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PALEOECOLOGY OF GLACIAL AND NON GLACIAL CARBONIFEROUS FAUNAS DURING THE LATE PALEOZOIC ICE AGE IN PATAGONIA

by

Nicole L. Braun

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ABSTRACT

PALEOECOLOGY OF GLACIAL AND NON GLACIAL CARBONIFEROUS FAUNAS DURING THE LATE PALEOZOIC ICE AGE IN PATAGONIA

by

Nicole L. Braun

The University of Wisconsin-Milwaukee, 2015
Under the Supervision of Dr. Margaret Fraiser

The Late Paleozoic Ice Age (LPIA) records the only icehouse to greenhouse transition in Earth's history that involved complex marine and terrestrial life and serves as an analogue for Quaternary climate change. Identifying biotic responses to paleoenvironmental variations during the LPIA is important in order to understand how our modern fauna may respond to contemporary climate change. Low-paleolatitude (far-field) marine faunas far from ice centers have been recognized and used as a global proxy for biotic responses to the LPIA, but the biotic responses in high-paleolatitude (near-field) regions close to Gondwanan ice centers have received much less attention. We tested the hypothesis that paleocommunities within polar latitudes in glacially influenced marine environments differed ecologically from paleocommunities distal to glacial influence. This study focused on the paleoecology of the Tepuel-Genoa Basin located in central Patagonia, Argentina to determine how conditions during the LPIA influenced marine paleoecology in a near-field region. Quantitative stratigraphic and paleontological analyses were conducted on sections near the base of the Pampa de Tepuel Formation. Results from this study suggest that paleocommunities located near the base of the formation were affected by stressful physical processes from glacial influences and possible small debri flows. Paleoecommunities were dominated by sessile epifaunal suspension feeders, abundant crinoid populations, and a lack of durophagus predation. This data suggests that Paleozoic marine invertebrate communities in a near-field region during the LPIA can be used as a potential proxy for modern glacial-marine communities. It is interpreted that shifts in taxonomic composition occur throughout this basin depending on environmental influences. The paleoecological changes observed in the Pampa de Tepuel Formation could be indicative of the waxing and waning of glaciation or of glacial and non-glacial intervals during this ice age.

To my parents,
Mike and Kellee Braun
and my sister,
Natalie Braun

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1. INTRODUCTION

The Late Paleozoic Ice Age (LPIA), which spanned most of the Carboniferous and into the Permian (~70 myr), was an important climatic event in Earth's history as it was the longest and largest icehouse interval of the Phanerozoic (e.g. Fielding et al., 2008; Montañez and Poulsen, 2013). The end of the LPIA records the only icehouse to greenhouse transition that involved biologically complex marine and terrestrial life (Gastaldo et al., 1996; Isbell et al., 2003; Montañez and Soreghan, 2006; Fielding et al., 2008) and the subsequent shift to a greenhouse state serve as the most recent and complete analogue for Quaternary climate change (Gastaldo et al., 1996; Montañez and Soreghan, 2006; Isbell et al., 2008a). Evidence suggesting a similar climatic shift today can be observed in retreating glaciers, increasing sea levels, and increasing global temperatures (e.g. Kaser et al., 2004; Harris et al., 2006; IPCC, 2014). Both intervals are also characterized by low atmospheric CO_2 and multiple glacial intervals (Isbell et al., 2003, Fielding et al., 2008a; Isbell et al., 2012, 2013; Frank et al., 2015).

Much LPIA research has focused on the extent and duration of glaciation in Gondwana, the supercontinent that included present-day South America, Africa, India, Australia, and Antarctica (e.g., Crowell and Frakes, 1970; Visser, 1997; Isbell et al., 2003, 2012; Fielding et al., 2008a, 2008b; Stollhofen et al., 2008; Gulbranson et al., 2010). Early hypotheses proposed that a single, massive ice-sheet covered Gondwana during this time (Frakes and Crowell, 1969; Scotese et al., 1999). However, improved chronostratigraphy and regional-scale sedimentologic analysis suggest that glaciation in Gondwana during the LPIA fluctuated and consisted of multiple restricted ice sheets of 1-8 million years in duration (Fig. 1) (e.g., Isbell et al. 2003, 2012; Fielding et al. 2008;

Gulbranson et al., 2010). The pacing of glaciation in this emerging LPIA concept is supported by radiometrically-calibrated reconstructions of eustasy from paleo low-latitude settings (Eros et al., 2012). Geochemical, stratigraphic, and tectonic records reveal evidence for multiple glacial episodes separated by nonglacial intervals (Fig. 2) (Fielding et al., 2008b, Gulbranson et al., 2010, López-Gamundí and Buatois, 2010). These environmental changes likely had profound effects on the composition and diversification of marine ecosystems during the LPIA (Clapham and James, 2008).

