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Cisuralian and Guadalupian global paleobiogeography of fusulinids in response to tectonics, ocean circulation and climate change

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Abstract

During the Permian, major icehouse-greenhouse climate shifts and tectonic reconfiguration had important biogeographic implications, especially for climate-sensitive organisms such as fusulinids. Here we present multivariate methods on a global fusulinid species dataset including 1546 species from 58 localities in the Early (Asselian, Sakmarian, Artinskian and Kungurian) and Middle (Roadian, Wordian and Capitanian) Permian. Our results show that fusulinid global provincialism was high in the Asselian, Sakmarian, and Artinskian, driven by the development of multiple fusulinid bioregions in and near the Tethys Ocean. During the Asselian, Uralian sites and nearby regions of western Tethys were distinct from eastern Tethys, while stations in Arctic Russia and Norway formed a separate Boreal bioregion. Tectonic closure of the oceanic gateway in the southern Urals resulted in progressive isolation of the Uralian and Boreal bioregions during the Sakmarian and Artinskian and their ultimate disappearance by the Kungurian. Climate warming likely was the most important control on the Sakmarian formation of the distinct peri-

Gondwana bioregion, because its development coincided with deglaciation following the late Paleozoic ice age but preceded the separation of the Cimmerian terranes from northern margin of Gondwana. On the other hand, northward movement of the Cimmerian blocks following Artinskian-Kungurian rifting ultimately led to the merger of the peri-Gondwanan bioregion with tropical Tethyan faunas, resulting in lower provincialism in the Guadalupian and minimal faunal differentiation across Tethys. In contrast, faunal similarity between Tethys and eastern Panthalassa (the McCloud region and southwestern United States) was higher in the Asselian-Artinskian but decreased in the Kungurian and Middle Permian, perhaps as the result of sluggish ocean circulation following the warming episode of Late Paleozoic deglaciation.

Key words

Permian, Multivariate analysis, Faunal provinces, Latitudinal temperature gradient, Biogeographic connectedness

1. Introduction

Biogeographic distributions are influenced by a complex suite of physical, environmental, ecological, and evolutionary controls. Temperature is one of the primary limits on the latitudinal ranges of marine organisms (Hall, 1964; Sunday et al., 2012), reflecting the interaction between climate variability or extremes and an organism's physiological tolerances (Bozinovic et al., 2011). Although temperature is an important overarching control on latitudinal range, other attributes of the environment, such as the distribution of preferred habitat types, may also limit the distribution of marine organisms (Foote, 2014). Even when environmental

conditions are appropriate, species may be further limited in their ranges due to ecological interactions or exclusion by incumbent species that prevent establishment (Valentine et al., 2008). Finally, ocean currents and continental distributions act as conduits for and barriers against dispersal in marine realm (Lessios 2008; Watson et al., 2011).

The Permian (298.9-251.9 Ma) was a time of major climate change following the peak of the Late Paleozoic Ice Age, tectonic plate reconfiguration during the assembly of Pangaea, and dramatic change of faunal communities (Qie et al., 2019). There was an overall warming trend from peak glacial conditions in the early Cisuralian (Early Permian) to deglaciation in Guadalupian (Middle Permian). Despite the previous hypothesis that deglaciation happened in the late Sakmarian (Korte et al., 2005; Montañez et al., 2007; Peyser and Poulsen, 2008), conodont apatite oxygen isotope measurements in South China (Chen et al., 2013) and a decrease in the magnitude of glacioeustatic fluctuations (Ross and Ross, 1978) suggest the largest waning of the ice sheets was in the Kungurian. The late Paleozoic icehouse-to-greenhouse shift was a dynamic climatic transition, including multiple glacial and non-glacial episodes superimposed on an overall warming trend (Fielding et al., 2008), associated with increased CO₂ and changes in oceanic and terrestrial systems (Liu et al., 2017a,b,c).

After the collision of the Laurasia and Gondwana in the Carboniferous, the assembly of the supercontinent Pangaea was completed through the Uralian Orogeny, resulting from the southwestern movement of Siberian Plate (Scotese, 2001; Stampfli and Borel, 2002; Puchkov, 2009). The Neo-Tethys Ocean opened along the northern margin of Gondwana while Paleotethys was narrowing by subduction along the southern margin of Eurasia. A strip of microcontinental blocks known as Cimmerian terranes was split off from the Gondwana as a consequence of Neo-Tethys opening and drifted northward to subequatorial paleolatitude in the

70 Middle to Late Permian, finally colliding with the southern margin of Eurasia in the Cimmerian
71 Orogeny (Sengör, 1979; Metcalfe, 2006; Ruben et al., 2007). These continental reconfigurations
72 provided opportunities for dispersal but also created barriers that altered ocean currents and
73 environmental conditions (Reid et al., 2007).

74 These tectonic movements and climate changes potentially had important
75 paleobiogeographic implications, especially for climate-sensitive organisms such as fusulinid
76 foraminifera. Fusulinids were the most diagnostic Late Paleozoic warm-water benthic
77 foraminifers because they were widespread within tropical and subtropical settings (Kobayashi,
78 1999; Ueno, 2003) and they evolved rapidly and reached high taxonomic diversity during their
79 short biostratigraphic ranges (Ross, 1967; Ross and Ross, 2003; Hada et al., 2015). It appears
80 that larval or juvenile individuals of fusulinids, like other benthic foraminifera, had a planktonic
81 stage that would have been sensitive to changes in ocean circulation during dispersal (Alve and
82 Goldstain, 2003, 2010; Shi and Macleod, 2016). Fusulinid distributions were also influenced by
83 habitat factors, as they predominantly occurred in shallow water carbonate and mixed
84 siliciclastic-carbonate environments (Davydov and Arefifard, 2007; Huang et al., 2015; Ross,
85 1967; Ross and Ross, 1987, 1988; Ueno, 2003); however, as the result of turbidity currents and
86 storms they can also be reported from outer ramp and slope deposits (Koehrer et al., 2010;
87 Sonnenfeld and Cross, 1993). The large size and complex morphology of fusulinids, similar to
88 modern larger benthic foraminifers (Beavington-Penney and Racey, 2004; Murray, 2006;
89 Hallock and Pomar, 2008), suggest that fusulinids hosted photosynthetic symbionts (Ross, 1982;
90 Vachard et al., 2004; Shi and MacLeod, 2016). Symbiosis can explain the high diversity and
91 rapid evolution of fusulinids, as well as their low-latitude distribution and restriction to the
92 euphotic zone (Della Porta et al., 2005; Groves and Wang, 2009). Although photosymbiotic

93 fusulinids predominantly occur in tropical carbonate deposits with high production rates, their
94 symbiosis also makes fusulinids highly sensitive to temperature, which has important
95 biogeographic consequences during times of major climate fluctuations (Weidlich, 2007). Thus,
96 fusulinids represent one of the best benthic foraminiferal groups to study Late Paleozoic
97 paleobiogeography.

