Significance of "Tethyan" Fossils in the American Cordillera

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Equatorial faunas of the ancient Tethyan seaway, which extended from western Europe to southeastern Asia, comprise some of the most diverse marine taxa in the fossil record. Comparable or identical "Tethyan" species that occur far from the Tethyan seaway in Paleozoic and Mesozoic rocks of the North and South American Cordillera have long been considered as a major biogeographic anomaly. Two leading theories to account for the occurrence of these anomalous "Tethyan" faunas in the Cordillera are that they were transported long distances to the east on tectonic blocks (suspect terranes that originated near the Tethys) or that they migrated westward via undiscovered marine corridors through continental areas of Pangea. An alternative model is that these "Tethyan" fauna were pantropic species that extended with attenuated diversities into the eastern proto–Pacific Ocean. This pantropic model can better account for the distribution patterns of many Paleozoic and early Mesozoic "Tethyan" species in the American Cordillera and provides a steady state hypothesis against which the other models can be tested. The distribution of pre-Cretaceous "Tethyan" faunas is similar to the known pantropic distribution of many Cretaceous and Cenozoic tropical biotas. During the Cenozoic, taxa were most diverse in the Tethys and Indo–West Pacific regions but extended with attenuated diversity to many parts of the equatorial Pacific Ocean, including the west coasts of North and South America. The eastern Pacific occurrence of many Indo–West Pacific species provides a modern analog for the occurrence of many anomalous "Tethyan" fossils in the American Cordillera.

PALEOBIOGEOGRAPHY HAS PLAYED A CENTRAL ROLE IN THE identification and paleogeographic reconstruction of suspect terranes—fault-bounded blocks with stratigraphic and tectonic histories that are commonly different from those of neighboring terranes and of adjoining continental masses (Fig. 1) (*1*). Suspect terranes now accreted to circum-Pacific continental margins include both continental fragments and the remnants of ancient island arcs and oceanic plateaus. Paleobiogeographic and paleomagnetic data from many suspect terranes in the Cordilleran region of western North and South America suggest that these terranes have been latitudinally displaced great distances before they were finally accreted to the continental margin (*2–8*). Some workers have also proposed that some North American suspect terranes had a western Pacific origin and have been displaced thousands of kilometers to the east (*9–11*). This latter hypothesis has been based primarily on interpretations of biogeographic data, particularly occurrences of anomalous "Tethyan" fossils in western North and South America.

These anomalous "Tethyan" Cordilleran fossils are comparable or identical to species from areas of the vast, equatorial Tethyan seaway (Fig. 2, A and B), which in Paleozoic through mid-Cenozoic time extended from western Europe to southeast Asia and harbored diverse and abundant shallow-marine biotas. Although the term Tethyan originally referred only to this paleogeographic region (*12*), it has subsequently been used also for (i) a faunal province that was restricted to the geographic seaway (*13*); (ii) a low-latitude faunal province of variable longitudinal extent—for example, Jurassic Tethyan and Boreal ammonoids (*14*); and (iii) fossil groups occurring elsewhere but having various biogeographic affinities to faunas occurring in the geographic Tethyan seaway (*15, 16*). To avoid propagating this regrettable nomenclatural confusion, I will use the designation "Tethyan" (in quotes) to indicate those Cordilleran fossils that are identical or comparable to fossils known from the Tethyan seaway [that is, as a substitute for the last usage (iii) above] and the modifier Tethyan (without quotes) for fossils found only in the Tethyan geographic region.

The occurrence of "Tethyan" fossils in the American Cordillera has been difficult to explain because many of these taxa are known only from Tethys and from the American Cordillera and have not been found in other regions. Resolution of this biogeographic anomaly is critical because fossils have been widely used to reconstruct the paleogeography of the circum-Pacific region. Two interpretations have generally been suggested to account for the occurrence of "Tethyan" Cordilleran fossils. In the tectonic model, the suspect terranes originated in the western or mid-Pacific (Fig. 2A), where the "Tethyan" faunas lived, and were displaced to their present-day position in the American Cordillera; thus, in this model, the disjunct (discontinuous) distributions of fossils resulted from longitudinal tectonic displacement and does not represent primary biogeographic patterns of "Tethyan" species (*9–11*). In contrast, in the marine-corridor model, seaways through early rift basins separating the enormous Pangeic continent allowed faunas to migrate westward via the west Tethys to western North or South America (Fig. 2B) (*17–21*). As different as these two models seem, they have been used to interpret comparable patterns—disjunct distributions of species known only from various parts of the Tethyan seaway and from the American Cordillera.