Paleobiologic studies suggest temperature associated with climate change can often have consequences on the distribution and survival of species through indirect changes in reproductive potential, abundance, or interspecific interactions (Clarke, 1993). Factors such as viscosity, oxygen solubility, and carbonate equilibria of the oceans can fluctuate with changes in climate and influence the physiology of many organisms (Clarke, 1993). Much remains to be understood about the effects on the marine paleoecology during this prominent climatic event.

Biotic responses to LPIA climate fluctuations in low-paleolatitude marine regions far from ice centers (far-field) have been recognized and used as a global proxy. Upper Mississippian marine paleocommunities in the far-field subtropics of North America suggest a common biotic response to the onset of the LPIA is an increase in eurytopic organisms (Bonelli and Patzkowsky, 2008, 2011). Other North American studies show climatic fluctuations had little effect on the diversity of marine paleocommunities across the Mississippian-Pennsylvanian boundary (Heim, 2009). A large-scale macroevolutionary study showed that sluggish diversification and narrowly distributed brachiopod genera did not recover to their preglacial configuration until after the LPIA

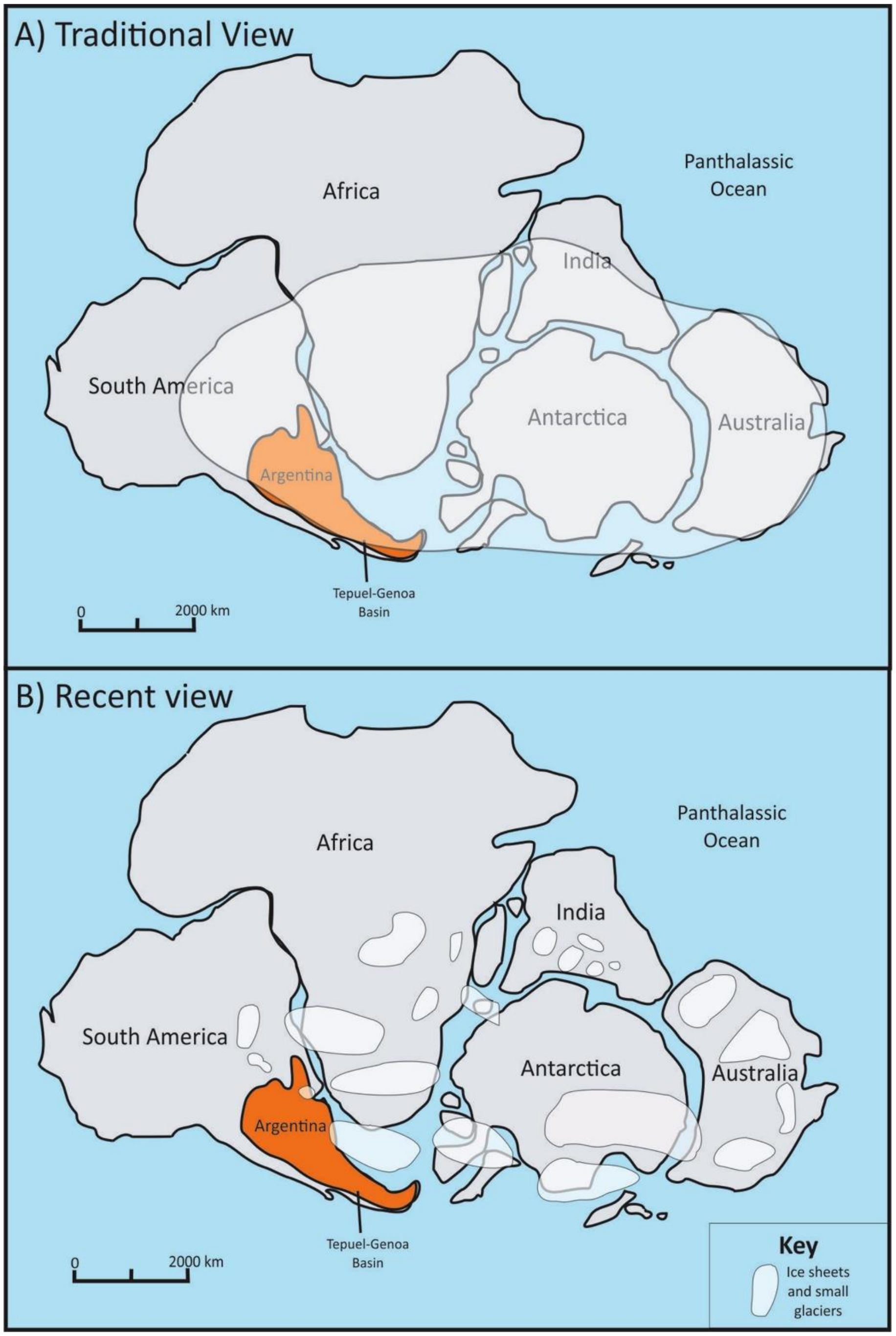


Figure 1. Traditional and recent reconstructions of maximum glaciation in Gondwana during the late Paleozoic. A) Traditional reconstruction showing a massive ice sheet. B) Reconstruction during maximum glaciation during the Gzhelian to early Sakmarian (Pennsylvanian–Early Permian). Data from Isbell, 2012.