98 Late Paleozoic foraminiferal assemblages have generally been divided into three major
99 biogeographic realms: the Midcontinent-Andean (sub-Arctic North America other than accreted
100 terranes, and northwestern South America), the Tethyan (northern margin of Gondwana,
101 southeastern margin of Euramerica, central and southeast Asia, Middle East, Africa and India)
102 and the Boreal (Arctic Alaska, Norwegian and Canadian Arctic, Russian platform, Franklinian
103 Shelf, and Uralian Trough as far south as the central Urals) (Groves and Lee, 2008; Reitlinger,
104 1975, Ross and Ross, 1985). The accreted terranes in western North America are characterized
105 by another biogeographic realm known as McCloud (Ross, 1997) which exhibited close
106 similarity with the North American realm during Late Carboniferous and early Cisuralian but
107 later developed greater resemblance with Tethyan elements (Skinner and Wilde, 1965). Two
108 extra antitropical transitional zones were recognized in the Late Paleozoic, on the northern and
109 southern margins of Tethys. The northern transitional temperate province or Arctic province (Rui
110 et al., 1991) includes areas from the northern Urals in the East to Canadian Arctic in the West
111 along the northern margin of the Pangea and was the consequence of cool water conditions
112 characterized by fusulinids with low taxonomic diversity. This province appeared in the late
113 Moscovian to Gzhelian and again in the late Asselian to early Sakmarian. The southern
114 transitional temperate fusulinid zone, including terranes along the Gondwanan margin (Leven,

1993; Kalvoda, 2002; Ueno, 2006), was also developed in the late Sakmarian and early Artinskian.

With a few exceptions (e.g. Davydov et al. 1996), these biogeographic regions have been recognized qualitatively and/or at coarse temporal resolution, making it difficult to evaluate environmental controls on fusulinid paleobiogeography. Many studies have also considered paleobiogeographic patterns within a single time interval or geographic region, so longer-duration shifts driven by climatic or tectonic changes cannot easily be documented. Here we quantitatively examine the changing global paleobiogeography of Early and Middle Permian fusulinid species, using species-level data at stage resolution, to decipher how climate changes, plate tectonic reorganization, and ocean circulation impacted fusulinid distribution.

2. Material and methods

We compiled presence-absence occurrence data for 1546 fusulinid species grouped into 58 geographic areas (Tables 1, S1 and S2), resolved to stage level and including the Asselian (444 species, 26 stations), Sakmarian (367 species, 25 stations), Artinskian (322 species, 26 stations), Kungurian (367 species, 26 stations), Roadian (181 species, 18 stations), Wordian (373 species, 34 stations), and Capitanian (184 species, 19 stations). Although some biostratigraphic correlations remain debated, we used a holistic approach incorporating evidence from conodonts, ammonoids, and radiometric constraints to assign fusulinid records to the global timescale with the current best information. Taxonomic assignments were standardized to the extent possible, and stations were included if they contained five or more species. Although the dataset does not include every published fusulinid species, biogeographic patterns are unlikely to be completely

obscured by incompleteness, or by oversplitting or misidentification of species (see supplementary material).

To analyze paleobiogeographic patterns, we performed cluster analysis on the presence-absence data for each time period. The Forbes coefficient, which measures faunal similarity well even when sample sizes are unequal (Alroy, 2015), was used to quantify dissimilarity between station pairs. Stations were grouped into clusters with the average linkage method. We also performed principal coordinate analysis (PCoA), using the Forbes coefficient to measure dissimilarity. PCoA ordination provides a complementary method of visualizing multivariate similarity, displaying gradients in faunal composition to go with the discrete groupings generated by cluster analysis.

We also calculated biogeographic connectedness, a measure of provincialism that compares the number of shared species links between sites to the total possible number of shared links (Sidor et al., 2013). A value of zero indicates that each species is endemic to a single site, whereas a biogeographic connectedness of one indicates that all species occur at all sites. This measure of provincialism is complementary to the number of discrete bioregions, and provides information on the dispersal potential and impact of barriers on geographic distributions. We estimated confidence intervals on biogeographic connectedness via bootstrapping, resampling the species list with replacement but keeping the distribution of each species unchanged (Sidor et al., 2013).

3. Results and interpretation

3.1. Asselian

Asselian fusulinids are recorded from 26 stations worldwide, including 444 species. Many stations were dominated by endemic species, with few species occurring at multiple sites. As a result, biogeographic connectedness was low during the Asselian (Fig. 1) and there is good differentiation between bioregions.

The first group is represented only by the Klamath Mountains (Western United States) of island-arc origin, situated on the western margin of Pangaea (Fig. 2). This region contains especially distinctive and endemic fusulinid species, previously distinguished as the McCloud province (Miller, 1987; Stevens et al., 1990). This characteristic fusulinid species assemblage differs considerably from all other regions, even from nearby sites in the Bird Spring Formation of southeastern California and southern Nevada, and in New Mexico (Big Hatchet Mountains) and the Glass Mountains (Texas, USA). Those three sites, all in the southwestern United States, form a group in both cluster and PCoA analyses, although there is considerable heterogeneity among the three stations.

The southwestern United States cluster is most similar to a cluster including East Tethys regions of Indochina, South China, North China, and Japan (Akiyoshi, Mino and Chichibu, Hida terranes). The East Tethyan localities themselves form a discrete cluster on the dendrogram (Fig. 3) and group closely on the PCoA plot (Fig. 4). The southwestern United States groups with East Tethys localities primarily because of the shared presence of the widespread paleoequatorial species *Pseudoschwagerina uddeni* and *Schubertella kingi*, although *Schwagerina neolata* is shared only between the southwestern US and South China. Some East Tethys localities, such as South and North China, also contained a few species found in the McCloud fauna of the Klamath Mountains (California, USA), including *Rugosofusulina retusa* and *Schubertella pusilla*. The faunal similarities between East Tethys and both the southwestern United States localities and

McCloud fauna imply some fusulinid dispersal across Panthalassa and even throughout the paleoequatorial region.