An alternative explanation is that many "Tethyan" faunal occurrences in the Cordillera reflect pantropic distributions of some marine species (Fig. 3A) and do not require explanation by either longitudinal tectonic displacement or the formation of marine corridors. Paleozoic and Mesozoic pantropic fossil groups include many benthic taxa in addition to planktonic groups (such as

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ammonites and microcrinoids), which have long been known to have had wide tropical distributions (*7, 14, 22*). This type of biogeographic model has been briefly discussed by several workers in studies of the paleontology of a few suspect terranes [for example (*16, 23*)]. In this article, I develop the pantropic model more fully by comparing the distribution patterns of Paleozoic and early Mesozoic Cordilleran "Tethyan" species with known distributions of strictly Tethyan species in Cretaceous through mid-Cenozoic time and with modern distribution patterns of Indo–West Pacific (IWP) mollusks. I also summarize equatorial circulation patterns that may have contributed to these biogeographic distributions. The distribution of modern faunas demonstrates that there can be significant eastward dispersal of tropical Pacific invertebrates.

Paleozoic "Tethyan" Faunas in the American Cordillera

Paleozoic "Tethyan" faunas in the western Cordillera (Table 1) provided some of the first evidence that parts of the North American Cordillera may be exotic or far-traveled. Thick [0.2 to 2 km (*24*)] sequences of Carboniferous and Permian biogenic carbonate rocks in the Cache Creek terrane (Fig. 1) contain abundant "Tethyan" faunas, including verbeekinid fusulinids and waagenophyllid corals. Because similar fossils had not been found in rocks known to be part of North America at the time, these fossils were put forth as evidence that the Cache Creek terrane originated in the central proto–Pacific Ocean, far to the west of its present position (*10, 11*). Waagenophyllid rugose corals with "Tethyan" affinities also occur in upper Paleozoic rocks of the eastern Klamath and Hayfork terranes (Fig. 1). Although the relative abundance and diversity of the "Tethyan" faunas in the Klamaths are not as high as those in the Cache Creek terrane, their occurrence was also considered as evidence that the Klamath terranes were located in the central or western Pacific during the late Paleozoic (*10, 13*).

Subsequent investigations revealed that some of these Paleozoic biotas were not confined strictly to the Tethyan seaway and to these suspect terranes. "Tethyan" verbeekinid fusulinids (*Yabeina texana*)

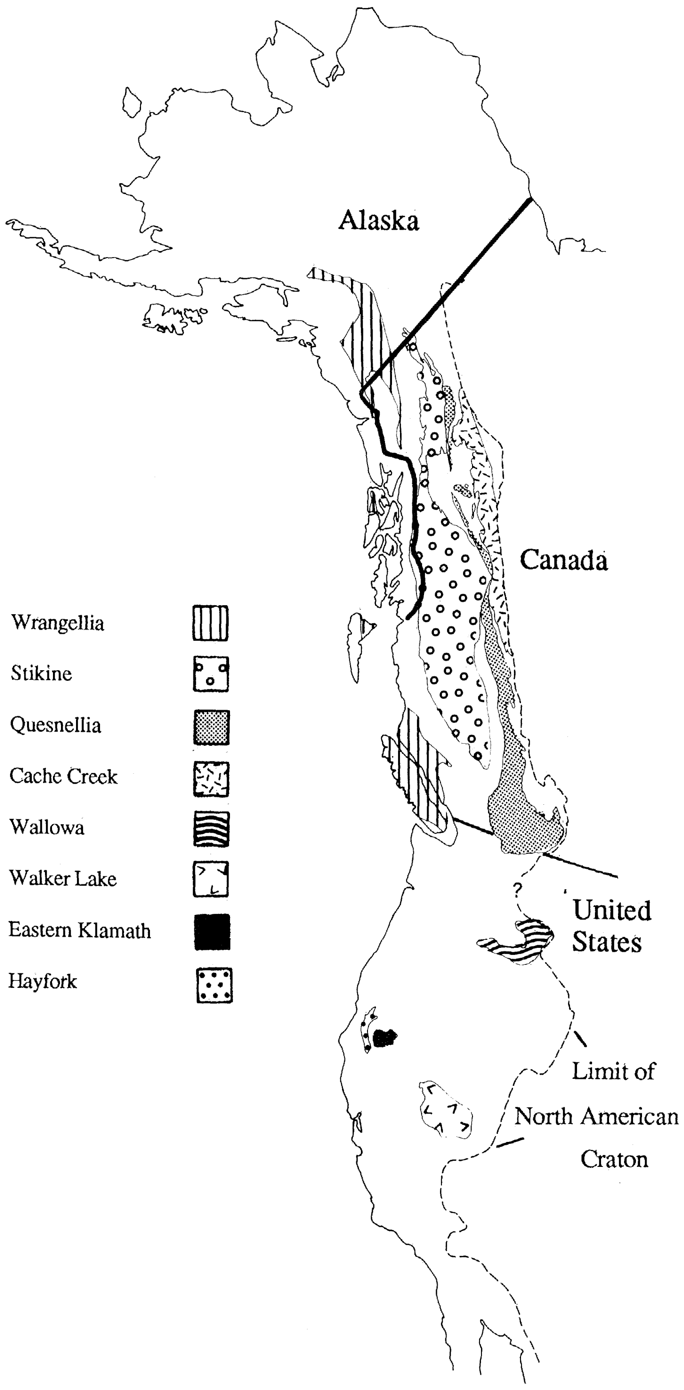

Fig. 1. Location of major North American suspect terranes discussed in text, relative to the western limit of North American cratonal rocks (dashed line). Distribution of terranes from (*61*).