(Powell, 2005). However, far-field faunas undoubtedly responded differently compared to those from high latitudes (near-field) (Waterhouse and Shi, 2010) and regional ecological patterns in response to climate change do not always parallel global patterns (Heim, 2009). Further analysis on near-field faunas during specific transitions from glacial to non-glacial intervals of the LPIA is necessary to more fully understand how faunas respond regionally to environmental change.

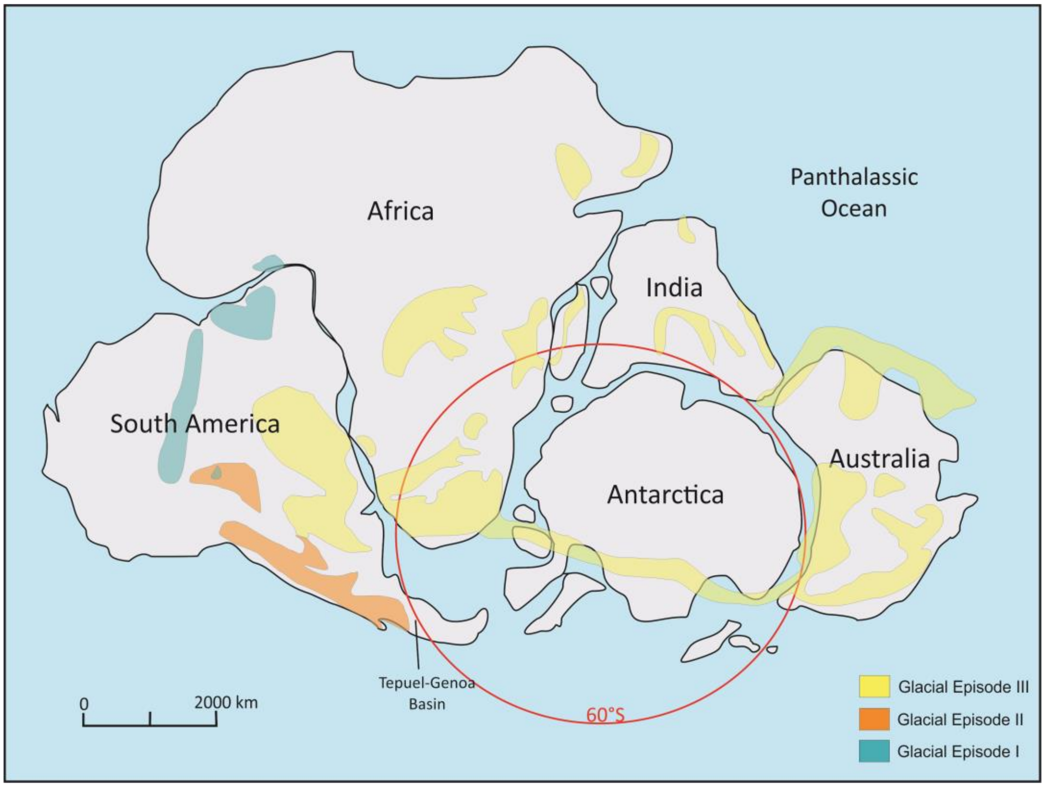


Figure 2. Gondwana Supercontinent and the Late Paleozoic Ice Age basins with glacial evidence in their stratigraphic record highlighted. Modified from López-Gamundí and Buatois, 1997, 2010; Isbell 2010.

1.1 Hypothesis

The objective of this study was to determine how conditions during the LPIA influenced marine paleoecology in a near-field region. The overarching hypothesis that was tested is that paleocommunities within and proximal to glaciomarine environments differed ecologically from paleocommunities distal to glacial influence (near-field faunas differed from far-field faunas). The specific aim of this study was to document the paleoecological characteristics along an environmental gradient in a high-paleolatitude region of Gondwana. The fauna within the Tepuel-Genoa Basin in the Chubut province of Argentina was examined to more fully understand how biota at high paleolatitudes responded to climate change. The two working hypotheses are: 1) faunas from glacial-proximal environments were characterized by low diversity and were dominated by genera with a broad latitudinal range (based on previous work by Powell, 2005); and 2) faunas from glacial-distal environments were more diverse, larger in body size, and more ecologically complex (based on previous work by Clarke et al. 2004; Dineen et al., 2012). These regional ecologic patterns were compared to large-scale, global ecological patterns in order to get a more robust understanding of how climate affected the biota.

2. GEOLOGIC SETTING

During the late Paleozoic, the supercontinent Gondwana included now-recognized continents of Australia, India, Antarctica, and parts of South Africa and South America. The western margin of Gondwana is represented by numerous Upper Paleozoic basins in southern South America and provides a well described and radiometrically-calibrated record of paleoenvironmental change (Limarino and Spalletti, 2006; Gulbranson et al., 2010; Césari et al., 2011), such as variations in sea level, tectonic activity, and changes in climate during the LPIA (Lopez-Gamundi, 1997; Pazos et al., 2002; Limarino and Spalletti, 2006; Henry et al., 2008, 2010, 2014, Limarino et al., 2014; Gulbranson et al., 2015). The Tepuel-Genoa Basin located in central Patagonia, Argentina contains a rich paleontological record and an exceptionally exposed succession (Limarino and Spalletti, 2006; Pagani and Taboada, 2010).