Uralian sites (Moscow Basin (Russia), South Urals (Russia), Pre-Caspian Basin (Kazakhstan), and Pre-Donets (Ukraine)) group with sites from the northern Tethyan margin (Fergana (Kyrgyzstan) and Darvaz (Tajikistan)) in both cluster and PCoA analysis. Other sites in Tethys formed smaller clusters, including one with east central Iran, Turkey, Carnic Alps (Austria/ Italy), and North Afghanistan, and another with North Iran and Abadeh (west central Iran) (Fig. 2). These subgroups are most similar to the Uralian cluster, forming a larger group on the dendrogram, along with the isolated Tethyan locality of North Qiangtang (Tibet, China). The grouping of North Afghanistan closer to Turkey, the Carnic Alps, and east central Iran in both analyses, despite its close geographic proximity to Darvaz, could suggest that Uralian and western Tethyan sites are all best grouped as a broad Uralian bioregion. These sites are also arranged in a continuum on the PCoA plot, suggesting a faunal gradient between Tethys and the Uralian seaway. However, Uralian sites form a distinct and coherent subgroup in both analyses, so could be separated as a different biogeographic region.

Arctic Norway, the Pre-Urals (Russia), and Timan are grouped into a broad gradient on the PCoA plot, but are scattered on the cluster dendrogram. The Pre-Urals and Arctic Norway are not grouped closely with any other site on the dendrogram, due to highly endemic faunas, while Timan groups with other Uralian sites. The PCoA analysis suggests grouping Arctic Norway and the Pre-Urals into a distinct bioregion at the Boreal extent of fusulinid distributions, perhaps also including Timan (Russia) or with that station as a transitional zone with the Uralian sites.

3.2. Sakmarian

In the Sakmarian, 367 fusulinid species are recorded from 25 stations worldwide, exhibiting low biogeographic connectedness, similar to the Asselian (Fig. 1). This high provinciality indicates well-defined fusulinid bioregions dominated by endemic species. The Klamath Mountains (McCloud bioregion) and southwestern U.S. (New Mexico and the Glass Mountains) both contain distinctive and endemic fusulinids in the Sakmarian. Although the two southwestern U.S. sites are grouped together with the Klamath Mountains by the cluster analysis (Fig. 3), they do so at quite low similarity levels. Also, the three sites do not form a distinct grouping on the PCoA plot, further suggesting that they are distinct from each other, as in the Asselian. However, North China plots close to southwestern U.S. localities with both methods. Despite the consistent pattern between both analysis, North China only includes 5 species, with a single species (*Pseudoschwagerina texana*) shared with New Mexico and the Glass Mountains. As a result, the exact biogeographic placement of North China is uncertain, although there may have been some degree of similarity across Panthalassa, as in the Asselian.

Other localities in eastern Tethys or Panthalassa (South China, South Kitakami (NE Japan), the Mino and Chichibu terranes (Japan), and North Qiangtang) are widely scattered on the cluster diagram, although only connected at low similarity values with neighboring clusters. South China is very loosely grouped with Uralian sites and Norway by the cluster analysis, while North Japan (Kitakami terrane) is connected at low similarity with the northern and western Tethyan localities of North Afghanistan, Turkey, and the Carnic Alps. North Qiangtang shares low similarity with the combined Uralian-West Tethys cluster, and the Panthalassa seamounts of the Mino and Chichibu terranes form an isolated location in the cluster analysis. However, all of these sites are more closely associated with each other in the PCoA analysis (Fig. 4), although

with South China closer to Uralian sites than to other Tethyan localities. Overall, this is most consistent with a continuation of the East Tethys bioregion, but with substantial heterogeneity within that region.

Uralian sites (Pre-Urals, southern Urals, Pre-Caspian depression, Timan, and Arctic Norway) retain their distinctive character in the Sakmarian, with Arctic Norway and Timan perhaps representing a different Boreal bioregion. The Pre-Urals, which was not closely associated with Uralian sites in the Asselian, is instead more similar to the southern Urals in the Sakmarian. Localities in northern and western Tethys, including North Afghanistan, Turkey, and the Carnic Alps, form a coherent group in cluster analysis but form more of a gradient in the PCoA plot, with the Carnic Alps closer to Uralian sites. As in the Asselian, this gradient suggests some faunal connection among Uralian and western Tethyan sites, although the two regions still have some distinctive elements.

The Sakmarian also included the appearance of a cooler biogeographical region at southern mid latitudes of peri-Gondwana, including Karakorum (Pakistan), central Pamir (Tajikistan), Hindu Kush (Pakistan), Kalmard (central Iran), Oman, southern Afghanistan, Baoshan (Yunnan, China), and Tenchong Block (Yunnan, China). These sites form a highly distinct grouping on both the cluster dendrogram and PCoA plot, particularly the core peri-Gondwanan sites in central Asia (Karakoram, central Pamir, Hindu Kush, Kalmard, and Oman). The Tenchong block is affiliated with peri-Gondwanan sites in the cluster analysis, but is more distant on the PCoA, perhaps as the result of less shared peri-Gondwanan fusulinid species or more species shared with eastern Tethyan localities

3.3. Artinskian

The Artinskian data includes 323 species from 26 stations, mostly distributed in the Tethyan Realm. Biogeographic connectedness remained low, as in the Asselian and Sakmarian (Fig. 1), indicating high levels of endemism.

The western U.S. McCloud bioregion remained distinct in the Artinskian, including the Klamath Mountains, northwestern Nevada, and central Oregon, forming a discrete group on both the cluster dendrogram (Fig. 3) and PCoA plot (Fig. 4). Other sites in the southwestern US (Hueco Mountains (Texas, USA) and Glass Mountains (Texas, USA)) form a distinct cluster and grouping on the PCoA plot, emphasizing the continued biogeographic separation between the McCloud fauna and other localities on the Laurentia margin. However, other sites in the southwestern United States (Inyo Mountains and Bird Spring of eastern California) also each have completely endemic faunas (16 species found only the Inyo Mountains and 6 species found only in the Bird Spring), forming isolated tips on the cluster dendrogram. As a result, the biogeographic affinity of these localities remains unclear.