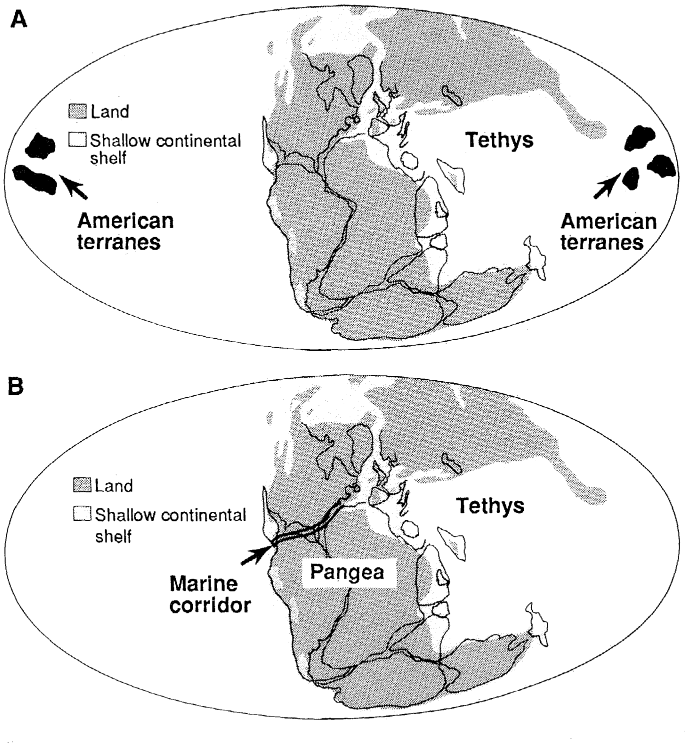

Fig. 2. Models that have been suggested to account for "Tethyan" faunal occurrences in rocks of the North and South American Cordillera. Base maps modified slightly from Hettangian reconstructions in (*62*). (**A**) Longitudinal tectonic-displacement model, showing an inferred western Pacific origin of North American suspect terranes [generalized from (*10, 11*)]. (**B**) Marine-corridor hypothesis, showing "Hispanic" corridor that has commonly been proposed to explain Jurassic faunal patterns in both North and South America; for example (*17–19*). However, current reconstructions of Pangea (*36, 62*) show that the site of the inferred corridor is represented by nonmarine sedimentary rocks; there is no direct sedimentological or faunal evidence for such a seaway.

have been found in rocks deposited in the Permian basin of West Texas (*13, 25*), which was clearly part of the North American plate at that time. This occurrence is incontrovertible evidence that verbeekinid fusulinids were introduced into cratonal North American communities (albeit in low diversity and abundance) and were therefore not completely restricted to the Tethyan seaway. Furthermore, Stevens *et al.* (*26*) have shown that Permian faunas from the eastern Klamath terrane represent a mixture of North American and "Tethyan" species, and that "Tethyan" biotas are more abundant in the Hayfork terrane to the west. These Paleozoic "Tethyan" fossils have been explained with revised models of marine corridors through Pangea (*13*) or with expanded tropical distributions (*23*).

Lower Mesozoic "Tethyan" Faunas in Cordilleran North and South America

Upper Triassic faunas. Upper Triassic molluscan faunas of many North American suspect terranes commonly contain "Tethyan" genera and species (Table 1). For example, "Tethyan" faunas in lower Norian bivalve assemblages from the Wallowa terrane of Oregon include the distinctive bivalve species *Cassianella angusta*, *Cultriopsis angusta*, and *Mysidioptera spinigera*, and the bivalve genera *Arcavicula*, *Cultriopsis*, *Krumbeckiella*, *Lopha*, and ?*Enantiostreon*. Overall, "Tethyan" bivalves compose a minor fraction of the total bivalve species diversity in the Wallowa terrane [approximately 18 to 19% (*27, 28*)]. In addition to the bivalves, some gastropods from the Wallows block also have "Tethyan" affinities (for example, the gastropod genera *Delphinulopsis* and *Kokenella*). Some of these "Tethyan" bivalve and gastropod taxa are known only from the southern Alps and Cordilleran North America, although others were evidently widespread throughout the Tethyan region [for example, *Arcavicula*, which ranged from the Alps to China and western North America (*27, 28*)].