There are currently two conflicting hypotheses explaining the paleogeographic position of Patagonia during the LPIA. The first proposes Patagonia as an autochthonous block, or native terrane (eg. Forsythe, 1982; Dalla Salda et al. 1990) and the second proposes Patagonia as an allocthonous terrane, or accreted terrane (Pankurst et al., 2006; Ramos, 1984, 2008; Rapalini et al., 2010). After further analysis on magmatic belts and their deformation and metamorphism, it is suggested that the basement of Patagonia is not exotic to Gondwana (Ramos, 2008). This evidence, along with recent fossil discoveries (Taboada, 2008; Pagani and Taboada, 2010), best supports the explanation that Patagonia is a paraautochthonous terrane (Ramos, 2008; Rapalini, 2010). However, this problem is not resolved at the present time. The basement rock of Patagonia consists of two tectonic blocks: the North Patagonian Massif and the Deseado Massif in the south

(Leanza, 1958; Harrington, 1962). It is suggested that western Patagonia and the Antarctic Peninsula collided first with the North Patagonian Massif and then both collided with Gondwana in the Late Paleozoic (Ramos, 2008).

In central Patagonia, Late Paleozoic rocks overlie Devonian granite and underlie Lower Jurassic strata (Pagani & Taboada, 2010). The fossiliferous section of interest in this study is located in the Tepuel-Genoa Basin with its outcrops located between latitudes S 42°50’ – S 44°40’ and W 69°30’ – W 71°20’ (Fig. 3). The tectonic setting of the basin is controversial. It has been interpreted as either a forearc basin or a retroarc basin with minor deformation and a lack of metamorphism (Fig. 4) (Limarino and Spalletti, 2006).

The high-paleolatitude proximity to glaciation of the Tepuel-Genoa Basin during the LPIA, coupled with its near stratigraphic completeness of Mississippian to Early Permian stratigraphy (cf. Isbell et al. 2003, Fielding et al., 2008; Isbell et al. 2012, 2013), makes this an ideal study site. The Tepuel-Genoa basin includes three formations including the Jaramillo, Pampa de Tepuel, and Mojon de Hierro formations. The Jaramillo Formation includes yellow-gray to greenish-gray sandstone with a few siltstones and diamictites and poor fossil content. The sediments that make up this unit were deposited in a nearshore environment (Andreis et al., 1987, 1996; Pagani and Taboada, 2010). This study focuses specifically on the Pampa de Tepuel Formation (overlying the Jaramillio), which contains conglomerate, mudstone, sandstone, and diamictite of probable fluctuating glacial and non-glacial influence (Fig. 5) (Taboada, 2010). Evidence for a glacially influenced interpretation of these strata is the presence of lonestones and glacial pavements (e.g. González et al., 2003; González and Glasser, 2008; Pagani and Taboada, 2010). Taboada (2010) has identified six diamictite levels, interpreting them as representing six separate glacial intervals. However, the glacial pavements may be the result of glide planes beneath slide blocks and the diamictites may also be the result of debris flows in a basinal slope setting (Isbell et al., 2013; Pauls, 2014). Therefore, caution should be exercised in working with these sediments. The overlying Mojón de Hierro Formation includes yellowish to greenish sandstone with intercalated siltstone and conglomerate (Pagani and Taboada, 2010), interpreted as a postglacial sea level rise (López-Gamundi, 1989, 1997).

Figure 3. Map of Tepuel-Genoa Basin located in central Patagonia, Argentina. Modified from González and Díaz Saravia, 2010; Dineen et al., 2012.

