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Paleoecology of brachiopod communities during the late Paleozoic ice age in Bolivia (Copacabana Formation, Pennsylvanian-Early Permian)

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ABSTRACT

Studies of modern ecological communities demonstrate that climate change may trigger changes in diversity and taxonomic composition; however, these studies are fundamentally limited to short timescales and therefore cannot demonstrate the full impact of major climate change. Understanding the ecological response of marine invertebrate communities to the Late Paleozoic Ice Age (LPIA), the last complete transition from icehouse to greenhouse, can establish a more complete picture of the climate-faunal relationship. We analyzed brachiopod community structure in Moscovian-Sakmarian (mid-Pennsylvanian to Early Permian) samples spanning the greatest extent of the LPIA, collected from four localities of the Copacabana Formation in Bolivia: Ancoraimes, Yaurichambi, Cuyavi, and Yampupata. Cluster analysis reveals three main groups that appear to coincide with pre-, syn-, and post-glacial times. Genus richness was significantly greater in samples during the Asselian glacial episode; however, the difference may be due to a combination of smaller body size and time averaged mixing of genera from different depths during more rapid glacioeustatic sea level change. Genera present in Bolivia consistently

had warm-water affinities, even during the main glaciation, but warm-water taxa increased in abundance over time and the samples became increasingly dominated by characteristically North American genera. Overall mean body size and the size of particular genera were smaller in the Asselian cluster. These size changes likely reflect variations in substrate because marine invertebrates should be larger at cooler temperatures due to oxygen limitation at higher temperatures. The monotonic increase in abundance of warm-water genera and increasingly North American biogeographic affinity imply that community change was most likely the result of the northward drift of Bolivia rather than a response to late Paleozoic glacial-nonglacial cycles. This lack of climate related faunal change was probably a result of Bolivia's mid-latitude location during the late Paleozoic because both the rate of temperature change and its magnitude were likely smaller at lower latitudes, reducing the impact of climate change on marine communities.

Keywords: Paleoecology; climate change; thermal tolerance

1. Introduction

Temperature is one of the basic controls on both marine and terrestrial community composition through its influence on organism physiology, geographic distribution, and interactions. Changes in temperature can force physiological changes in organisms' respiration, metabolic rate, and ability to perform critical biological functions, which can lead to death (Pörtner 2001; Peck et al. 2004). As temperature increases a rise in metabolic rate leads to a mismatch between oxygen supply and demand, which progressively lowers long-term fitness by causing tissue hypoxia and eventually forcing organisms to anaerobic metabolism (Melzner et al. 2007; Pörtner 2010; Somero et al. 2012). It is possible for organisms to withstand higher

temperatures using heat shock proteins, however, this is an energy intensive process and leaves less energy for feeding and reproduction (Somero et al. 2012). Studies have shown that temperature limits for long-term survival occur at much lower values than those which cause rapid death (Peck et al. 2009). In addition to these direct physiological consequences, temperature change can cause changes in the relative abundance of species in communities, range shifts, altered species interactions, and extinction, all of which can have profound consequences for the overall structure and functioning of communities (Clarke 1993; Petchey et al. 2004; Harley et al. 2006). Many of these temperature driven ecological changes are already evident in modern species (Peck et al. 2004), including range shifts and disruptions in the coordinated life cycles of interacting species (Walther et al. 2002; Parmesan 2006). These physiological and ecological changes lead to a greater possibility of extinction for many species, which could have further ecological consequences.

The fossil record provides evidence that faunal change has occurred in conjunction with climate change throughout geologic history. Studying ancient episodes of climate change can help to establish the biotic response to long term natural warming, thereby providing a baseline from which to assess more extreme events such as modern anthropogenic climate warming. During Pleistocene glacial-interglacial transitions faunal turnover in the Sea of Japan occurred when warm-water mollusk species migrated into the area, accompanied by a northward contraction of ranges of both warm-water and cool-water taxa and extinction of cool-water species (Kitamura et al. 2000). Similar faunal change has also been observed at the end of the Late Paleozoic Ice Age (LPIA), the last glacial period before the Pleistocene. Dramatic shifts in floral assemblages occurred with rapid temperature fluctuations during later LPIA glacials, with deglaciation resulting in a complete floral regime change from fern dominated to conifer

dominated (Gastaldo et al. 1996; Montanez et al. 2007). Global data indicate a distinct mid-Permian diversification, especially in the tropics, due mainly to a radiation of strophomenate brachiopods (Alroy 2010) and assemblages in Australia show compositional and relative-abundance changes during deglaciation as well as potentially higher extinction rates during times of rapid climate shifts (Clapham and James 2008; Clapham and James 2012).

The LPIA was characterized by dynamic climate fluctuations lasting nearly 70 Ma from the mid-Carboniferous to the mid-Permian (Fielding et al. 2008) (Figure 1). Our study spans the Moscovian to the Sakmarian, corresponding with the C4 nonglacial, P1, and P1 nonglacial of Fielding et al. (2008). The C4 glaciation waned in the Moscovian and was followed by a long, warmer nonglacial extending to the Carboniferous-Permian boundary. Asselian-early Sakmarian glaciation extended over a broader region of Gondwana, indicating that the P1 glaciation was the peak of the LPIA. Following the decline of the P1 glacial in the Sakmarian, temperature increased sharply, though cooling occurred in the beginning of the Artinskian during the P2 glacial (Montanez et al. 2007; Korte et al. 2008).

The majority of late Paleozoic geological and paleontological work has been conducted in eastern Australia (high southern paleolatitude) and North America and China (equatorial paleolatitude). The paleontology of South America has been relatively unstudied and offers a look at how glaciation, and the subsequent deglaciation, affected marine invertebrate communities in the climatically highly variable mid-paleolatitudes. The lateral and time continuity of marine and glaciogenic deposits in the basins of South America imply that steep climate gradients existed in the region (Grader et al. 2008). This regional climate variability is likely to result in highly variable ecological conditions, and therefore fauna, as glaciers waxed and waned throughout the LPIA.

2. Geological Setting

We assessed biotic change during the LPIA using data collected from four locations of the Copacabana Formation in the Lake Titicaca region of Bolivia (Figure 2). The four sections range in age from Moscovian to Sakmarian (Grader, 2003), spanning the greatest extent of the LPIA and its major deglaciation (Figure 3). The section from Cuyavi spans the largest amount of time (from the Moscovian to Sakmarian; Grader, 2003); however, only four samples come from this section – three from the Moscovian and one most likely from the Sakmarian. Yampupata samples are contained entirely within the Moscovian (Fujikawa et al., 2003). The Yaurichambi section ranges from the Gzhelian into the Asselian (most of the section is likely Asselian; Charles Henderson, pers. comm.) with samples coming from the bottom and middle of the section. Samples from the section at Ancoraimes cover the lower two-thirds of the section, ranging in age from the Gzhelian to the Sakmarian (possibly late Asselian) (Grader, 2003). The precise positions of stage boundaries are not well constrained in any of our sections.

Lithologically, the four sections are broadly similar and composed mainly of marly lime mudstones and wackestones, pure wackestones and packstones, and terrigenous siltstone. Samples from Cuyavi come from bioclastic-dominated wackestones, representing deposition below fair-weather wave base in a mid- to distal ramp setting, and from green calcareous sandstones from slightly shallower environments. Fossiliferous units at Yampupata are composed of mid-ramp green calcareous sandstones similar to those at Cuyavi. In contrast to the other sections, exposed units at Yaurichambi are dominated by lime mudstone and wackestone, with most of the section covered. Two samples from the base of the section are derived from light grey limestones representing deposition in a restricted inner ramp environment. Most samples are from cyclical mid- to inner ramp sediments in the middle part of the section, ranging

from shallower bioclastic and fusulinid wackestones to more distal sandstones and siltstones. The majority of the Ancoraimes section is composed of marly lime mudstone or wackestone with a few largely unfossiliferous shale-dominated intervals and increasingly high-energy packstones above our study section. Ancoraimes samples come from marly lime mudstone or wackestone beds, representing distal to mid-ramp environments close to storm wave base.

3. Methods

We collected 47 bulk samples of about 100 specimens each from measured sections at Ancoraimes (31 samples), Yampupata (6 samples), Cuyavi (4 samples), and Yaurichambi (6 samples) for identification and counting in the lab. Each sample was collected from the entire exposed length of a single bed, which ranged from <1 m to >10 m. Samples consist almost entirely of strophomenate and rhynchonellate brachiopods, with trilobites and mollusks occurring rarely and mostly in the samples from Yampupata. Because brachiopods comprise nearly 99% of our specimens, our analysis is restricted to that group. It is possible, although we think unlikely, that different groups may have exhibited a stronger (or weaker) response to late Paleozoic climate changes or that brachiopods were affected by changes in the diversity of other taxa. We identified specimens to genus and, where possible, species level and counted all identifiable specimens. All analyses are done at the genus level. We also measured the length, width, and height of all complete specimens. We assessed environmental conditions using standard sedimentological criteria in the field and data from Grader (2003). No sorting or grading of specimens was observed in the field and counted specimens mostly exhibit low to moderate abrasion, indicating that little transportation occurred. Sample age was determined from correlation with sections in Grader (2003) and conodont biostratigraphy of the Yaurichambi

section (C. Henderson, pers. comm.). All abundance counts and size data are stored in the Paleobiology Database (reference 41985).