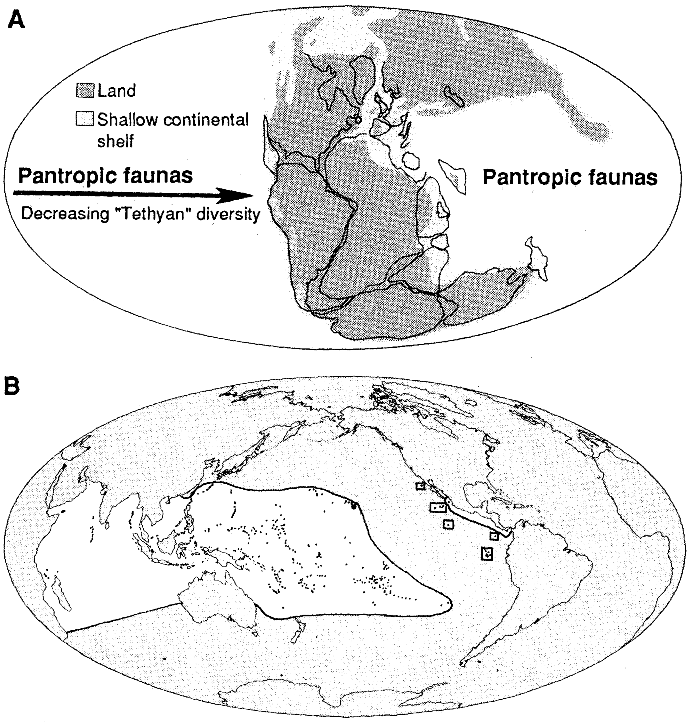

Fig. 3. (**A**) Pantropic model to account for "Tethyan" faunal occurrences in western North and South America. "Tethyan" faunas decrease in diversity eastward in the proto–Pacific Ocean; close to the North and South American continents, American tropical endemic species would constitute a substantial fraction of the biota, with only minor "Tethyan" species. (**B**) Extent of IWP influence (outlined) in the modern ocean (*41–43*). Indo–West Pacific species extend to the East Pacific and, occur in islands off central America (boxes) as well as along the central American continental margin (white). In these easternmost occurrences, IWP taxa are generally subordinate in importance to species of the tropical Panamic province (*43*).

Wrangellia, one of the largest suspect terranes, contains bivalve assemblages with the "Tethyan" species *Cassianella angusta* and *Mysidioptera spinigera.* Norian rocks from the Tatsenshini map area in British Columbia (probably part of the Wrangellia terrane) contain *Palaeonucula subaequilatera*, a species also known from Peru (*29*) and from the western Tethys. In Cordilleran South America, upper Norian carbonate rocks of Peru also contain bivalve assemblages with minor proportions of "Tethyan" bivalves (*30*). The tropical bivalve *Monotis salinaria*, which was widespread in Tethys, also occurs in many Cordilleran terranes (*5*); this species was clearly a circumequatorial species (*5, 7*).

Distributional patterns of other Triassic invertebrates in the Cordillera also indicate "Tethyan"-American faunal interchange in the eastern Pacific region. Pelagic microcrinoids, benthic foraminifers, and anomuran crustacean ichnofossils have all been reported to have "Tethyan" and western North American distributions (*22*); some of these "Tethyan" fossil groups occur in terranes (for example, the Walker Lake terrane) that were close to North America during Triassic time. Corals and spongiomorphs also show "Tethyan" affinities, with one Norian patch reef in the Wallowa terrane containing eight "Tethyan" coral and spongiomorph taxa (*9*). Some terranes that were close to North America at this time have coral faunas with high proportions of "Tethyan" species. For example, the Karnian coral fauna of the Pilot Mountains in the Walker Lake terrane contains 70% "Tethyan" species (*31*). Some species of ammonoid cephalopods are also known to be broadly distributed throughout the Tethyan seaway, occurring in rocks associated with stable North America as well as in suspect terranes (*7*).

As in the lower Norian, many of the upper Norian "Tethyan" fauna in Cordilleran terranes were actually widespread at low latitudes, whereas a few taxa are known only from Europe and the American Cordillera.

Lower Jurassic faunas. The distribution of Lower Jurassic "Tethyan" faunas in the American Cordillera (Table 1), in particular, has been cited as evidence in support of marine corridor hypotheses. Among 45 species of Jurassic Argentinian bivalves in a recent study (*32*), 11 (24%) have "Tethyan" affinities. One well-studied genus, the bivalve *Weyla*, occurs in the Cordillera of North and South America and in western Tethys localities but has not been found in the western Pacific or eastern Tethys region; several workers (*17, 18, 32*) have therefore speculated that a marine corridor ("Hispanic Corridor") through Pangea allowed *Weyla* to migrate westward to the American Cordillera. One potential flaw in this interpretation is that *Weyla*'s inferred ancestor, *Tosapecten*, was predominantly a western Pacific genus, with only a single, questionable occurrence in the Wallowa terrane of western North America. If *Tosapecten* was the ancestor of *Weyla*, this lineage likely developed in the western Pacific–East Tethys region.