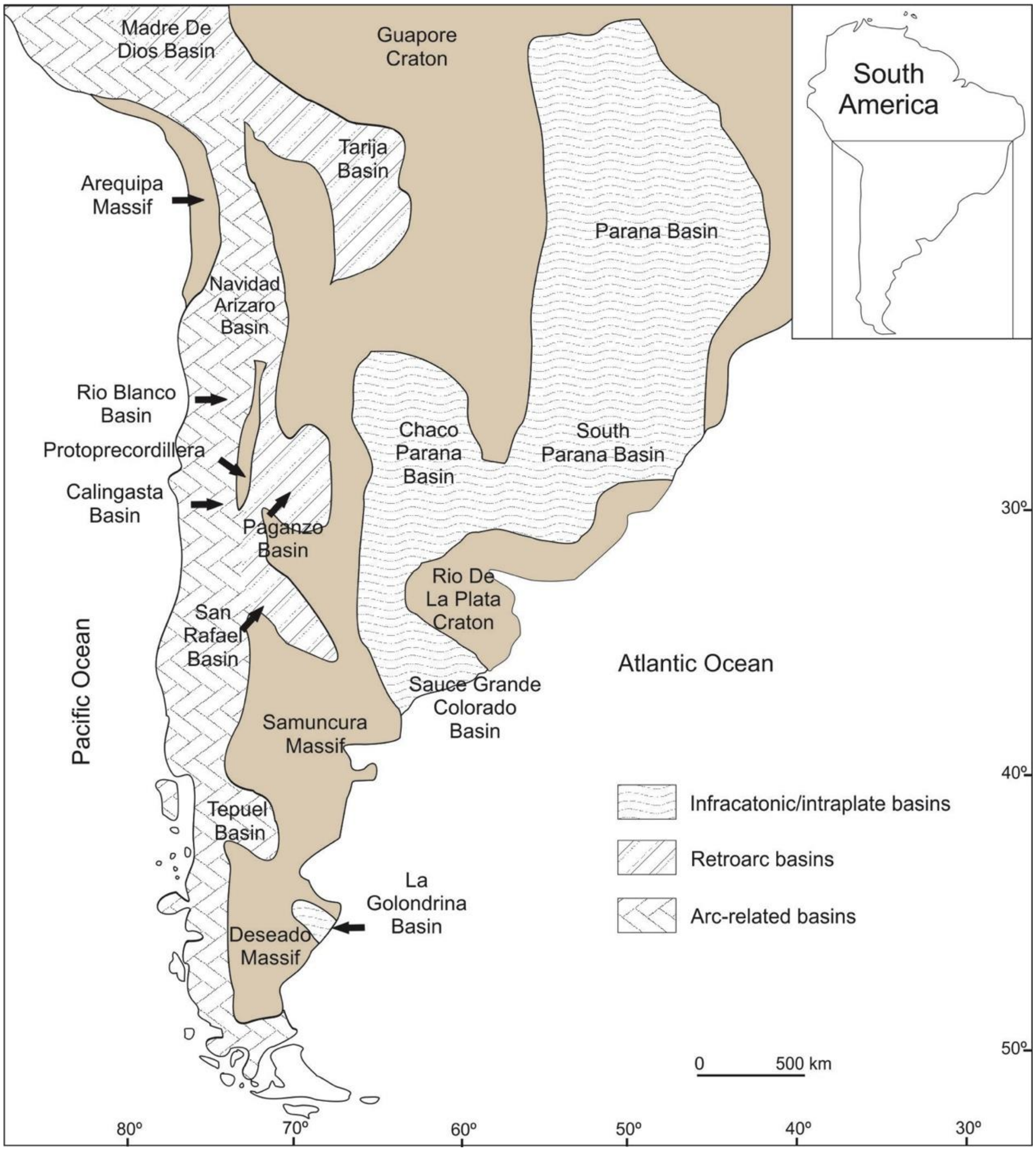


Figure 4. Major basins of southern South America. Modified from Limarino and Spalletti, 2006.