Multivariate analyses (cluster analysis and non-metric multidimensional scaling [NMS]) were performed in R using the Vegan package (Oksanen et al. 2012). We performed a square root transformation on the count data used in multivariate analyses to reduce the influence of abundant taxa, such as *Crurithyris*, which are common in most samples and could obscure trends in the data. Using global Carboniferous and Permian occurrence data downloaded from the Paleobiology Database (PaleoDB; http://paleodb.org) on 17 May 2012, we calculated the preferred latitude of each genus found in Bolivia using the method described in Clapham (2010) and (Clapham and James 2012). Due to the high sampling frequency of the tropics a latitudinal bias may be introduced by simply using the mean latitude of all occurrences. To counteract this bias the preferred latitude of each taxon is adjusted using the latitudinal density of all occurrences (Clapham and James 2012).

We also used the PaleoDB data to determine the provinciality and temperature classification (warm or cool) of each genus. The globe can be divided into two cool biogeographic realms above 30° north (Boreal) and below 30° south (Gondwanan) and two tropical realms between 30° north and south: Panthalassic on the west coast of Laurentia and Tethyan surrounding the Tethys Sea. We assigned each occurrence of a genus to one of the four biogeographic realms based on its occurrences in the Paleobiology Database. We considered a genus to be characteristic of the biogeographic realm in which it was most common only if the number of occurrences in that realm was at least twice as large as the number in the next most common realm. If a taxon is not considered characteristic of a particular realm it is classified as cosmopolitan.

4. Results

4.1. Taxonomic Composition

Cluster analysis reveals three clusters of samples: 1) Moscovian samples from before the main LPIA glaciation, 2) Asselian samples from the P1 glacial, and 3) Sakmarian samples from the end of the P1 glacial and (possibly) interglacial (Figure 4). Cluster 1 consists of the lower Cuyavi samples and the majority of the Yampupata samples. A greater abundance of *Gypospirifer condor* and *Linoproductus cora* is characteristic of this cluster, which lacks a group of taxa (*Fimbrinia cristatotuberculata*, *Orthotichia latirostrata*, *Rhipidomella cora*, *Chonetinella*, *Quadrochonetes*, *Hustedia*, and *Stenoscisma thevenini*, called the *Hustedia* group) typical of cluster 2. This cluster also includes sample Ya2 in which *Isogramma* is common. Samples from the lower two-thirds of Ancoraimes and Yaurichambi make up cluster 2, which is characterized by the presence of the *Hustedia* group. This cluster also more commonly contains *Kozlowskia capaci* and *Hystriculina*. Cluster 3 is mainly from the upper third of Ancoraimes and, like cluster 1, is distinguished by the lack of the *Hustedia* group. Though *Composita subtilita* and *Dasysaria inca* are present in most samples they are more common in cluster 3 samples. Three samples unassociated with these main clusters are of note: 1) sample A24 is composed of entirely *Kozlowskia capaci*, 2) *Waagenoconcha humboldti* makes up the vast majority of sample A31, and 3) sample A32 contains mostly *Neochonetes variolata*.

These clusters are also apparent when count data is analyzed using non-metric multidimensional scaling (Figure 5). The majority of samples occur in a single large group; however, samples from the clusters identified by cluster analysis plot together. Samples from

cluster 1 plot to the right on axis one and in the bottom two-thirds of axis two, cluster 2 plots on the left on axis one and spans a greater amount of axis two than cluster 1, and cluster 3 plots at an intermediate axis 1 position but at high values on axis 2. The samples that are unassociated with any of the three clusters plot around the edges of the main group, with many of them (especially the high-dominance, low-diversity samples A24, A31, and A32) clearly separated from the rest of the samples.

4.2. Richness

Overall, mean within-sample genus richness was 10 genera, but there were significant variations among clusters (ANOVA, $p<0.001$). Because richness is a proxy for the 'health' of a system that may have been influenced by late Paleozoic climate fluctuations it is important to look at any variations among the clusters. Cluster 2 had the highest richness, with a mean of 12.5 genera per sample, whereas cluster 1 (mean richness of 9.9 genera) and cluster 3 (mean richness of 8.2 genera) had lower diversity (Figure 6). The increase from cluster 1 to cluster 2 is weakly significant (Tukey test, $p=0.045$), but the decrease from cluster 2 to cluster 3 is highly significant (Tukey test, $p<0.001$). Richness did not differ significantly between clusters 1 and 3 (Tukey test, $p=0.35$). Sample richness varied greatly within clusters of samples, including some samples containing only 1-2 genera, but no consistent trends or regular patterns can be observed among samples from single stratigraphic sections.

4.3. Preferred Temperatures and Biogeographic Affinity

If climate changes contributed to the community restructuring, the changing faunal composition of the three clusters may also have led to shifts in the proportion of warm- and cool-

water genera. For each genus, we quantified its preferred temperature (warm or cool water) by calculating the mean paleolatitude of its global occurrences (termed 'preferred latitude'). We assessed the climatic affinity of the fauna in two ways. First, we calculated the mean preferred latitude of all genera found in each of the three clusters. Overall, the mean preferred latitude of all genera present in each cluster was very consistent through time (25.4° in cluster 1, 26.4° in cluster 2, and 25.3° in cluster 3) and is relatively low in all clusters (Figure 7). Second, we calculated the preferred latitude of each sampled brachiopod assemblage by assigning each specimen the preferred latitude based on its genus and calculating the mean value of all specimens in each sample. Though the preferred latitude of genera within clusters shows very little variation, the mean preferred latitude of specimens within samples (which weights the genus preferred latitude by relative abundance) consistently decreased with time (Figure 8). Samples in cluster 1 have the highest mean preferred latitude (mean of 23.8°), followed by cluster 2 (mean of 20.4°), and finally cluster 3 (mean of 17.9°). The range of preferred latitude values remained consistent through the three clusters.

Although the preferred latitude of genera is very stable throughout our study interval, indicating a consistently warm-water composition, the biogeographic affinity of those genera may have varied due to changing climate or oceanographic patterns. We assigned genera to five different regions (Boreal, Gondwanan, Tethyan, Panthalassic, and Cosmopolitan) and compared the relative proportion of specimens from each region to test for shifts in the biogeographic composition of each cluster. Biogeographic affinity shows a trend of increasing Panthalassic association with time, increasing from 36% of specimens in cluster 1 to 71% in cluster 2, and to 88% in cluster 3 (Figure 9). Cosmopolitan genera show a corresponding decrease: cluster 1 is composed of 56% cosmopolitan specimens, whereas clusters 2 and 3 contain 23% and 12%,

respectively. Boreal, Gondwanan, and Tethyan genera make up a negligible percentage of each cluster, comprising no more than 5% of specimens.

4.4. Body Size

In the fossil record, changes in body size can be indicative of physiological stress. Although many factors can influence body size, maximum body size in marine invertebrates is primarily controlled by oxygen (Pauly 2010). Due to the mismatch between oxygen supply and demand during times of ecological stress organisms can be forced to suspend non-vital functions such as growth, leading to smaller body size. The mean body size (measured by the geometric mean of shell length and width) of genera in cluster 2 is 7.3 mm, which is significantly smaller than the mean size of genera in either cluster 1 (11.5 mm; Welch t-test, $p<0.001$) or cluster 3 (11.3 mm; Welch t-test, $p<0.001$). Because these body size shifts may reflect changes in the relative proportion of larger- and smaller-bodied taxa or in the identity of taxa present, it is also important to assess within-genus size changes of taxa present in multiple clusters. Eleven of the 12 genera present in both cluster 1 and cluster 2 decrease in body size (exact binomial test, $p=0.006$) (Figure 10). Ten of 13 genera increase in size between cluster 2 and cluster 3; although the number of size increases is weakly non-significant (exact binomial test, $p=0.09$), the magnitude of increase is generally greater than the decrease from cluster 1 to cluster 2.