In Jurassic rocks of western North America, Cordilleran ammonoids and belemnoids include taxa that were abundant in the West Tethys region (*21, 33, 34*). The Jurassic bivalve *Lithiotis*, a "Tethyan" genus, formed small biostromes that are preserved in Pliensbachian (Lower Jurassic) rocks of North America and in Toarcian (uppermost Lower Jurassic) rocks of South America (*20*). To explain the distribution of these mollusks, a number of workers have argued that a marine corridor through Pangea had opened by Pliensbachian time (*20, 21*).

Alternative Model: Pantropic Distributions

Two aspects of these "Tethyan" occurrences deserve particular emphasis. First, many "Tethyan" taxa in the American Cordillera are not simply endemic to West Tethys but rather occur over a wide area between the Alps and China or Japan. Second, "Tethyan" species represent only a minor part of the diversity in most Cordilleran faunas: molluscan associations in the East Pacific "Tethyan" genera or species typically represent at most 20 to 25% of the overall species richness; in upper Norian assemblages, "Tethyan" taxa commonly compose less than 10% of the total number of molluscan taxa (*28, 30*).

A pantropic model can accommodate many of the observed biogeographic patterns more completely than the tectonic displacement or marine-corridor hypotheses. Because of the widespread geographic ranges and small proportion of "Tethyan" taxa in most Paleozoic and Mesozoic Cordilleran assemblages, these faunas may have been cosmopolitan tropical taxa that dispersed widely from the Tethys–West Pacific region using current systems and island chains as stepping stones (*7, 22*). The North and South American continents and many of the suspect terranes would have been positioned on the distal, eastern edge of this tropical belt.

No single model must account for all "Tethyan" fossil occurrences in the American Cordillera. Therefore, the pantropic model is not intended as a universal substitute for the longitudinal tectonic displacement or corridor dispersal explanations (*35*). Rather, the pantropic model provides a steady state hypothesis against which other hypotheses can be tested on a case-by-case basis. The principal weakness of a longitudinal tectonic displacement model as a unifying model for Cordilleran "Tethyan" faunas is that it does not adequately account for "Tethyan" occurrences in craton-related rocks of the Americas—for example, verbeekinid fusulinids in West Texas, Triassic "Tethyan" foraminifera in Nevada, and Jurassic "Tethyan" bivalves in areas of both North and South America. Rigorous testing of the longitudinal displacement model is also very difficult, even though longitudinal displacements of some magnitude have probably occurred during the evolution of the western Cordillera. The flaw in the marine corridor hypothesis as a unifying model is that there is no sedimentological or paleontological evidence for such a seaway; the sites of inferred Permian, Triassic, and Lower Jurassic marine corridors are represented by nonmarine sedimentary rocks in all current reconstructions of Pangea (*36*) (Figs. 2 and 3). The alternative, pantropic model more fully accounts for observed "Tethyan" distribution patterns, has significant predictive power, and is readily testable.

Examples of Cretaceous and Cenozoic Pantropic Marine Biotas

Several Cretaceous, Cenozoic, and modern biotas that may be counterparts of pre-Cretaceous Tethyan biotas, had exceptionally broad longitudinal distributions; these data provide additional evidence for pantropic distributions of pre-Cretaceous "Tethyan" faunas in the American Cordillera. Among Cretaceous marine faunas, many coral and rudist taxa are pantropic, occurring in western North America as well as in the Tethyan region (*37*). Other Cretaceous groups, such as trochacean gastropods of the subfamily Chilodontinae and the mesogastropod family Cassiopidae, also show wide longitudinal distributions (*37, 38*).

For Cenozoic faunas, numerical modeling of marine molluscan diversity in Tethys indicates that geographic ranges expanded in pulses, during which Tethyan taxa migrated eastward to Pacific islands or westward into northwestern Europe (*39*). These pulses of range expansion seem to have been associated with changes in plate geometries and also with climatic and sea-level variations. The half-value distance, where the number of molluscan taxa common to two sites is reduced by 50%, averaged about 2000 km during much of Cenozoic time. Half-value distances for Cenozoic Tethyan mollusks were at a maximum during early Eocene and early Miocene time (*39*), which suggests that the geographic ranges of Tethyan molluscan taxa were greatest in relatively warm, equable climatic intervals (*40*). By comparison, half-value distances for modern Gulf Stream and western North American benthic molluscan assemblages are small, 1500 and 1000 km, respectively (*39*). Even in our present, less equable, climate, mollusks inhabiting the more uniform environments, such as those influenced by the Gulf Stream, have far greater distributions than those of more variable regions (*39*).

In the modern Pacific Ocean, IWP species have demonstrably dispersed very long distances (in some cases more than 10,000 km)

Table 1. Some representative examples of Paleozoic and Mesozoic "Tethyan" fossils in the American Cordillera.