East Tethys sites of South China and Indochina also form a group in both analyses, although Kitakami and Akiyoshi (SW Japan) are closer to West Tethyan sites of Abadeh, and east-central Iran, while South Qiangtang (Tibet, China) is grouped with the large cluster including all other Tethyan locations. North Qiangtang instead groups at low similarity with the remaining Uralian localities of the South Urals and Pre-Caspian basin, but only because of two species (*Oketaella provecta* and *Pseudofusulina valuda*). On the PCoA analysis, these localities form a broad region in the center of the plot, consistent with the continuation of an East Tethys bioregion. The apparent similarity of Kitakami and Akiyoshi to Western Tethyan sites is primarily due to shared occurrences of widespread species, such as *Pamirina darvasica*, *Levenella leveni*, *Leeina fusiformis* and *L. krafftii*. However, the Hida terrane (central Japan) in

central Japan groups with Western Tethyan sites in both analyses, including close to North and South Afghanistan in the cluster analysis. The links with N and S Afghanistan are based on the shared presence of *Chalaroschwagerina vulgaris*, *Leeina krafftii* and *Neofusulinella giraudi*, but the terrane also had species (*Neofusulinella giraudi* and the widespread *Chalaroschwagerina vulgaris*) in common with Akiyoshi and Kitakami. Although Hida was geographically located in Panthalassa, we leave it as unplaced due to the ambiguity of its fauna. Finally, NE Russia (Koryak) may represent a separate Panthalassan bioregion, particularly given the endemic fauna (7 of 8 species) or may represent an open-ocean subgroup of the East Tethys bioregion.

Central and western Tethyan localities (Darvaz, North Afghanistan, East-central Iran, Abadeh, Turkey, Karakorum, and the Carnic Alps) make a well-defined grouping in both cluster and PCoA analyses. Sites belonging to this West Tethys bioregion are fully separated from the remnants of the Uralian bioregion (South Urals (Russia) and Pre-Caspian depression), continuing the divergence of those areas that was partially developed in the Sakmarian. The two Uralian sites are closely grouped in both analyses due to shared endemic species such as *Parafusulina solidissima*, *Concavutella concavatus*, *Kutkenella kutkanensis*, and *K. solida*. No peri-Gondwanan sites are represented in the Artinskian and the development of the bioregion is unclear due to a lack of data, however the age of the fusulinid species in some peri-Gondwanan regions have been extended to early Artinskian especially based on conodont biostratigraphy.

3.4. Kungurian

The Kungurian includes 369 fusulinid species at 26 sites in West Tethys and eastern Panthalassa. The Uralian bioregion had disappeared by the Kungurian due to a barrier between the Uralian seaway and Tethys, with resulting cooling in northern Pangea. Biogeographic

connectedness increased from the Artinskian to Kungurian (Fig. 1), indicating more numerous shared species and reduced endemism.

The Western U.S. McCloud bioregion persisted in the Kungurian and was characterized by a low-diversity fusulinid fauna containing *Parafusulina complexa*, *P. halli*, *P. owensensis*, *Concavutella klamathensis*, *C. fiski*, *Skinnerella davydovi* and *S. hexagona*, all of which are endemic to that bioregion. The Glass Mountains and Baylor Mountains also contain a distinctive Kungurian fauna representing the continuation of the southwestern US bioregion, the cluster also contains the Koryak terrane (NE Russia). However, the two regions only share a single species (*Skinnerella magna*, present in both the Koryak terrane and the Baylor Mountains (Texas, USA)), while the Koryak terrane is separated in the PCoA analysis. This implies limited faunal dispersal across Panthalassa, as documented to a greater degree in Kungurian brachiopods (Shen et al., 2011). Due to the otherwise highly endemic nature of the NE Russia fauna, it may be best identified as a distinct Panthalassan bioregion. The Inyo Mountains fauna also remained completely endemic, including six species found at no other station, resulting in uncertain biogeographic placement.

Stations in eastern Tethys and Panthalassa form several distinct clusters on the dendrogram, and occupy a broad but coherent region in the PCoA analysis. South China groups with Indochina, North China, North Qiangtang, and the East Hindu Kush. Darvaz, Kitakami, and Sibumasu (Thailand) also form a grouping in both cluster analysis (Fig. 3) and PCoA (Fig. 4), whereas South Qiangtang and the Mino and Chichibu terranes (Japan) are more distinct in the cluster analysis and, in the case of South Qiangtang, also on the PCoA plot. Darvaz grouped with western Tethyan sites in the Artinskian, but both it and the East Hindu Kush are geographically located at the transition between the eastern and western Tethys bioregions, so shifting

assignment does not necessarily indicate a major biogeographic shift. Indeed, with the exception of *Parafusulina diabloensis*, *Pseudofusulina fukasensis*, *Schubertella pseudogiraudi*, and *Shichanella ambigua*, all species shared between Darvaz and eastern Tethys also occur in western Tethyan regions. The Akiyoshi terrane, an isolated Panthalassan seamount, instead groups within a cluster of western Tethyan localities, largely on the shared presence of *Armenina asiatica*, *A. salgirica*, and *Leeina quasifusuliniformis*, which are not recorded in east Tethyan localities. However, given the considerable geographic distance between Akiyoshi and western Tethys, the biogeographic placement of Akiyoshi is uncertain.

Western Tethyan sites, including Karakorum, the Southern Pamirs, North Afghanistan, South Afghanistan, Abadeh, east central Iran, Transcaucasus (Azerbaijan/Armenia), Crimea, Turkey, and the Karakaya Complex (Turkey), are clearly grouped in the cluster analysis and also exhibit similarity on the PCoA plot. These sites form two subgroups, largely corresponding to more westerly localities (Abadeh, Crimea, Turkey, and Karakaya Complex) in one and more easterly localities (east central Iran, North and South Afghanistan, and Karakorum) in the other. The close faunal similarity of Turkey and South Pamirs (Tajikistan) is unusual given the considerable geographic separation between those sites, although both are considered as Cimmerian continents.

3.5. Radian

The Radian dataset contains 182 fusulinid species from 18 stations, primarily in West and East Tethys but also including the southwestern U.S. in eastern Panthalassa and Panthalassa seamounts of Central and southwest Japan. Biogeographic connectedness reached its highest

value in this time interval (Fig. 1), indicating a greater proportion of species shared among sites, but remained low in an absolute sense.