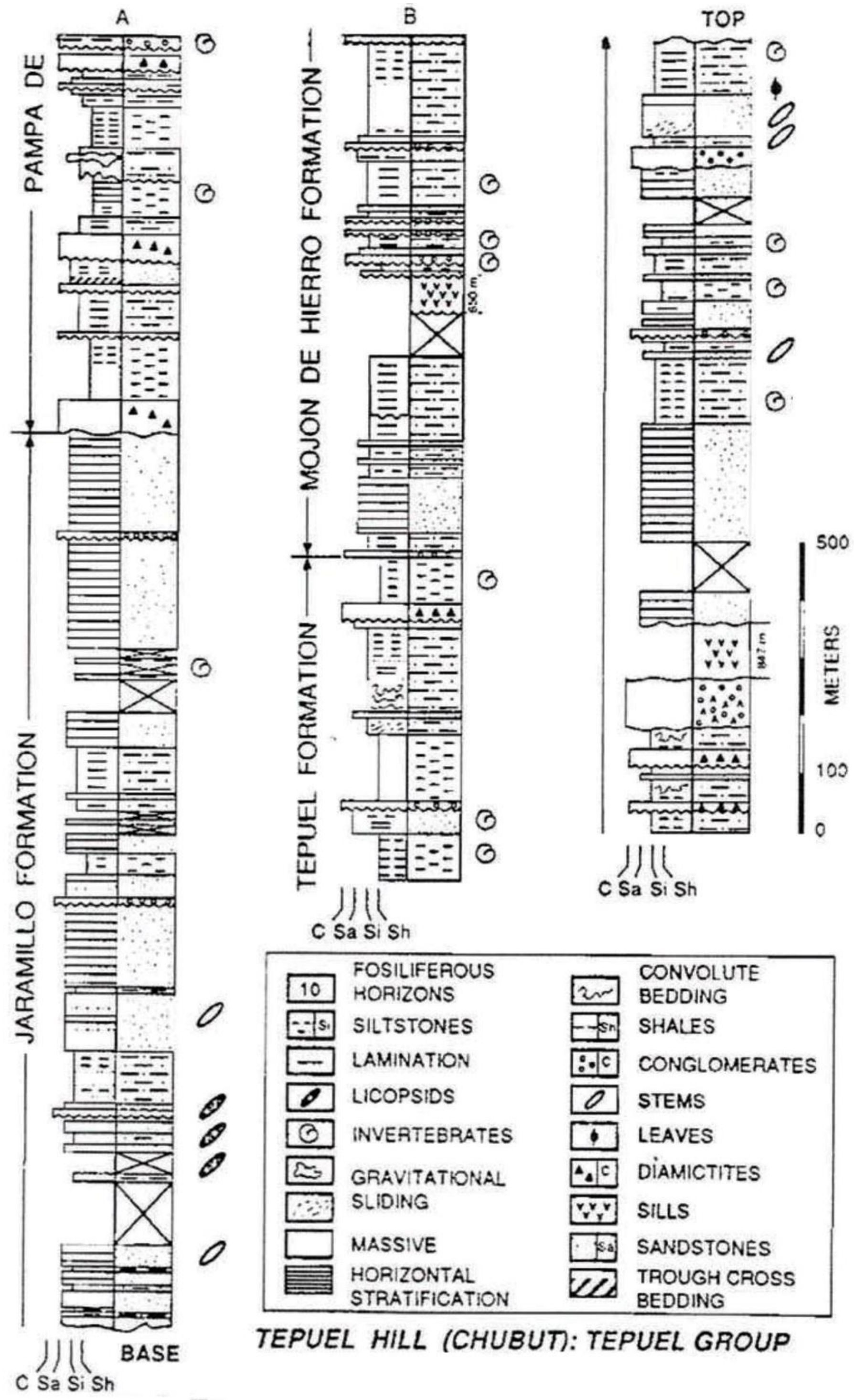


Figure 5. Stratigraphy of the Tepuel group (Jaramillo, Pampa de Tepuel, and Mojón de Herro formations) from the Tepuel-Genoa Basin. Modified from Suero, 1948.

2.1 Biostratigraphy

Studies by Pagani and Taboada (2010) focus on biostratigraphic correlation and attempt to integrate the different faunal associations in order to create a unified biozonation scheme for this region. Most skeletonized, macroscopic, marine invertebrate groups are represented as body fossils throughout the Tepuel-Genoa Basin, with the most diversified being brachiopod, bivalve, bryozoan, and gastropod groups (Pagani & Taboada, 2010). The invertebrate fossils within the Pampa de Tepuel Formation are divided into five units based on brachiopod and bivalve generic classifications (Simanauska and Sabattini, 1997). Biostratigraphic schemes are based on faunal distribution in the northern section of the Tepuel-Genoa Basin (Pagani and Taboada, 2010). The Pampa de Tepuel formation includes the *Lanipustula* biozone, characterized by the presence of the *Lanipustula* brachiopod (Fig. 6). The fauna found within this formation is suggested to be middle Carboniferous to early Permian in age.