Terrane or area	Age	Taxonomic group	Reference
Cache Creek	Carboniferous, Permian	Fusulinid foraminifers, rugose corals	(*13, 16*)
East Klamath	Permian	Rugose corals	(*23*)
Hayfork	Permian	Foraminifers, rugose corals	(*23, 26*)
Quesnellia	Permian	Rugose corals	(*10, 58*)
Stikine	Triassic	Foraminifers	(*59*)
	Jurassic	Ammonoids	(*21*)
Walker Lake	Triassic	Scleractinian corals, bivalves	(*31*)
	Jurassic	Ammonoids	(*21*)
Wallowa	Triassic (early Norian)	Bivalves, gastropods, scleractinian corals, spongiomorphs, sponges	(*27, 28, 60*)
	Triassic (late Norian)	Bivalves, scleractinian corals, microcrinoids	(*22, 30, 60*)
	Jurassic	Ammonoids, bivalves	(*20, 21*)
Wrangellia	Jurassic	Ammonoids	(*21*)
?Wrangellia	Triassic (late Norian)	Bivalves	(*30*)
Sonora*	Triassic	Microcrinoids	(*22*)
Alaska*	Triassic	Microcrinoids	(*22*)
Nevada, Oregon*	Triassic	Foraminifers	(*22*)
California*	Triassic	Anomuran crustacean ichnofossils	(*22*)
Cerro de Pasco, Peru	Triassic	Bivalves	(*30*)
Argentina	Jurassic	Bivalves	(*17, 18, 32*)
Numerous terranes	Triassic	Ammonoid cephalopods	(*7*)

*Detailed locations and terrane assignments are not available for "Tethyan" occurrences mentioned in (*22*).

to reach isolated Pacific islands. Marine mollusks have a substantial IWP influence, albeit with attenuated diversity, northward into the Japanese islands, northeastward to the Hawaiian islands, and eastward to the Marquesas (Fig. 3B) (*41*). Even Easter Island, located outside the tropics at 26°S and far to the east of most Pacific islands (105°W, or approximately the same meridian as Baja California) has an attenuated but substantial IWP molluscan biota (86% of Easter Island molluscan species are known from some area of the IWP; 24% range throughout the Indo-Pacific region) (*42*). Thus, the influence of the IWP province, in many ways the modern counterpart of the Mesozoic "Tethyan" biogeographic realm, extends far eastward into the Pacific Ocean.

Indo–West Pacific influence reaches even into the easternmost Pacific Ocean (Fig. 3B). For example, in offshore islands of the modern eastern Pacific Ocean, 49 gastropod species and 7 bivalve species have IWP affinities (*43*). These taxa are wholly distinct from "tropicopolitan" species that also occur in the western Atlantic and are thought to have been introduced during Tertiary time, before closure of the Panamanian Isthmus. In contrast, these 56 taxa apparently arrived during geologically recent times. These occurrences include 38 species from Clipperton, 6 species from Revillagigedo, 4 species from Cocos, 9 species from the Galápagos, and a species from Guadalupe (*43*). The Clipperton Island marine molluscan fauna is particularly notable in having subequal proportions of IWP and Panamic species (38 of the 70 species are of IWP affinities) (*43*). Although most of the IWP molluscan species are limited in the eastern Pacific to offshore islands, 15 species also occur on the western American continental shelf. In addition to the mollusks, other marine groups in the eastern Pacific also have IWP affinities. The hermatypic coral fauna of the Galápagos Islands is predominantly IWP, as are the majority of nonendemic ahermatypic scleractinians (39%) (*44*). Marine shore fishes, spiny lobsters, gammaridean amphipods, and coral-dwelling crabs show varying degrees of biogeographic relationship with IWP taxa (*44, 45*). These concordant biogeographic patterns provide compelling evidence for outliers of IWP taxa in the easternmost Pacific Ocean. In most areas these IWP species occur in minor abundance relative to endemic Panamic species, but in a few areas (as in the case of the Clipperton mollusks) they represent a substantial fraction of the total fauna. Most of these central and eastern Pacific occurrences are thought to reflect relatively recent (Quaternary) eastward dispersal of IWP taxa [(*43–48*); for a dissenting opinion see (*49*)].

These modern and ancient examples of broadly dispersed tropical faunas provide insights into the expected patterns of tropical diversity in Paleozoic and Mesozoic seas. For instance, the occurrence of some IWP species off western North America indicates that even in today's relatively seasonal global climate the influence of this tropical province reaches from the East African margin to western America, some 230° of the globe (approximately 25,000 km). These case studies have also demonstrated that there is a fundamental historical link between climatic equability and the geographic range of tropical taxa, with mean present-day geographic ranges perhaps only 50 to 75% as large as those in earlier, more equable Cenozoic intervals (*39*). Hence, extensive, pantropic ranges for warm-water species during the climatically equable early Mesozoic would be predicted by modern distribution patterns. Furthermore, the 260° extent of such "Tethyan" early Mesozoic faunas is not extraordinary when compared with the wide geographic range of the modern Indo-Pacific biota.