5. Discussion

5.1. Taxonomic Composition

Separation of samples into three primary clusters that occur during pre-, syn-, and post-glacial times is potentially consistent with the hypothesis that long-term climate change

restructured marine communities. Although clusters occasionally contain samples of different ages (e.g., a Moscovian sample from Yampupata groups with primarily Sakmarian cluster 3), there is a strong relationship between age, and therefore climate, and cluster membership. It is possible that clusters reflect facies rather than time, but this seems unlikely because samples within clusters span multiple lithologies and, occasionally, come from multiple sections. For example, cluster 1 is composed of samples from both bioclastic-dominated wackestones at Cuyavi and calcareous sandstones at Yampupata. In contrast, clusters 2 and 3 are both dominated by samples from Ancoraimes (cluster 2 from the lower two-thirds of our section and cluster 3 from the upper one-third) and come from very similar lithologies and environments, yet have different faunal compositions. Both clusters are from lime mudstones and wackestones, representing distal to mid-ramp environments, but cluster 2 is dominated by the *Hustedia* group, *Kozlowskia capaci*, and *Hystriculina*, whereas cluster 3 almost completely lacks the *Hustedia* group and contains *Composita subilita* and *Dasysaria inca* in greater abundances. Because there are no clear patterns in either lithology or location in the composition of clusters, it seems unlikely that clusters are simply a result of differing facies.

Although the faunal change associated with the clusters seems to coincide with climate change due to the P1 glacial, the clusters are distinct but not clearly separated by MDS analysis, suggesting that cluster analysis may impose artificial breaks on a continuous gradient of gradual faunal change related to slow northward drift of Bolivia. The preferred latitude of genera in clusters was low and very consistent through time, indicating that the genera present did not dramatically change with either the onset of glaciation or deglaciation. Although the preferred latitude of genera did not change, the preferred latitude of individual samples based on specimens consistently decreased between clusters. Constant cluster-level but decreasing sample-

level preferred latitude was due to an increase in the abundance of warmer-water genera rather than the replacement of cooler-water genera by warmer-water taxa. The decrease in sample preferred latitude is uninterrupted through the glacial period, when cool-water genera and therefore preferred latitude should have increased. The continuous change from cosmopolitan to Panthalassic genera is also consistent with a gradual shift rather than effects of glacial climate change (Figure 11).

In contrast, community restructuring during post-glacial warming has been observed at high latitudes in Australia (Clapham and James 2008). Similar faunal shifts may not have occurred in Bolivia, which was located at mid-latitude, because the rate or magnitude of change at lower latitudes may have been slow enough that organisms were capable of migrating, adapting, or evolving (Holland and Bitz 2003; Hofmann and Todgham 2010; Miller et al. 2010). Modern high-latitude organisms have low aerobic scopes because of their low metabolic rates, an adaptation to permanently cold conditions, and therefore are less able to meet metabolic oxygen demands as temperature increases (Peck et al. 2004). In contrast, mid- and low-latitude organisms experience greater seasonal fluctuations and are therefore more able to cope with changes in temperature (Pörtner 2001). Similarly, high-latitude Permian taxa may also have been more vulnerable to temperature changes, whereas mid-latitude taxa, such as those in Bolivia, would not have been as greatly affected.

5.2. Diversity

Despite the gradual faunal change rather than climate-driven restructuring, the richness of samples in cluster 2 is higher than that of either cluster 1 or cluster 3. This higher diversity apparently coincides with the P1 glacial; however, diversity is higher in the tropics today and

among Pennsylvanian-Permian brachiopods (Powell, 2009), and the onset of cooler glacial conditions should have been accompanied by a drop in diversity (Roy et al. 1998; Alroy 2010). This apparent decoupling of temperature and diversity could be due to an increase in surface ocean nutrient levels from more vigorous ocean circulation during the glacial. The importance of increased nutrient levels in Bolivia is unclear because Bolivia was located in a partially enclosed basin with limited connection to wider ocean circulation during the Late Carboniferous and Early Permian.

The higher richness of samples in cluster 2 could perhaps be explained by smaller body size of taxa in the cluster. Because the size-frequency distribution of species is log-normal, many species are small (Clauset and Erwin 2008). Therefore, samples that contain smaller taxa in addition to large ones, like those in cluster 2, may contain greater diversity relative to the other clusters where small specimens are less abundant.

Mixing of warmer and cooler water faunas due to time averaging is another possible explanation for increased diversity during the glacial (Figure 12). The faunal boundary between warmer and cooler water taxa may have shifted northward and southward with climate changes (Angiolini et al. 2007), causing shifts in local faunal composition at Mikankovich timescales. Time averaging is a pervasive phenomenon that mixes shells over scales of hundreds to thousands of years in a single shell bed. Time averaging during deposition of the sample may have mixed genera from warm and cool water faunas and inflated the diversity of these samples relative to samples from climatically more stable time periods. This is unlikely, however, because the range of preferred latitude of samples is fairly consistent in all three clusters. The fauna of cluster 2 do not span a greater range of latitudes than the other clusters so it is unlikely that they would represent a mix of both warm and cool water faunas. The effect of faunal mixing

would have been minimal because the timescales of Milankovitch cyclicity are much longer than those of time averaging.

Time averaging may have mixed genera from a greater range of depths during the glacial, which could also have caused the increased diversity in cluster 2 (Figure 13). Sea level changes would have been more rapid and of greater magnitude during the P1 glacial (Rygel et al. 2008), which would have superimposed a living community from one depth over recently dead shells from a different depth. These shells from different habitats would then get mixed into a single bed by time averaging.

5.3. Biogeographic Affinity

There was a shift from Cosmopolitan to Panthalassic taxa with time, with a dramatic increase occurring from Carboniferous cluster 1 to Permian cluster 2. Most of these Panthalassic taxa are genera found in the western U.S., especially west Texas. Although Texas is extremely well-sampled, this signal of increasing proportion of Panthalassic taxa is not simply a sampling bias, because we normalized each genus to the total number of occurrences in each region. Increasing dominance by Texas taxa may reflect warming sea surface temperatures in Bolivia during this time period as Bolivia drifted north from more than 35° S to close to 30° S. This sort of faunal similarity between Bolivia and the western U.S. has also been seen in corals (Wilson 1990). Studies of brachiopod biogeography have variously identified a separate Andean province based on chonetids (Archbold 1983) or were unable to group Bolivia with any defined province because of the cosmopolitan nature of the few taxa previously reported in the literature (Shen et al., 2013).

346 *5.4. Body Size*

347 Genera are smaller in cluster 2, roughly during the LPIA glacial, than in either cluster 1
348 or 3. This reduction in body size is evident in both the mean body size of all specimens in each
349 cluster and the within-genus size comparisons between clusters. Body size is closely related to
350 composition because samples with a larger number of smaller taxa will have a smaller overall
351 size. Clusters 1 and 3 are characterized by larger taxa, such as *Gypospirifer condor* and
352 *Linoproductus cora* in cluster 1 and *Composita subtilita* and *Dasysaria inca* in cluster 3. They
353 also lack the *Hustedia* group, which is characteristic of cluster 2 and composed of generally
354 smaller taxa, such as *Hustedia* and the chonetids *Chonetinella* and *Quadrochonetes*. While this
355 appearance and increase in abundance of larger genera in clusters 1 and 3 explains the larger
356 mean sizes of those clusters, it does not explain the within-genus trend of reduced body size in
357 cluster 2. The reduction in size during cluster 2 also cannot be explained by cooling related to
358 glaciation, because the principles of oxygen-limited thermal tolerance would predict larger body
359 size during cooler temperatures (Pauly 2010; Forster et al. 2012). The most likely explanation for
360 reduced body size in cluster 2 is a sampling issue related to lithology, because cluster 2 comes
361 almost entirely from the lower two-thirds of Ancoraimes, which is typically finer grained and
362 more fissile. This fissile nature makes it easier to find smaller specimens and harder to find
363 larger ones. Finer-grained sediments are likely to reflect softer substrates that may also have
364 favored smaller individuals (Thayer 1975). The smaller grain size of Ancoraimes can explain the
365 decrease in body size from cluster 1 (collected from Cuyavi and Yampupata) to cluster 2 but the
366 increase from cluster 2 to cluster 3 (also from Ancoraimes) is less clear because Ancoraimes is
367 lithologically and environmentally consistent throughout our section, potentially suggesting that
368 the increase is a real phenomenon.

6. Conclusions

Faunal changes are evident in Bolivia, but are most likely due to gradual northward drift of Gondwana rather than climate change related to the LPIA. The shift in sample preferred latitude towards lower latitudes and the increasingly Panthalassic biogeographic affinity are consistent with this. Diversity is higher during the glacial period, contrasting with the anticipated decline in diversity associated with the onset of cooler glacial conditions. The higher diversity in cluster 2 is likely due to some combination of the mixing of genera from different habitat depths from Milankovitch-scale glacioeustatic sea level changes during time averaging and the sampling of a greater range of body sizes, including small taxa.