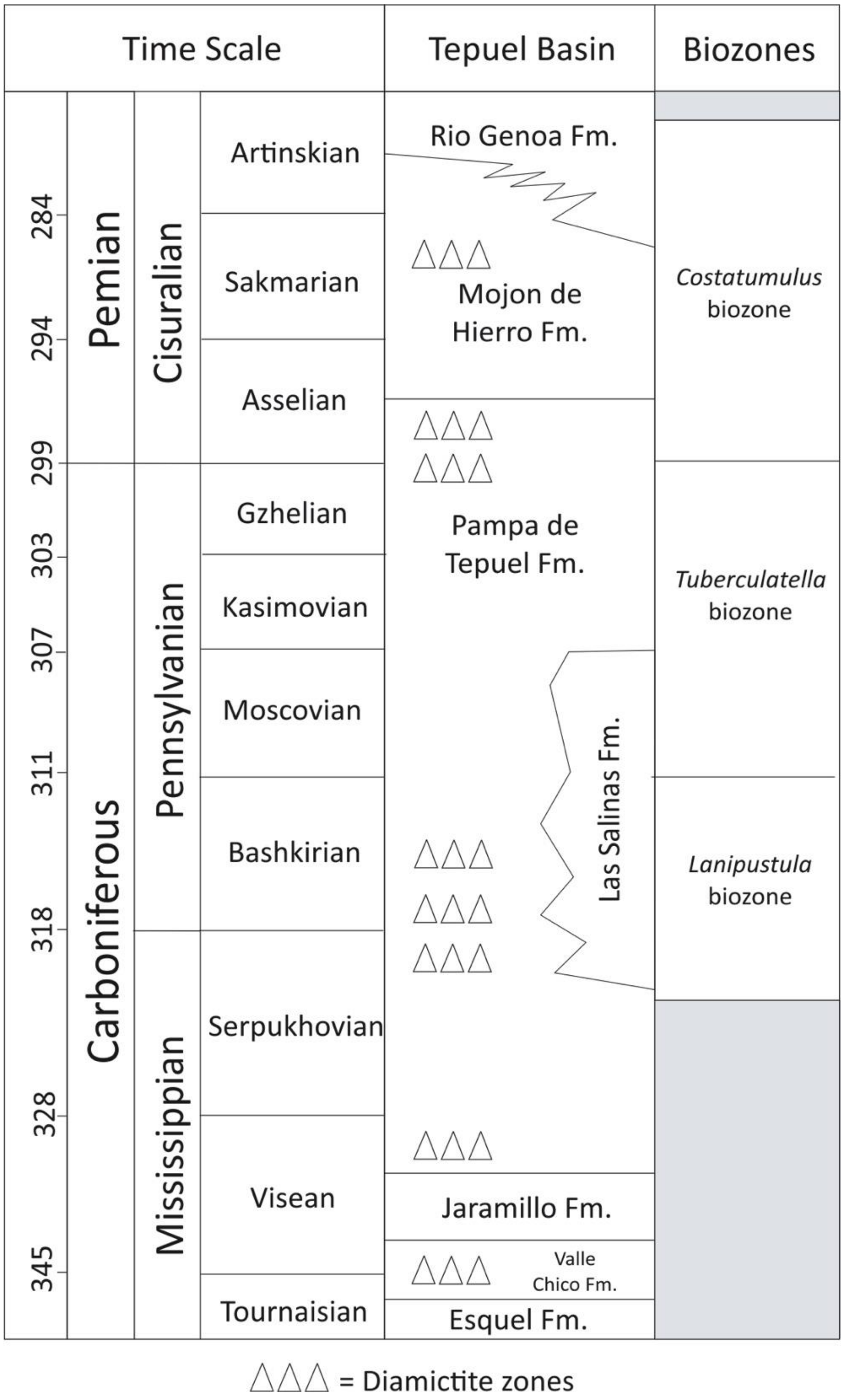


Figure 6. Lithostratigraphy and biostratigraphy of the Late Paleozoic in the Tepuel-Genoa Basin. Modified from Taboada, 2008, 2010; Cesari et al., 2011.

3. METHODS

In late March 2014, paleoecological and sedimentological fieldwork was completed in Patagonia along with Dr. John Isbell (UWM), Dr. Arturo Taboada (LIEB), Dr. Alejandra Pagani (CONICET), and UWM students Kathryn Pauls (Ph.D.) and Sarah Survis (M.S.). Sedimentological and paleocological data were collected and used in construction of stratigraphic columns, in paleoecological statistical analysis, and construction of a regional paleoenvironmental map in order to determine the physical processes that affected marine organisms in the Tepuel-Genoa Basin.

3.1 Sedimentological Methods

I examined two sections of marine strata with the UWM contingent near the base of the Pampa de Tepuel Formation in the Tepuel-Genoa Basin. Stratigraphic sections were measured using standard sedimentological techniques using a Brunton compass, abney level, and Jacob’s staff. Sedimentary structures and stratigraphic surfaces were identified and lithologies were determined in the field. This data was used to create stratigraphic columns in order to establish paleoenvironmental context and identify potential physical stresses that may have affected the paleocommunities in this basin. The total stratigraphic thickness measured was approximately 290.3 meters.

3.2 Paleoecological Methods

It has been suggested that in order to produce a more thorough paleoecological study, information such as counts of relative abundance of individuals, ecological niches, and lithofacies descriptions should be included (e.g., Clapham et. al, 2006). All macroscopic taxa were identified and recorded in the field, with the help of our Argentine