The eastward decrease in the proportion of "Tethyan" faunas in many Paleozoic-Mesozoic Cordilleran sites resembles gradients of declining IWP diversity eastward in the islands of the modern Pacific Ocean resulting from dispersal of marine organisms over large distances ("jump" dispersal). Although the pantropic model may best account for the distribution of Cordilleran "Tethyan" species occurring as minor proportions of the total fauna, it also warrants consideration even for faunas dominated by "Tethyan" species, in light of some anomalous occurrences of faunas with mostly IWP affinities in the modern eastern Pacific Ocean. Temporal variations in the proportion of "Tethyan" species have also been observed in some Cordilleran terranes; in a pantropic model this variation could be interpreted as climate-related dispersal pulses analogous to the episodic dispersal of Cenozoic Tethyan mollusks in the Pacific Ocean.

Circulation Patterns and Dispersal of Modern Equatorial Organisms

Many of the isolated oceanic islands of the central and eastern Pacific region that contain IWP faunas are geologically young and have formed entirely on oceanic crust. Colonization of these islands must have required long-distance dispersal of shallow marine organisms over distances of hundreds or thousands of kilometers. Although long-distance dispersal of sessile organisms may occasionally occur by attachment to logs, pumice rafts, or even other organisms (*50*), the most quantitatively important dispersal mechanism is the transport by oceanic currents of long-lived (teleplanic) pelagic larvae (*41, 51*). An estimated 80 to 85% of shallow benthic tropical species have a pelagic larval phase (*52*). The larvae of many of these species are able to reside in the water column for weeks, months, or even a year before settling (*51, 53*) so that currents of only moderate velocity may transport these teleplanic larvae over great distances before settlement. As an example, in a plankton survey in the Pacific South equatorial current, larvae of coastal species were recovered in more than 92% of the open-ocean sites, and these data suggest that such larvae may be transported up to 2000 to 4000 km during their residence in the water column (*51*). Teleplanic larvae have also been recovered from many plankton tows in the tropical eastern Pacific between 120° and 140°W; groups represented include gastropods, bivalves, polychaetes, sipunculids, decapods, echinoderms, and cnidarians (*48*). Thus the configuration and intensity of equatorial currents may strongly influence long-distance dispersal of tropical, shallow-water organisms between widely separated islands or continental margins.

Equatorial surface currents in the modern Pacific Ocean consist of the broad Northern and Southern equatorial currents, which flow westward, and the intervening, narrow Northern equatorial countercurrent, located at 5° to 10°N and flowing eastward. These surface currents are diffuse and move at velocities of 25 to 75 cm/sec (0.5 to 1.5 knots) (*54*). In addition, the intensity and configuration of surface equatorial currents vary seasonally and in response to El Niño events.

Because of the large geographic areas represented by the westward-flowing Northern and Southern equatorial currents, many workers have emphasized the east-to-west transport of larval stages of equatorial organisms. In this model, Cordilleran "Tethyan" taxa originated in the eastern Pacific and migrated westward to the Tethyan seaway (*22*) (Fig. 2B); eastward migration of western Pacific biotas via equatorial currents is considered less likely (*10*). However, data on modern Pacific molluscan distributions unequivocally indicate that IWP taxa have migrated eastward to the eastern Pacific; in contrast, no westward migration of American molluscan species to the IWP realm is known (*43, 48*). Several workers have proposed that eastward-flowing equatorial surface countercurrents are responsible for this eastward transport of IWP faunas (*46*). An alternative explanation of this asymmetric, west-to-east dispersal is that the strongest component of Pacific equatorial circulation is not a surface current but rather the intense, jetlike equatorial undercurrent (termed the Cromwell current in the Pacific Ocean, where it is best developed), which flows rapidly eastward (*47*). Unlike the diffuse, more slowly moving surface currents, the Cromwell current is laterally compressed, with widths of only 300 km, and flows rapidly, with maximum velocities of 150 cm/s (3 knots) (*54*). This undercurrent flows nearly along the geographic equator, varying seasonally in intensity but not greatly in position (within 100 km of the equator). The Cromwell current occurs at relatively shallow depths (50 to 300 m; maximum velocities at 75 to 150 m), with its core generally coincident with the thermocline; in the central Pacific at 140°W much of this swiftly moving jet consists of warm water (22° to 26°C) (*54*), although in the easternmost Pacific near the Galápagos this undercurrent sinks deeper and consists of colder water (15° to 17°C) (*55*).