This lack of climate related faunal change in Bolivia was probably a result of its mid-latitude location. Both the rate of temperature change and its magnitude were likely smaller at lower latitudes than at high-latitudes, thereby reducing the impact of climate change on marine communities. Furthermore, this lack of change implies that mid- and low-latitude organisms are less vulnerable than high-latitude organisms during climate change, which is consistent with predictions from biologists based on aerobic scope and metabolic rate. More broadly, variable responses across latitudes during slow, long-term climate change implies that geographic distribution would likely have been a significant predictor during more severe climate change events such as the end-Permian or end-Triassic mass extinctions and suggests that high-latitude organisms are likely to be at greatest risk during modern climate change.

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Figure Captions

Fig. 1. Summary of Late Paleozoic Ice Age glaciations and temperature records. Glacial records come from Australia (Fielding et al., 2008) and basins throughout Gondwana (Isbell et al., 2003).

Permian temperature records from high and tropical latitudes show decreasing temperatures during the early Permian glacial (Korte et al., 2008 and Montañez et al., 2007).

Fig. 2. Map showing the location of the four sections (Ancoraimes, Yaurichambi, Cuyavi, and Yampupata) sampled for this study in the Lake Titicaca region of Bolivia.

Fig. 3. Composite section showing the dominant lithology, approximate age correlation of each section, and stratigraphic height of samples. Stage boundaries are approximate because the precise age of sections is uncertain. The cluster affinity of each sample is indicated and shows a fairly robust correlation of cluster with stratigraphic position.

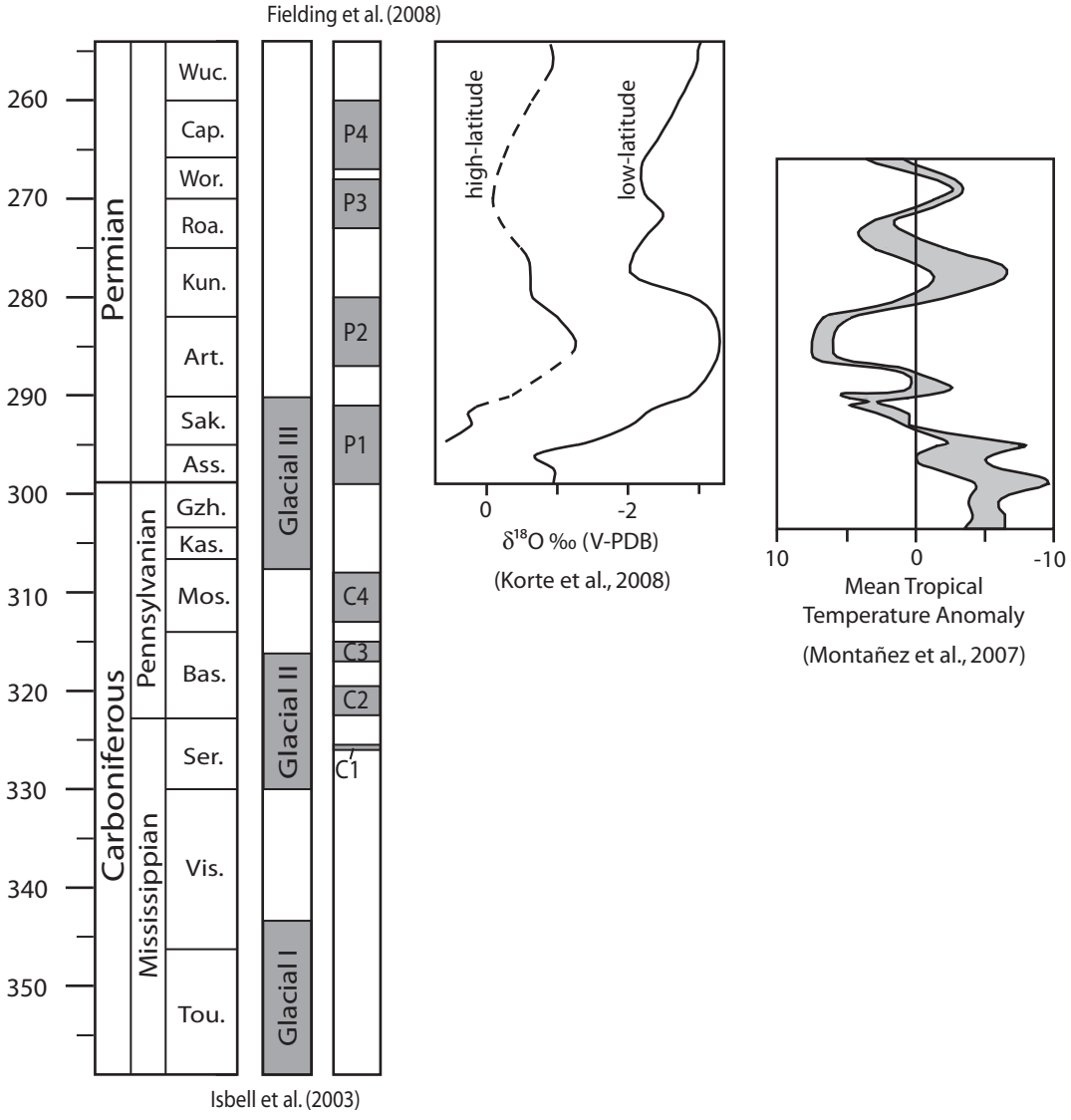
Fig. 4. Cluster-abundance diagram of all samples and genera. For each genus the abundance in a sample is shown using the size of the dot and the style (black, grey, or white) indicates temperature affinity. Samples are divided into three main clusters based on the presence or absence and relative abundance of genera.

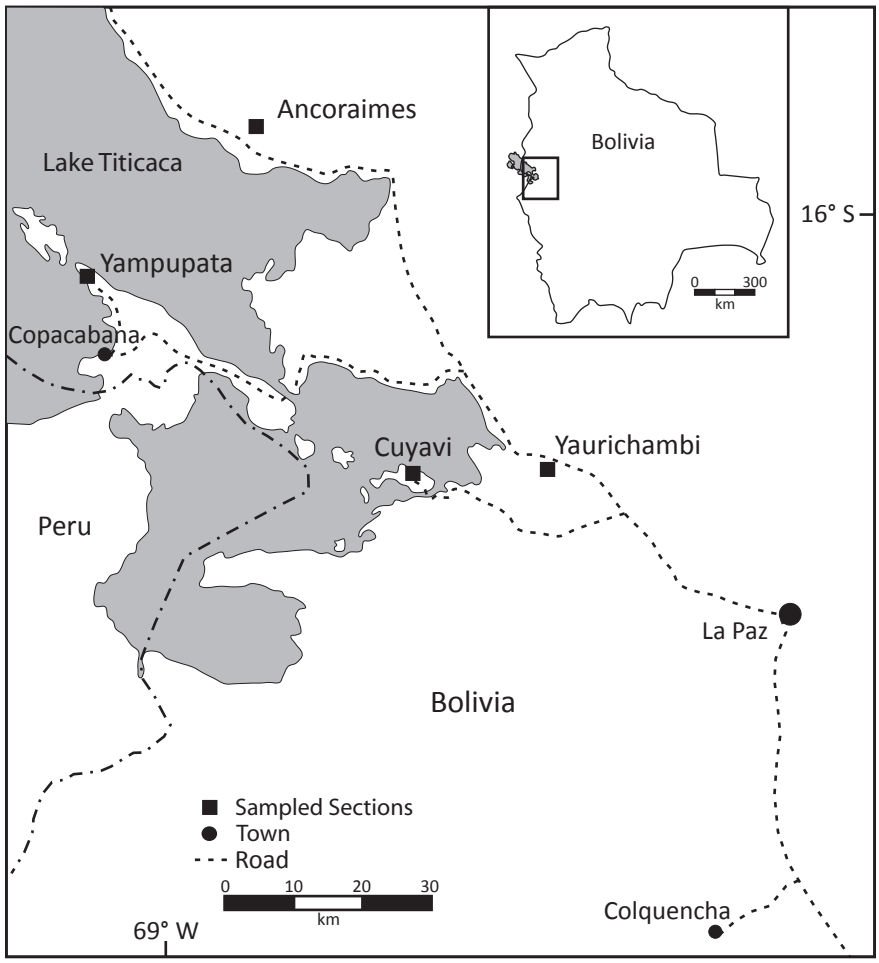
Fig. 5. Non-metric multidimensional scaling showing the grouping of samples from clusters identified by cluster analysis. Samples from these clusters group together with unassociated samples scattered on the fringes of the plot.