The Glass Mountains continued to have a highly distinct fusulinid fauna, representing the continuation of the southwestern US bioregion. Roadian fusulinids are not represented in NE Russia, but other Panthalassa seamount localities of Central and southwest Japan share no species with the southwestern U.S. Instead, those two localities (Hida and Akiyoshi) group with East Tethys sites of South China, South Qiangtang and Indochina in the cluster analysis (Fig. 5). Although the main East Tethys cluster also includes the Karakaya Complex in Turkey and the South Pamirs, those two sites are on the periphery of East Tethys stations in the PCoA analysis (Fig. 6). Likewise, the Akiyoshi station is separated from other East Tethys localities on the PCoA plot, despite grouping in the cluster analysis. The Mino and Chichibu terranes in SW Japan is not grouped with other East Tethyan sites in the cluster analysis, but in the PCoA plot it is close to East Tethyan localities. Finally, the Panthalassan seamount locality of Kuzu (central Japan) has a distinctive fauna that is clearly separated in both cluster and PCoA analyses, sharing only one species (*Parafuaulina yabei*) with East and West Tethys sites.

The West Tethys bioregion remains partly defined in the Roadian, although in several distinct clusters. Turkey, Transcaucasus, East-central Iran, and North and South Afghanistan form one group in the cluster analysis, with Crimea and the North Pamirs (Tajikistan) making another. The Karakaya Complex and South Pamirs are associated, despite their geographic distance, but within the cluster including most of the East Tethys localities. On the PCoA plot, one group includes Turkey, Transcaucasus, East central Iran, and North and South Afghanistan, similar to their grouping in the cluster analysis. Crimea and the North Pamirs are also associated in the PCoA analysis, but the Karakaya Complex and South Pamirs (Tajikistan) are more

separated, with the Karakaya Complex closer to Crimea and the North Pamirs, and the South Pamirs close to North and South Afghanistan. Zagros in SW Iran is an isolated site both in the cluster and PCoA analyses, grouping with low similarity to the large cluster that includes all other Tethyan and Panthalassan sites except Kuzu (Fig. 5). The biogeographic placement of Zagros is unclear, because some species are shared with West Tethys (*Eopolydiexodina persica*, with Transcaucasus) while other species instead occurred in East Tethys (*Parafusulina elliptica* and *Schubertella simplex* in Indochina and South China).

3.6. Wordian

The Wordian dataset contains 374 species from 34 stations. Most are in West and East Tethys, with the Glass Mountains representing eastern Panthalassa and the Koryak Terrane (NE Russia), Mino and Chichibu, and Hida terranes (Central Japan), and Akiyoshi Limestone (SW Japan) representing mid-Panthalassa seamount locations. Biogeographic connectedness declined and is obviously lower than that of in the Roadian (Fig. 1), indicating less numbers of shared species than in the preceding intervals.

Some biogeographic patterns in the Wordian are similar to the preceding Roadian stage, although Wordian clusters are less well-defined, particularly within Tethys. The Glass Mountains continued to have an endemic fusulinid fauna dominated by *Parafusulina* species, none of which occur in other regions, representing the continuation of the southwestern US bioregion. South Primorye also contained a distinctive fauna that differed considerably from other Tethyan and Panthalassan sites (Fig. 5), likely as a result of its location at temperate latitudes. Tethyan and Panthalassan stations form a large cluster with poor internal subdivision; most smaller clusters contain a mixture of sites from East Tethys, West Tethys, and sometimes

also Panthalassa seamounts. There is slightly stronger patterning in the PCoA analysis, with West Tethys localities such as Sicily, the Karakaya Complex, Batain (Oman), and North and South Afghanistan grouping together (Fig. 6). Some East Tethys localities are clustered in the central portion, including North and South Qiangtang, Baoshan, Indochina, South China, Kitakami, and the Hida Terrane. Weaker grouping of sites may suggest that the East Tethys bioregion perhaps was becoming more similar to other Tethyan localities but remained partially distinct. Despite the poor clustering, stations are assigned to either West Tethys or East Tethys, in part based on their biogeographic affinity in the Roadian and/or Capitanian.

3.7. Capitanian

Capitanian dataset includes 184 fusulinid species from 19 stations. As in the Wordian, most stations are located in West and East Tethys, along with the Glass Mountains (southwestern U.S.) on the eastern Panthalassa margin and the Mino and Chichibu terranes (Central Japan), Koryak terrane (NE Russia), and Akiyoshi (SW Japan) as central Panthalassa seamounts. Biogeographic connectedness was similar to the Wordian (Fig. 1), but remained higher than in the Asselian, Sakmarian, and Artinskian, suggesting less endemism among late Guadalupian fusulinids.

The distinctive southwestern US bioregion, represented by the Glass Mountains continued in the Capitanian, with only a single species (*Codonofusiella paradoxa*) shared with South China, Transcaucasus, Turkey and Tunisia. Panthalassan seamount sites of the Mino and Chichubi, Koryak, and Akiyoshi terranes are grouped together in both cluster (Fig. 5) and PCoA (Fig. 6) analyses, although have only moderate or low similarity among themselves. This grouping may represent a Panthalassa bioregion, containing the seamount sites.

As in the Wordian, South Primorye (NE Russia) has a distinctive fauna, but here grouped at low similarity with Kitakami (Japan). Both may represent a cooler-water region of the East Tethys bioregion, or exhibit some similarity with Panthalassa seamount sites. Other East Tethys sites, including South China, Indochina, Lhunzhub (Lhasa Block, Tibet, China) and North Qiangtang, form a group in cluster analysis and are close together in PCoA. Baoshan plots close on the PCoA analysis but cluster analysis groups it with a cluster including East Tethys as well as Turkey and Abadeh (Fig. 5). Baoshan only shares three species (3 out of 15) including *Sumatrina annae*, *Verbeekina verbeeki* and *Yangchienia haydeni* with Indochina, so its placement may indicate transitional characteristics between East and West Tethys.

West Tethyan sites form a broad grouping in both cluster and PCoA analyses Tunisia, Crimea, Transcaucasus, South Afghanistan, and South Pamir form a cluster, although the cluster also includes South Qiangtang, which had more affinity with East Tethys in the Cisuralian and Roadian. Turkey and Abadeh are a small cluster, but with greater similarity to the East Tethys cluster than to other West Tethys sites. In PCoA, Panthalassan sites are located in the upper half of the plot and in contrast, East and West Tethyan sites have occupied the right and left sides of the lower half of the plot. This may indicate stronger separation of Panthalassan sites from Tethyan sites during Capitanian despite weak separation in the Roadian and Wordian. Tethys also exhibits stronger biogeographic differentiation between eastern and western regions, similar to the Roadian and stronger than the Wordian.

