Pacific plates are included; any additional plates involved in terrane motion could change the model appreciably. Moreover, the motions implied by these models are sensitive to variations in docking times for individual terranes. In conclusion, these paleomagnetic models are excellent, but they should not be applied more literally than their authors intended.

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In Reply: Paleobiogeography of the Ancient Pacific

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