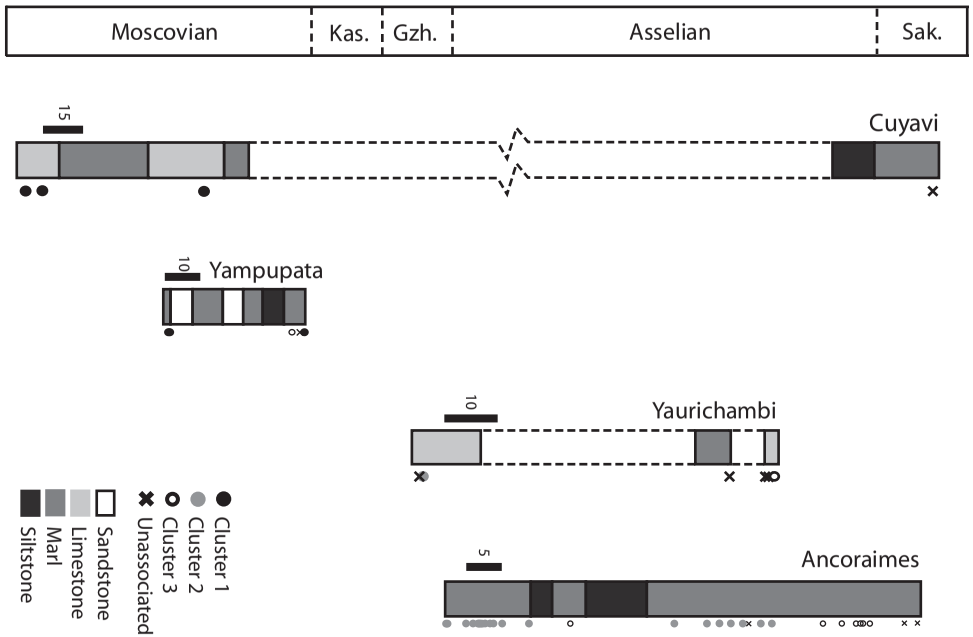
Fig. 6. Box and whisker plot showing median and first and third quartiles for genus richness of samples in each cluster.

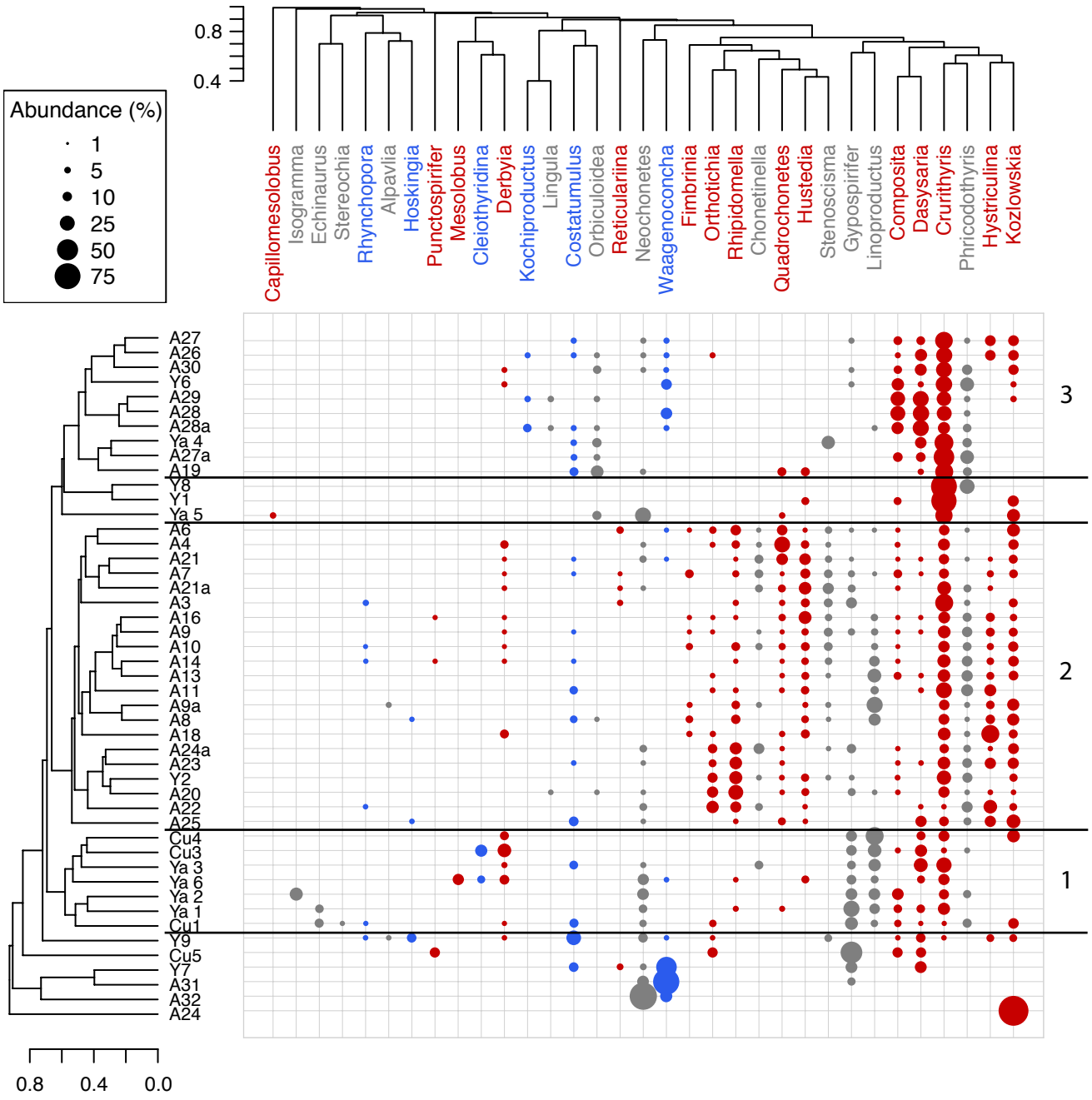
524 **Fig. 7.** Box and whisker plot of the preferred latitude of genera present in each cluster. In this
525 analysis, genera are recorded as present or absent (their relative abundance is not incorporated)
526 and the mean preferred latitude calculated for each cluster based on the taxonomic list of present
527 genera. All three clusters have similar values, indicating that the climatic affinity of genera
528 present in Bolivia did not change significantly over the study interval.
529
530 **Fig. 8.** Box and whisker plot of the preferred latitude of specimens within samples of each
531 cluster. Each specimen is assigned the preferred latitude of its genus, yielding a mean preferred
532 latitude for each sampled brachiopod assemblage, weighted by the relative abundance of genera
533 in that sample. Lower preferred latitude values for samples in cluster 3 indicate that the relative
534 abundance of tropical genera increased within samples from cluster 1 to cluster 3.
535
536 **Fig. 9.** Bar plot showing the provinciality of each cluster. Genera are assigned to Tethyan,
537 Panthalassic, cosmopolitan, Gondwanan, and Boreal regions based on the area with the largest
538 number of occurrences.
539
540 **Fig. 10.** Body size trends between clusters based on mean size of genera (solid circles) and
541 overall mean size of all specimens (open circles). Genera occurring in more than one cluster are
542 connected by solid lines to indicate between-cluster size changes.
543
544 **Fig. 11.** Richness (A), preferred latitude (B), proportion of Panthalassic taxa (C), and mean body
545 size (D) trends of samples from Yampupata (solid circles), Cuyavi (open squares), and