4. Discussion

4.1. Formation of a distinct peri-Gondwanan region in the Sakmarian

During the Sakmarian, localities at mid-latitudes along the margin of Gondwana developed a characteristic fusulinid fauna dominated by species of *Pseudofusulina* and *Eopolydiexodina*, marking the transition between non-fusulinid cold water communities and typical Tethyan warm water assemblages. This southern transitional temperate fusulinid zone, or peri-Gondwana province (Leven, 1993; Kalvoda, 2002; Ueno, 2006), included Cimmerian terranes such as Kalmard in central Iran, south and central Afghanistan, the central and southern Pamirs, Karakoram, Tengchong Block, east Hindu Kush, and Baoshan (Fig. 2). However, the development of the peri-Gondwana bioregion was transient. By the Kungurian, formerly peri-Gondwanan sites such as south Afghanistan and the southern Pamirs instead exhibited strong similarity with Darvaz and north Afghanistan on the northern Tethys margin.

The earliest Permian was part of the peak Late Paleozoic Ice age, with massive ice sheets widespread in the paleo-Southern Hemisphere (Isbell et al., 2003; Montañez and Poulsen, 2013). Pronounced warming and deglaciation occurred in the Sakmarian, suggested by decreasing oxygen isotope values (Korte et al., 2008; Chen et al., 2013) and a transition from glaciogenic to carbonate sediments in regions such as Oman or the Baoshan block (Stephenson et al., 2008; Shi et al., 2011). In other region, such as Kalmard (central Iran), Karakoram, east Hindu Kush, south Afghanistan, and the central Pamirs, no Sakmarian glacial deposits are reported but cold-water siliciclastics were also replaced by carbonates. Asselian and early Sakmarian faunas – for example in Tibet, the Baoshan block, and the Pamirs – lacked fusulinids and were instead characterized by cool-water brachiopod, bryozoan, and bivalve faunas with similarity to Gondwanan localities such as Western Australia (Shen et al., 2000; Angiolini et al., 2013; Zhang et al., 2013). In contrast, late Sakmarian carbonates were widespread in Cimmerian blocks, and contained warmer-water faunas including fusulinids. This Sakmarian transition from cool-water

siliciclastics to fusulinid-bearing limestones was rapid (Stephenson et al., 2008; Shi et al., 2011), consistent with a climatic driver that enabled the expansion of fusulinid faunas to a southern transitional region. Climate may also have contributed to the disappearance of the peri-Gondwanan bioregion, if continued warming into the Kungurian and Roadian (Chen et al., 2013) resulted in reduced latitudinal temperature gradients and more homogeneous conditions across Tethys.

The appearance of a distinct peri-Gondwanan fusulinid fauna was also coincident with the separation of the Cimmerian terranes from Gondwana and initiation of the Neo-Tethys Ocean in the Early Permian. Rift-related sedimentation began in the latest Carboniferous or earliest Permian across the Cimmerian blocks, from the Pamirs (Angiolini et al., 2013) to Baoshan (Shi et al., 2011). The transition to seafloor spreading and northward movement of the Cimmerian terranes was likely marked by Artinskian-Kungurian unconformities and basalt units (Ali et al., 2013; Angiolini et al., 2013). However, this northward drift postdated the development of Sakmarian peri-Gondwanan fusulinid faunas, suggesting that climate warming was a more important control on formation of the distinct biogeographic region. In contrast, northward drift of the blocks following Artinskian-Kungurian rifting likely played a key role in the merger of the peri-Gondwana bioregion into a broader Tethyan fauna by the Kungurian and Roadian, as Cimmerian blocks moved into more tropical latitudes.

In recent years paleomagnetic data has suggested that opening of Neo-Tethys and continental break-up from the eastern margin of the Gondwana might have been asymmetrical (Muttoni et al., 2009; Angiolini et al., 2013, 2015). Middle Cimmerian terranes (western Karakorum, South and central Afghanistan, South Pamir and Qiangtang) more likely moved much faster in the Middle Permian and decelerated in the Late Permian and Early Triassic,

whereas Iran and possibly the Sibumasu and Baoshan blocks did not appear to have moved much in the Middle Permian compared to their faster movement in Late Permian and Early Triassic (Muttoni et al., 2009; Angiolini et al., 2013, 2015).

However, Wordian and Capitanian fusulinids in Iran and Afghanistan do not reveal major diversity differences in terms of typical warm-water fusulinids, indicating that it is doubtful that Afghanistan reached an equatorial position in the Capitanian, while Iran joined to other Cimmerian terranes in tropical setting sometime in Late Permian. Furthermore, based on fusulinid data the frequency of occurrences of warm water fusulinids in Karakorum and Qiangtang were low in Middle Permian, suggesting a position within the subtropics.

4.2. Closure of the Uralian Seaway and disappearance of the Boreal and Uralian provinces

Uralian fusulinid assemblages belonged to a more extensive bioregion in the Asselian and Sakmarian, sharing species with localities in northern and western Tethys, but Uralian sites were isolated by the Artinskian and fusulinids disappeared by the Kungurian. Faunas at the northernmost end of the Uralian seaway –in Timan, the Pre-Urals, and Arctic Norway – exhibited a distinct composition in the Asselian and Sakmarian, but disappeared from northern sites by the Artinskian (Fig. 2). The disconnection between Boreal and Tethyan fusulinids resulted from closure of the southern end of the Uralian seaway, which dramatically changed oceanic circulation within Boreal and Tethyan realms. Closure of the oceanic gateway between Tethys and the Uralian seaway blocked the warm-water currents that previously flowed from the tropics toward the Uralian and Boreal regions during the Asselian and Sakmarian. Subsequent cooling in the Uralian seaway and on the northern margin of Pangea (Beauchamp, 1995; Beauchamp and Baud, 2002; Montañez et al., 2007; Reid et al., 2007), reduced the diversity of

505 fusulinids and created an endemic Artinskian fauna that completely went extinct during the
506 Kungurian.

