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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.

1. Introduction

Temperature is one of the basic controls on both marine and terrestrial community compositions 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

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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; Montañez 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, 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) (Fig. 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 (Montañez 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 (Fig. 2). The four sections range in age from Moscovian to Sakmarian (Grader, 2003), spanning the greatest extent of the LPIA and its major deglaciation (Fig. 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.

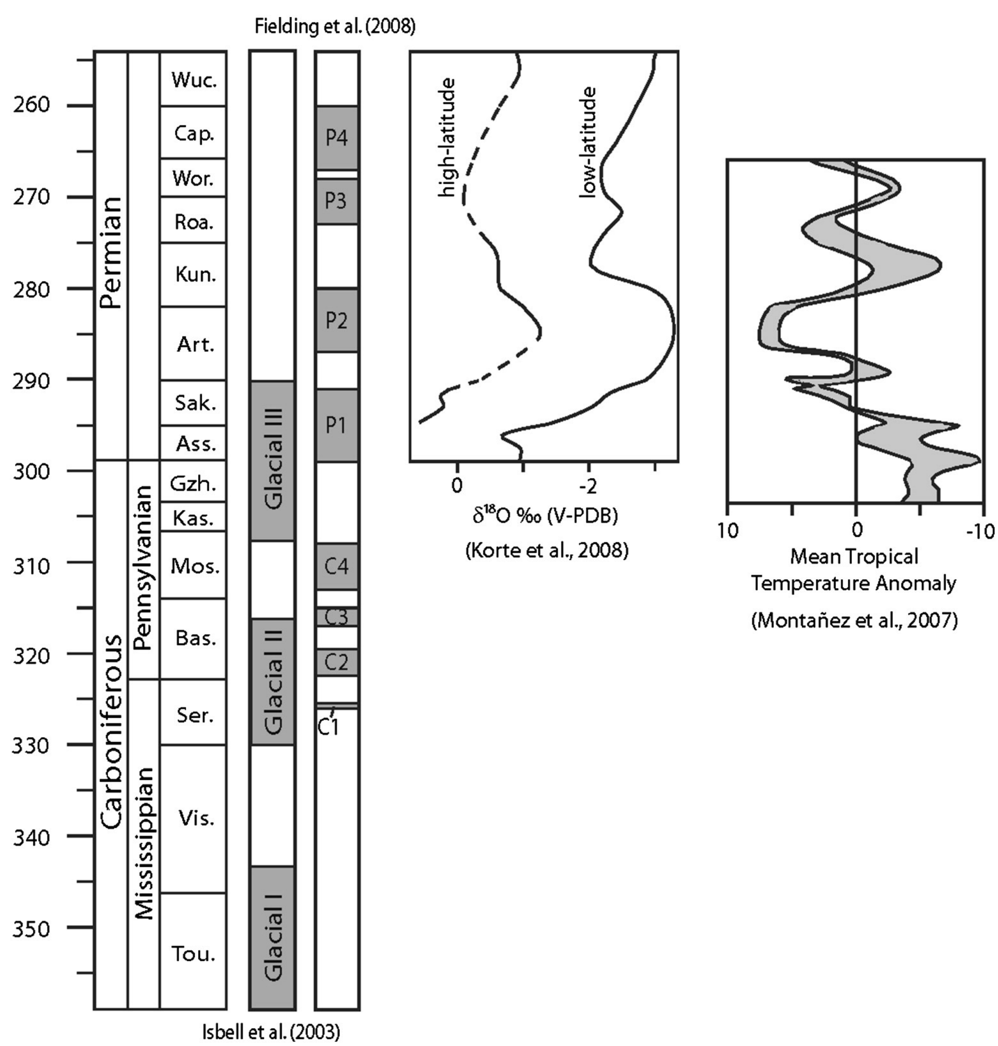

Fig. 1. Summary of Late Paleozoic Ice Age glaciations and temperature records. Glacial records come from Australia (Fielding et al., 2008) and basins throughout Gondwana (Isbell et al., 2003). Permian temperature records from high and tropical latitudes show decreasing temperatures during the early Permian glacial (Montañez et al., 2007; Korte et al., 2008).