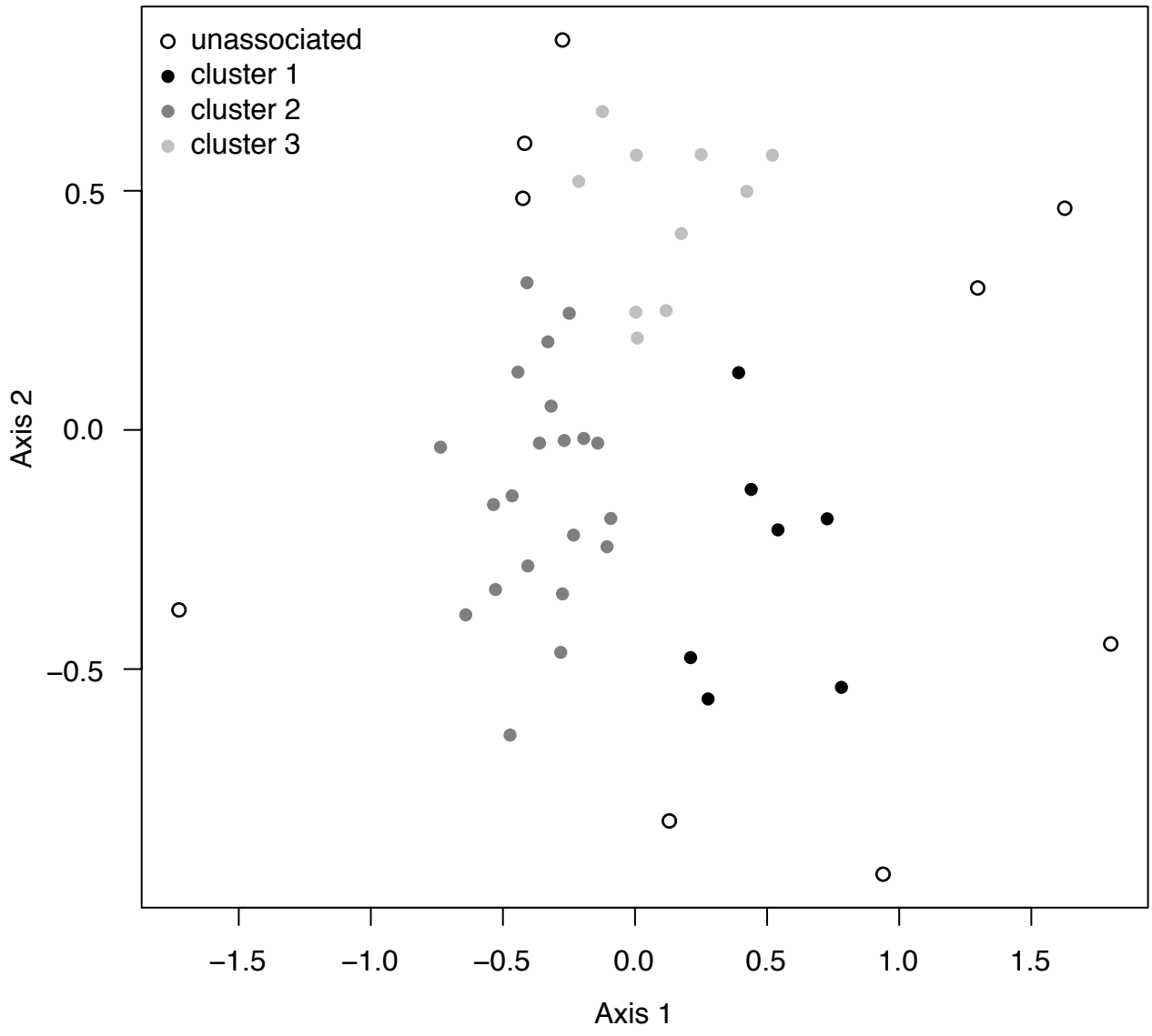
546 Ancoraimes (open circles). Yaurichambi samples are not included because they cannot be
547 correlated precisely with Ancoraimes.
548
549 **Fig. 12.** Base map showing hypothetical fluctuations of the faunal boundary between warm-
550 water and cool-water faunas (dashed lines) relative to Bolivia (black box) during glacial and
551 interglacial times. The latitudinal position of the faunal boundary is approximately based on data
552 from Angiolini et al. (2007).
553
554 **Fig. 13.** Cartoon showing Milankovich-scale sea level fluctuations (dashed lines) during glacial
555 and interglacial times, illustrating their effect on water depth at a hypothetical sample locality.
556 Time-averaged fossil samples would integrate specimens over a broad depth range.

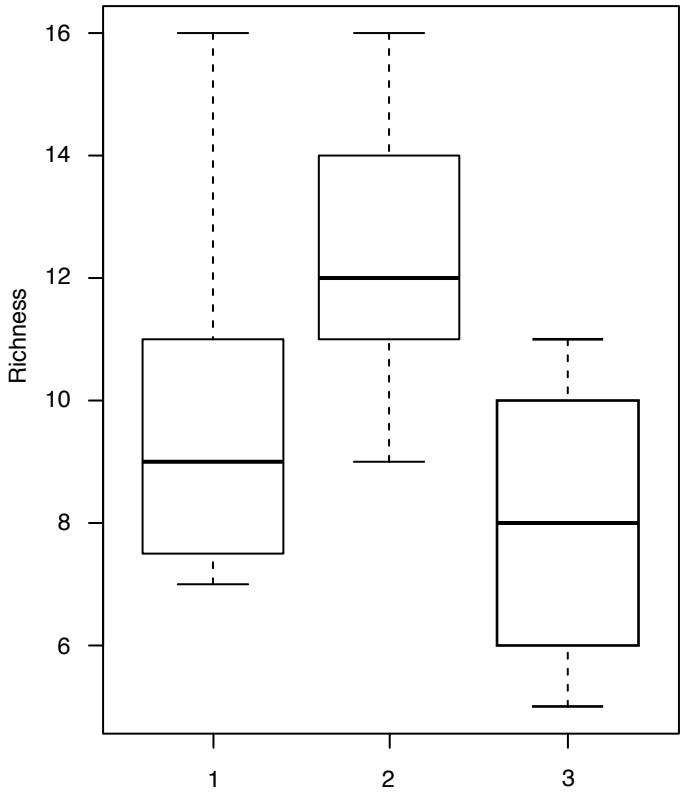

Fielding et al. (2008)
260
270
280
290
300
310
320
330
340
350
Permian
Carboniferous
Pennsylvanian
Mississippian
Wuc.
Cap.
Wor.
Roa.
Kun.
Art.
Sak.
Ass.
Gzh.
Kas.
Mos.
Bas.
Ser.
Vis.
Tou.
Glacial III
Glacial II
Glacial I
P4
P3
P2
P1
C4
C3
C2
C1
Isbell et al. (2003)
high-latitude
low-latitude
0
-2
δ18O ‰ (V-PDB)
(Korte et al., 2008)
10
0
-10
Mean Tropical
Temperature Anomaly
(Montañez et al., 2007)

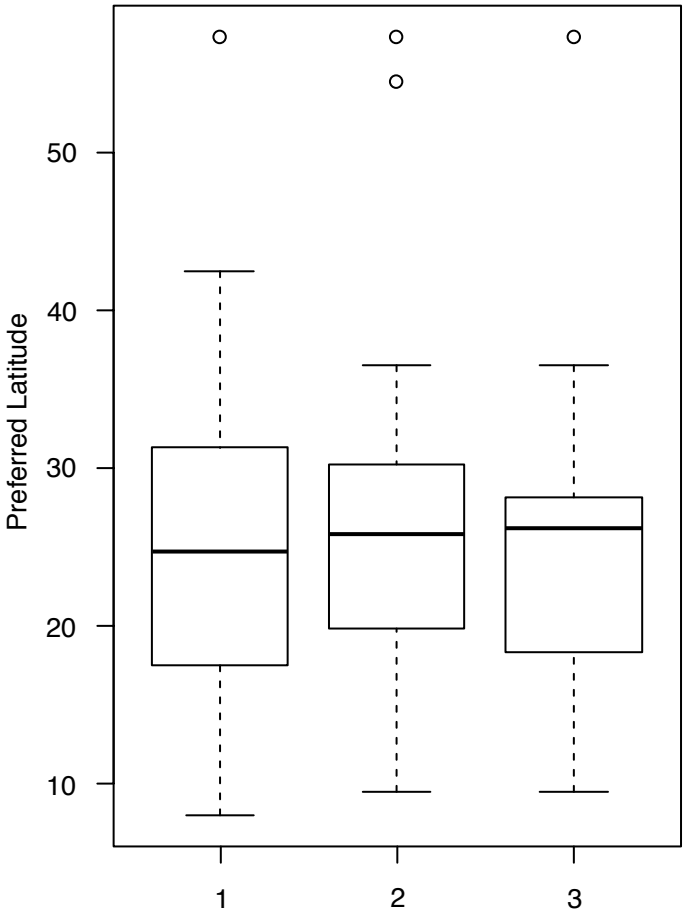

Ancoraimes
Lake Titicaca
Yampupata
Copacabana
Cuyavi
Yaurichambi
Peru
La Paz
Bolivia
Colquencha
Sampled Sections
Town
Road
0 10 20 30
km
69° W
16° S
Bolivia
0 300
km

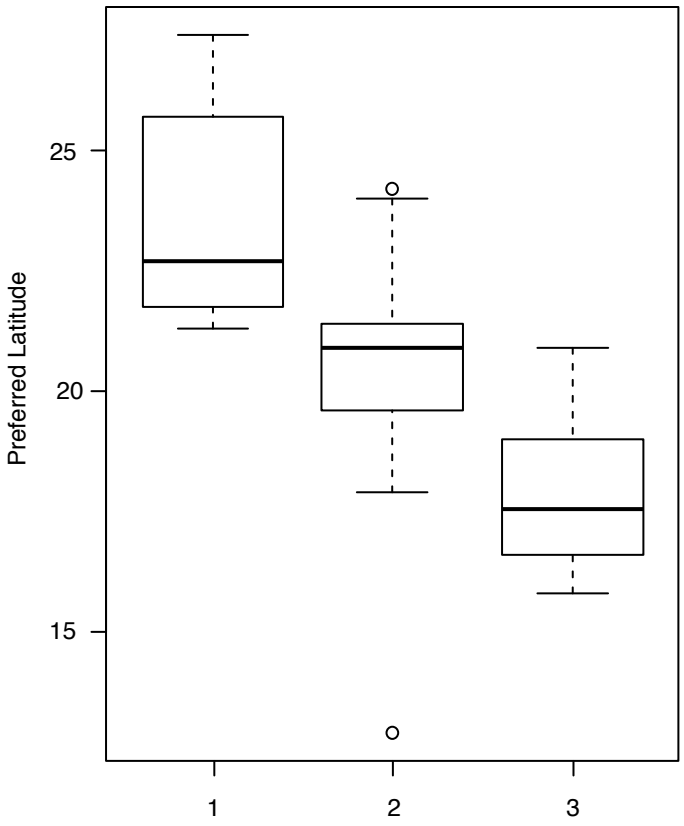

Moscovian
Kas.
Gzh.
Asselian
Sak.
15
Cuyavi
10
Yampupata
10
Yaurichambi
5
Ancoraimes
Siltstone
Marl
Limestone
Sandstone
Unassociated
Cluster 3
Cluster 2
Cluster 1