507 In contrast to previous arguments for isolation of the Uralian seaway in the early
508 Sakmarian (Davydov, 2008), our data suggest that closure of the gateway occurred later in the
509 Sakmarian. The widespread occurrence of *Schwagerina moelleri* in Tethys, Uralian, and Boreal
510 regions, as well as other shared species such as *Eoparafusulina tschernyschewi* and
511 *Pseudofusulina callosa*, suggest biotic interchange during the Sakmarian. However, Artinskian
512 faunas in the Urals and Pre-Caspian Depression contain only endemic species, such as
513 *Parafusulina solidissima*, *Pseudofusulina concavatus*, *P. kutkanensis*, and *P. solida*, and have no
514 faunal overlap with Tethyan regions. The Artinskian genus *Chalaroschwagerina*, which was
515 widespread in Tethys, also was absent from Uralian sites. These results are consistent with
516 paleoclimatic indicators suggestive of initial cooling at Boreal sites in the late Sakmarian (Reid
517 et al., 2007). Uralian brachiopod faunas also exhibited similarities with Tethyan sites in the
518 Asselian through Artinskian (Angiolini et al., 2007; Shen et al., 2013), but by the Kungurian
519 there was a distinct difference between the Uralian brachiopod fauna and those from Tethys
520 (Shen et al., 2013).

522 4.3. Middle Permian homogenization of Tethyan fusulinid faunas

523 The Tethys Ocean contained several distinct fusulinid faunas during the Early Permian.
524 In western Tethys, the remnant Uralian bioregion became separated from western Tethyan
525 localities in the Sakmarian and Artinskian, and a transient peri-Gondwanan region developed
526 during the Sakmarian (Fig. 2). At the same time, eastern Tethyan localities (the East Tethys
527 bioregion of South China, Indochina, and Japan) contained a different fauna, in some cases with

stronger links with Panthalassan seamounts. The east-west separation within Tethys weakened during the Roadian, and East and West Tethys sites were not clearly separated in the Wordian. Furthermore, there was faunal similarity even among geographically distant sites, such as Crimea and North Pamir in Roadian or Slovenia with Abadeh in Wordian. There was better separation in the Capitanian, as East and West Tethyan sites form groups in the cluster analysis and a continuous series in the PCoA plot, but biogeographic differentiation within Tethys was weaker in the Guadalupian than in the Cisuralian.

More detailed taxonomic studies may resolve these discrepancies, but the weak relationship between paleogeographic position and faunal similarity is also consistent with a greater proportion of widespread species that had distributions across Tethys. The pattern among fusulinids is similar to the paleobiogeography of brachiopods, where a distinct southern transitional or Cimmerian province became less distinct and merged with the paleoequatorial realm (Shi and Archbold, 1995; Shen and Shi, 2004; Shen et al., 2009; Angiolini et al., 2013).

Greater faunal similarity within Tethys was partly a consequence of the gradual northward movement of Cimmerian blocks following the opening of the Neo-Tethys in the late Early Permian (Metcalf, 1999; Muttoni et al., 2009; Angiolini et al., 2013) from mid-latitude settings marginal to Gondwana toward lower-latitude regions. Lower diversity among tropical verbeekiniid and neoschwagerinids suggests that many Cimmerian blocks were predominantly located at subtropical latitudes during the Middle Permian, including Transcaucasus (Leven, 1998), central Iran (Kobayashi and Ishii, 2003), and Baoshan (Huang et al., 2015). Climate warming following the late Paleozoic ice age, along with flattening of latitudinal temperature gradients, likely also contributed to the increased faunal similarity among Tethyan sites. Like all benthic foraminifera, fusulinids are poikilothermic organisms, i.e. their body temperature

depends on ambient water (Murray, 1973; Beavington-Penny and Racey, 2004). As a result, temperature is the most important factor influencing the distribution of fusulinid faunas (Hohenegger, 2004; Prazeres et al., 2016). The drift of Cimmerian blocks to subtropical latitudes, coupled with expansion of subtropical waters during Middle Permian warming, enabled more homogeneous faunas, perhaps with Cimmerian blocks acting as “stepping stones” for migration between eastern and western Tethys.

4.4. Faunal connectivity across Panthalassa

The western and southwestern United States contained distinctive fusulinid faunas throughout the Early and Middle Permian, differing considerably from each other and from Tethyan faunas. However, the presence of fusulinid species shared between eastern Panthalassa (either the western U.S. or southwestern U.S.) and Tethys indicates some degree of faunal connectivity across Panthalassa. In the Artinskian, the typical Tethyan fusulinid genus *Chalaroschwagerina* – especially *Ch. elkoensis*, *Ch. nelsoni*, *Ch. inflata*, *Ch. turgida* and *Ch. rotunda* – also occurred in the western U.S. (Dunbar and Skinner, 1937; Skinner and Wilde, 1966; Davydov et al., 1997; Stevens and Stone, 2009), indicating some connections between Tethys and eastern Panthalassa. This genus originated in the Tethys realm in the middle Artinskian (Davydov et al., 2014) but had a delayed appearance in the western U.S. about 2-2.5 Myr later in the late Artinskian. Davydov (2014) argued for strong provinciality between Tethyan and North American realms from the Kungurian to Wordian on the basis of the delayed appearance of *Yangchienia iniqua* (Yang and Yancey, 2000) in North America in late Kungurian, a time lag of 4-4.5 Ma compared to its first occurrence in Tethys in the early Kungurian. However, other fusulinid species, including *Skinnerella schucherti* and *S.*

diabloensis, also occurred in both Tethys and the southwestern U.S. during the Kungurian (Skinner, 1971), supporting the continuation of limited fusulinid interchange between these two realms.

Forbes dissimilarity values, comparing the McCloud bioregion or southwestern U.S. to a pooled species list of all Tethyan sites, suggest generally high dissimilarity on average across Panthalassa (Fig. 7). The southwestern U.S. was most similar to Tethys in the Kungurian and the most dissimilar in the Wordian, although the McCloud region had its lowest similarity with Tethys in the Kungurian. There are similar links across Panthalassa, for example between the southwestern U.S. and Japanese terranes, among Kungurian brachiopod faunas (Shen et al., 2011; Tazawa et al., 2016), consistent with dispersal via a westward-flowing equatorial current. Western U.S. sites instead were located at slightly higher latitudes and were influenced by cool currents flowing from the north (Clapham, 2010), both of which would have been less favorable for cross-Panthalassa fusulinid dispersal. On average, the southwestern U.S. displayed greater similarity across Panthalassa in the Guadalupian (aside from the Wordian) than in the Cisuralian (although the Asselian had somewhat greater similarity). Although the sample size is small, the trends are consistent with slowing ocean circulation during climate warming following the late Paleozoic ice age. Warming episodes in the late Cisuralian may have resulted in reduced latitudinal temperature gradients and sluggish ocean circulation.