Eastward faunal transport across the modern Pacific may thus derive partially from the vigor of the eastward flowing undercurrent (Cromwell current) (*47, 48*) rather than from the movement of surface equatorial currents (although in the eastern Pacific the undercurrent does consist of cooler waters that might form an ecologic barrier for some warm-water species). In the modern equatorial Atlantic Ocean, where relations between plankton distribution and circulation patterns have been extensively studied, the equatorial undercurrent contains abundant invertebrate larvae representing the phyla Cnidaria, Echinodermata, Arthropoda, Annelida, and Mollusca (*56*). Among the species represented in this warm (core temperature 25°C), shallow (60 to 90 m) undercurrent is a shallow-water, tropical zoanthid coral whose geographic range includes both the South American and African continental margins. The equatorial undercurrent thus provides a mechanism for long-distance dispersal of warm- and shallow-water organisms in the tropical Atlantic Ocean. By extension, an equatorial undercurrent in the Paleozoic and early Mesozoic proto–Pacific Ocean may have contributed to long-distance dispersal of tropical benthic organisms among low-latitude suspect terranes (depending on the temperature of the undercurrent and the thermal tolerance of the "Tethyan" species). Unfortunately, no quantitative paleocirculation models are available for the late Paleozoic or early Mesozoic proto–Pacific Ocean.

Fossil Versus Paleomagnetic Evidence for Terrane Displacement

Fossil and paleomagnetic data contribute the two primary lines of evidence for large-scale latitudinal movement of suspect terranes in the American Cordillera. Latitudinal displacement of terranes is clearly indicated by both faunal and paleomagnetic data from the North American Cordillera, and in most cases these two types of data are concordant. Several paleobiogeographic analyses have convincingly demonstrated that suspect terranes have been transported northward, with the juxtaposition of ancient tropical faunas against inboard temperate faunas [for example (*7, 8, 16*)]. The pantropic model is fully consistent with continued use of fossil data as an independent check on paleomagnetic models for latitudinal displacement of Cordilleran suspect terranes.

Longitudinal tectonic displacements of Paleozoic-Mesozoic suspect terranes cannot be resolved by paleomagnetic data. Paleobiogeographic data do have some potential to identify such displacement, but rigorous demonstration of longitudinal displacement on the basis of fossil evidence is far more difficult than most workers have presumed. To establish biogeographically that Cordilleran suspect terranes have undergone substantial longitudinal displacement and are entirely allochthonous requires extensive sampling of North and South American cratonal faunas of a given age and a wide range of facies; if all cratonal rocks of a given age are nearshore clastic rocks and terrane rocks open-ocean carbonate rocks, biogeographic comparisons may not be meaningful. Furthermore, demonstration of a western Pacific origin with the use of biogeographic data would require thorough documentation of craton-related Asian faunas, and even then the question of eastward, long-distance dispersal to oceanic islands would be difficult to disprove. A final complication is that even the modern biogeographic patterns of shallow-marine species in the islands of the Pacific Ocean are complex and overlapping, and islands as far distant from one another as Hawaii, Okinawa, and Easter are all only moderately differentiated parts of the IWP biogeographic region (*41, 57*); marine biogeographic patterns alone could not be used to identify the present-day spatial relations of these islands or to quantify the geographic distances that separate them (*28*). In light of these considerable uncertainties, use of Paleozoic and Mesozoic biogeographic data to resolve longitudinal tectonic displacements is, in most cases, premature.

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63. I thank W. K. Emerson for his assistance with literature on eastern Pacific Mollusca.

Energy Loss Mechanisms of Superconductors Used in Alternating-Current Power Transmission Systems

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The intrinsic hysteretic loss of superconductors carrying alternating current has been derived from simple models and verified experimentally. In practical cable designs the losses are increased by surface roughness, conductor configuration, and added metallic components. When possible applications by electric utility companies are being considered, such losses are only one of many factors that must be adjusted in an optimization that produces the lowest cost (including both capital and operating expenses) during the lifetime of the system.

THE DISCOVERY OF SUPERCONDUCTING MATERIALS WITH critical temperatures above 90 K (*1*) has rekindled interest in the practical application of superconductors. Will their high critical temperatures reduce refrigeration power or permit the use of nitrogen coolant, and are these important considerations in future applications? It is not clear if this is the case; such practical considerations depend on detailed analyses of prospective designs in which many factors are varied to optimize the overall system performance. It is possible that the new superconductors will find applications at temperatures below half the critical temperature, where enhanced current-carrying ability may be an attractive feature. In commercial applications of superconductivity the capital cost must be balanced against other considerations that affect the operating costs. These considerations include maintenance, the projected load (over the lifetime of the project), and the expected losses; in a superconducting system the losses are manifested as the power needed to run the cooling system. The objective is usually to minimize the total cost over the lifetime of the system. Optimizations of this kind are typical of conventional engineering practice (*2*). For example, overhead transmission lines can easily be designed to lower resistive losses if bigger conductors are used, but this feature must be balanced against the cost of the larger conductor, stronger towers, and bigger insulators. In a superconducting power transmission system the conductor losses are a component, but not necessarily the major component, in setting the power level of the cooling system.

During the past three decades numerous projects were initiated in

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