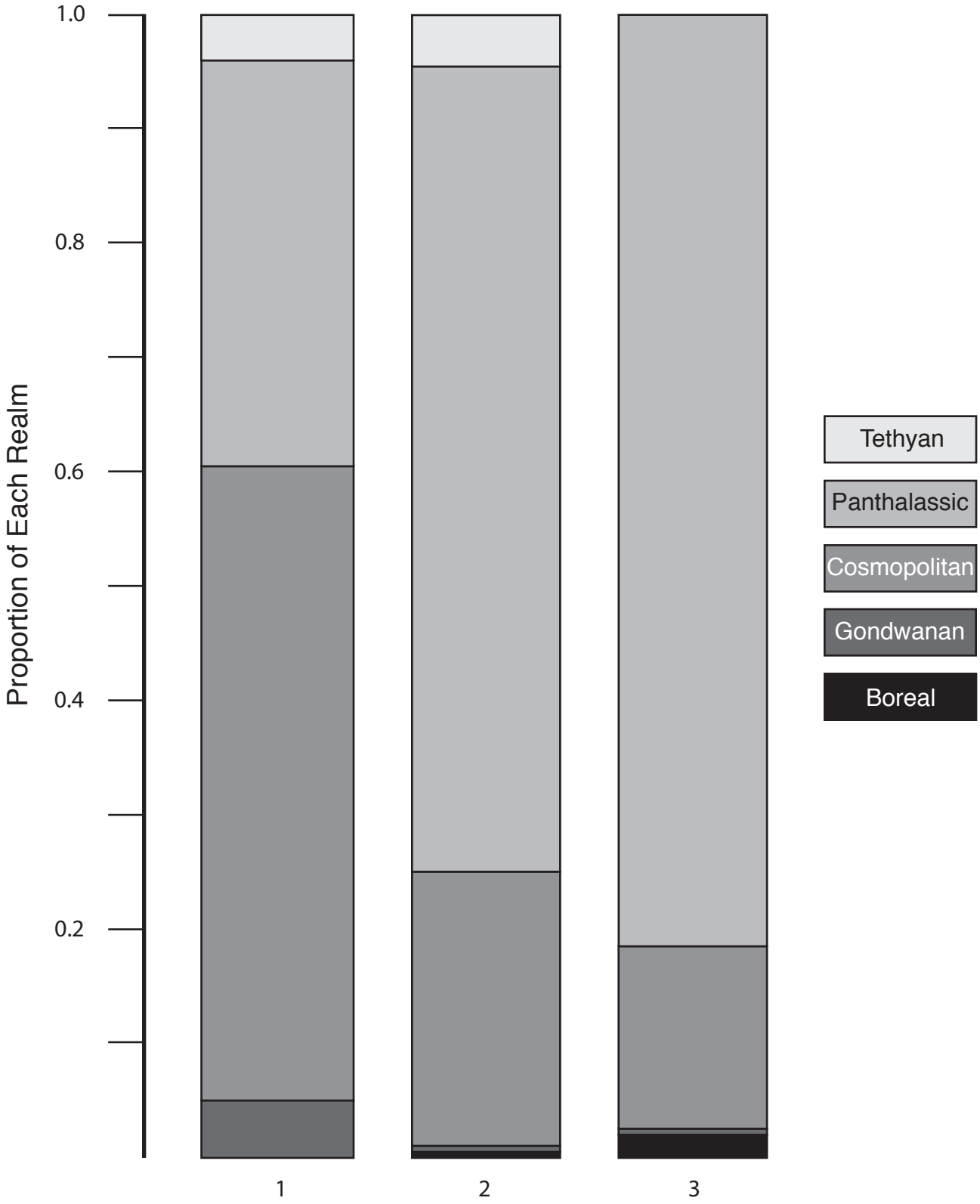

Abundance (%)
1
5
10
25
50
75
0.8
0.4
Capillomesolobus
Isogramma
Echinaurus
Stereochia
Rhynchopora
Alpavlia
Hoskingia
Punctospirifer
Mesolobus
Cleiothyridina
Derbyia
Kochiproductus
Lingula
Costatumulus
Orbiculoidea
Reticulariina
Neochonetes
Waagenoconcha
Fimbrinia
Orthotichia
Rhipidomella
Chonetinella
Quadrochonetes
Hustedia
Stenoscisma
Gypospirifer
Linoproductus
Composita
Dasysaria
Crurithyris
Phricodothyris
Hystriculina
Kozlowskia
A27
A26
A30
Y6
A29
A28
A28a
Ya 4
A27a
A19
Y8
Y1
Ya 5
A6
A4
A21
A7
A21a
A3
A16
A9
A10
A14
A13
A11
A9a
A8
A18
A24a
A23
Y2
A20
A22
A25
Cu4
Cu3
Ya 3
Ya 6
Ya 2
Ya 1
Cu1
Y9
Cu5
Y7
A31
A32
A24
3
2
1
0.8
0.4
0.0

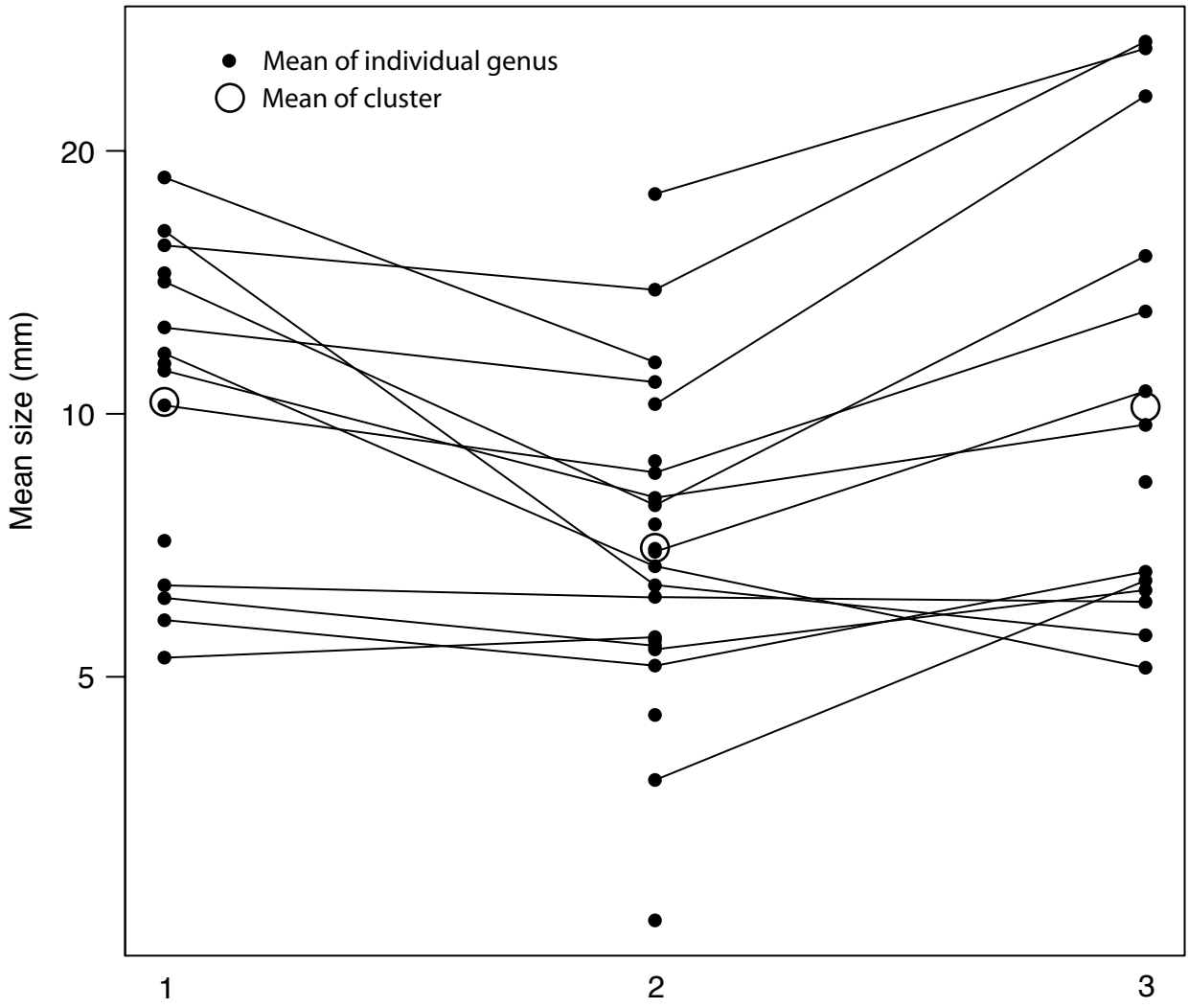

unassociated
cluster 1
cluster 2
cluster 3
0.5
0.0
−0.5
Axis 2
−1.5
−1.0
−0.5
0.0
0.5
1.0
1.5
Axis 1