4.5. Trends in faunal connectedness

Quantitative measures of biogeographic connectedness indicate greatest provinciality in the Asselian, Sakmarian, and Artinskian, with higher connectedness in the Kungurian and Guadalupian that reached peak values in the Roadian (Fig. 1). Absolute connectedness values are

low because of the species-level taxonomic resolution, but the trends match the number of distinct bioregions identified from cluster and PCoA analyses. During the Sakmarian, the Uralian and Boreal bioregions began to differentiated from Tethys, while a distinctive peri-Gondwanan bioregion formed. Similarity between Tethys and the western or southwestern U.S. was higher relative to other time intervals, but those two sites still had distinct and largely endemic faunas. In contrast, although similarity between the southwestern U.S. and Tethys decreased into the Middle Permian, the distinct Boreal and Uralian provinces had disappeared and Tethyan faunas became increasingly homogeneous.

Trends in biogeographic connectedness likely were influenced by changing climates throughout the Early and Middle Permian. The warming climate following the Asselian-Sakmarian peak of the late Paleozoic ice age reduced latitudinal temperature gradients, enabling more widespread distributions of temperature-sensitive organisms such as fusulinids, increasing connectedness. On the other hand, sluggish ocean circulation may have reduced dispersal potential, especially across the large Panthalassa ocean basin, leading to more endemic taxa and reduced biogeographic connectedness. Although climate changes were plausible contributors, plate tectonic reorganization may have had greater impacts on biogeographic connectedness. The closure of the oceanic gateway at the southern Uralian seaway isolated the Uralian and Boreal regions, ultimately causing extinction of the largely-endemic fusulinid faunas at cooler northern latitudes. Northward drift of the Cimmerian blocks also brought those regions into subtropical and tropical waters, helping establish a broadly-distributed Tethyan bioregion with greater number of species shared among sites.

5. Conclusions

Because fusulinids were temperature-sensitive organisms, large-magnitude Permian climate fluctuations likely were important controls on paleobiogeography. Development of the peri-Gondwanan bioregion in the Sakmarian is best explained by post-glacial warming that allowed expansion of fusulinids to higher latitudes and differentiation from contemporaneous tropical faunas. Continued warming and flattening of latitudinal temperature gradients may have contributed to the demise of the peri-Gondwanan bioregion as a distinct entity, although northward tectonic drift was likely more important. Finally, reduced faunal similarity across Panthalassa during the Middle Permian could also be consistent with slower ocean circulation in a greenhouse climate with flatter latitudinal temperature gradients.

Tectonics also played important roles in the development or demise of fusulinid biogeographic regions. In some cases, tectonics created barriers to ocean currents; for example, closure of the ocean gateway in the southern Urals blocked fusulinid dispersal and led to cooling in Uralian and Boreal regions, both of which created more distinct faunas and ultimately led to the disappearance of fusulinids from those regions. In other cases, plate reconfiguration provided opportunities for dispersal and may have led to greater faunal similarity. Northward drift of the Cimmerian blocks was likely responsible for the disappearance of the peri-Gondwana bioregion, as those blocks reached equatorial regions and the fusulinid faunas merged with tropical faunas. Likewise, the presence of Cimmerian blocks in the equatorial zone may have facilitated east-west fusulinid dispersal throughout Tethys, reducing provinciality between western and eastern margins of the ocean.

Overall, biogeographic connectedness was low throughout the entire interval, and most regions were dominated by endemic species. The trend toward greater connectedness in the Middle Permian may in part have been influenced by the tectonically-driven disappearance of

the Boreal and Uralian bioregions and the northward drift of Cimmerian blocks. However, the shift to a Middle Permian greenhouse climate was also a likely contributor, as a flatter latitudinal temperature gradient would have widened the extent of suitable tropical habitats. Fusulinid diversity and turnover also peaked during the late Paleozoic ice age (Groves and Wang, 2009), perhaps a result of the restricted ranges of many fusulinid species, suggesting that paleoclimate was the key control on fusulinid macroevolution.

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932 Figure 1. Trends in biogeographic connectedness during the Cisuralian and Guadalupian. Points

933 indicate the estimated values, with higher values indicating more shared species among sites.

934 The violin plot shapes illustrate the distribution of bootstrapped replicated, and 95%

935 bootstrapped confidence intervals are indicated by horizontal lines near violin edges.

936

Figure 2. Paleogeographic maps showing geographic distribution of stations and their assignment to bioregions. Station numbers correspond to the localities in tables S1 (Asselian, Sakmarian, Artinskian, Kungurian) and S2 (Roadian, Wordian, Capitanian). The paleogeographic positions of Panthalassan terrane stations (the Akiyoshi, Hida, Kuzu, Mino and Chichibu regions of Japan, and the Koryak Terrane in NE Russia) are approximate.

944
 945 Figure 3. Cluster dendrograms (Forbes dissimilarity, average linkage) for Cisuralian stages,
 946 showing faunal similarities among stations. Bioregion classification is indicated by colored
 947 circles at branch tips.

948

949 Figure 4. Principal Coordinate Analysis (using Forbes dissimilarity as the distance metric) for

950 Cisuralian stages, showing faunal similarities among stations. Color indicates bioregion

951 classification.

Figure 5. Cluster dendrograms (Forbes dissimilarity, average linkage) for Guadalupian stages, showing faunal similarities among stations. Bioregion classification is indicated by colored circles at branch tips.

957

958 Figure 6. Principal Coordinate Analysis (using Forbes dissimilarity as the distance metric) for

959 Guadalupian stages, showing faunal similarities among stations. Color indicates bioregion

960 classification.

Figure 7. Forbes dissimilarity coefficients between the McCloud region and pooled Tethyan locations, and between the southwestern U.S. and pooled Tethyan locations. Larger values indicate greater dissimilarity, or fewer shared species. The pooled Tethyan fauna is based on combining species occurrences from Abadeh, the Baoshan Block, Batain Carnic Alps, Central Iran, Central Pamir, Crimea, Darvaz, Fergana, Hindu Kush, Indochina, Kalmard, the Karakaya Complex, Karakorum, Kitakami, Lhunzhub, North Afghanistan, North China, North Iran, North Pamir, North Qiangtang, Oman, Primorye, Rutog, Saiq, Sibumasu, Sicily, Slovenia, South Afghanistan, South China, Southern Pamir, South Qiangtang, Transcaucasus, Tunisia, Turkey, Xainza, and Zagros. The McCloud region includes the Klamath Mountains, northwestern Nevada, and central Oregon, whereas the southwestern U.S. includes New Mexico, the Hueco Mountains, Baylor Mountains, and Glass Mountains.