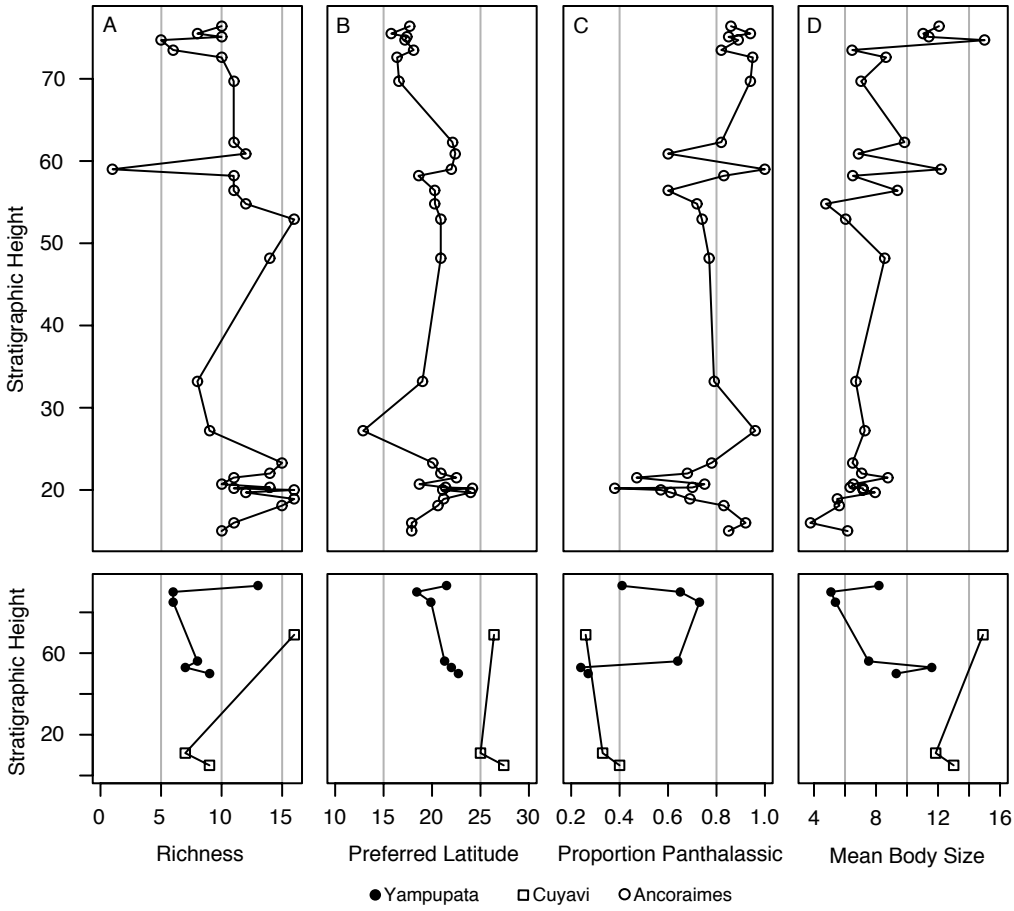

Richness
16
14
12
10
8
6
1
2
3

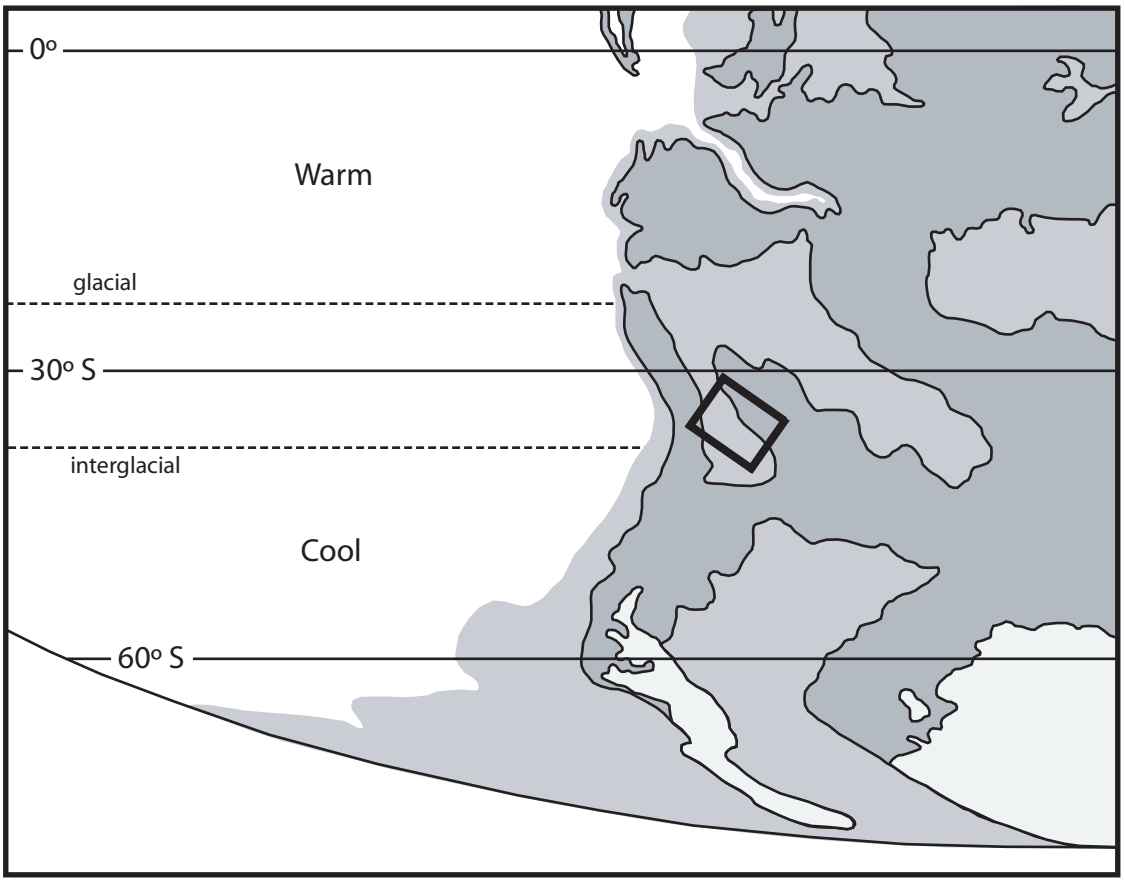

Preferred Latitude
50
40
30
20
10
1
2
3

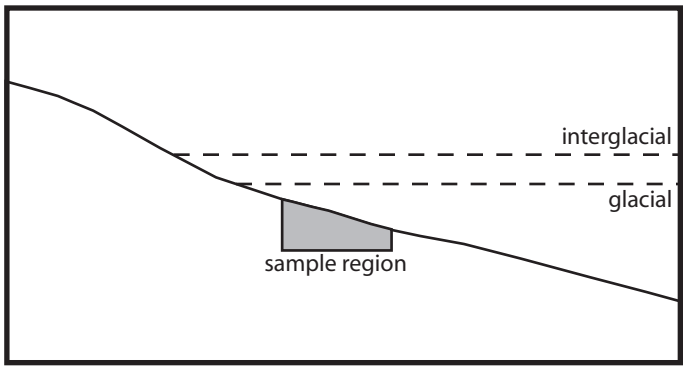

Preferred Latitude
25
20
15
1
2
3


1.0
0.8
0.6
0.4
0.2
Proportion of Each Realm
1
2
3
Tethyan
Panthalassic
Cosmopolitan
Gondwanan
Boreal


Mean of individual genus
Mean of cluster
Mean size (mm)
20
10
5
1
2
3


A
B
C
D
Stratigraphic Height
70
60
50
40
30
20
Stratigraphic Height
60
20
0
5
10
15
10
15
20
25
30
0.2
0.4
0.6
0.8
1.0
4
8
12
16
Richness
Preferred Latitude
Proportion Panthalassic
Mean Body Size
Yampupata
Cuyavi
Ancoraimes


0°
Warm
glacial
30° S
interglacial
Cool
60° S


interglacial
glacial
sample region