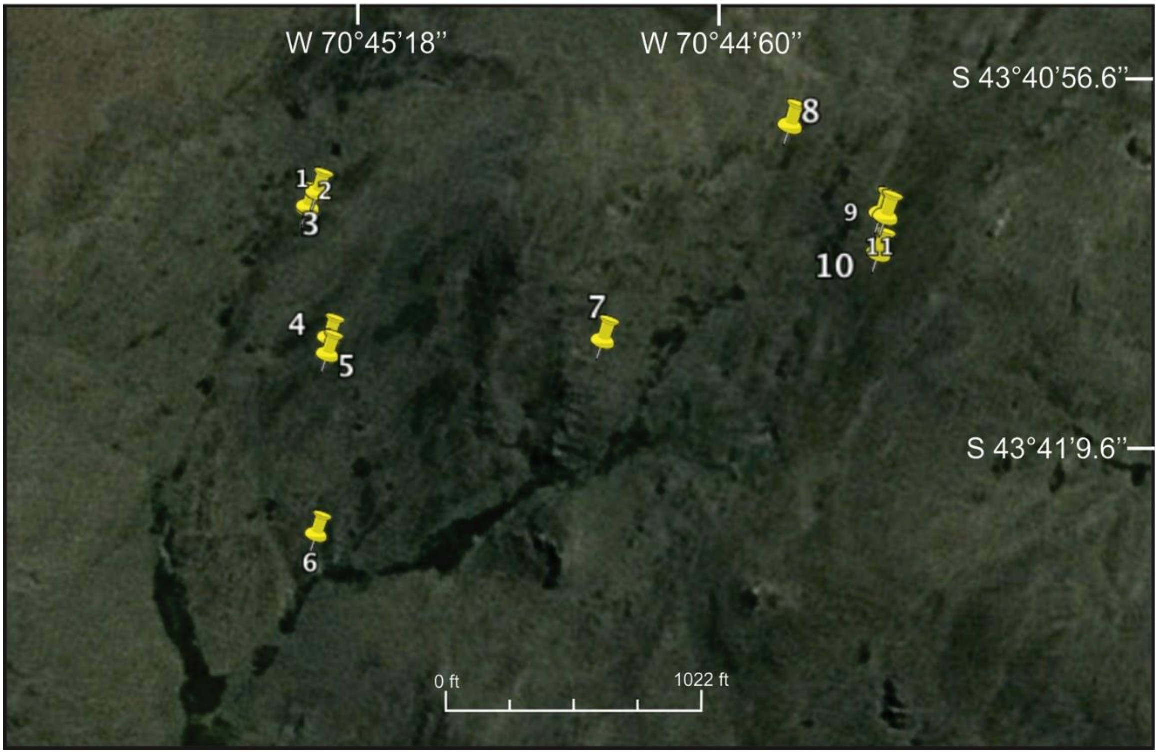


Figure 7. Google earth image of the Pampa de Tepuel Formation section including eleven sampling horizons (indicated by yellow pins).

colleagues, and the numbers of individuals (identified down to the genus level when possible) were counted from a total of eleven different sampling horizons (Fig. 7). The MNI (minimum number of individuals) method was used when counting brachiopod and bivalve fossils in order to avoid overestimation of organisms (i.e. right and left valves from a single bivalve individual were counted as only one individual) (Gilinski and Bennington, 1994). Bryozoan fossils were counted using a 10 cm^2 grid system with lines 1 cm apart (Forcino et. al, 2013). At each gridline intersection, a count of one was recorded for the bryozoan genus. If two taxa were occupying one intersection point, each bryozoan received a count of one. Crinoid fragments were not taxonomically distinctive and their ossicles and columnals were conservatively counted. Reliable and distinct methods for estimating the number of crinoids on the basis of fragments are not available

(Moore and Jeffords, 1968). In order to research the most effective approaches for quantifying disarticulated crinoids, I thoroughly reviewed primary literature regarding crinoid morphology and contacted crinoid specialists, such as Dr. Tatsuo Oji (Nagoya University). Following correspondence and morphological research, I decided to quantify crinoids based on stalk size differences and location in the sampling horizon. Articulated stalks and ossicles found less than 4 cm away were counted as one individual. Disarticulated fragments found grouped together (< 4 cm) were counted as one individual.

In order to obtain the most robust paleoecological information, it has been suggested that a count of at least 50 different individuals should be collected from each fossil horizon (Forcino, 2012). At least 50 specimens were recorded for each sampling horizon, with some horizons exceeding this count. For sampling horizons exceeding 50 counts, data were normalized by distributing random real numbers (greater than or equal to 0 and less than 1) to each individual genus using Microsoft Excel. The 50 specimens with the highest randomly assigned values were used in paleoecological statistical analysis. Randomization of collected data reduces the chance that confounding variables will influence our results. Constraining our data to 50 counts each will keep a statistical consistency among our data when used in different analyses.

The diversity of the paleocommunities was calculated using a variety of diversity indices including Simpson’s Diversity Index and Shannon-Weiner Index. Simpson’s Diversity Index gives the probability that two randomly picked organisms are the same species. Calculated diversity indexes that are close to a value of 1 indicate a very dominant taxon within the designated sampling horizon. Likewise, if the value is minimal it can be inferred that all taxa within the sampling horizon are even (Hammer and Harper 2006). The Shannon-Weiner Index indicates the ability to predict the next collected species. A high Shannon-Weiner value suggests that the sampling horizon possesses high diversity. Both the Shannon-Weiner Index and Simpson’s Index are useful when comparing paleocommunities within different environments (Hammer and Harper 2006).

Ecological dominance was determined through evenness, mean rank order, and breadth of distribution. Ecological dominance is important to account for in a community because dominant species have an equally, or more important influence on species diversity and trophic structures (Clapham, et al. 2006). Evenness is the inverse measure of dominance in a community and measures how evenly distributed the composition of species are (Hammer and Harper, 2006). Mean rank order values assigns a rank to each genera based on their general abundances. A breadth of distribution coefficient was determined in order to measure how certain individuals were among sampling horizons (Clapham et al., 2006). These types of analyses were conducted on each individual sampling horizon. This data could then be used to compare paleocommunity distributions between the two stratigraphic columns.

Z-test values were calculated in order to determine if there were statistically significant differences between populations or groups. (Whitlock and Schluter, 2009). A Z-test was completed between each of the beds in order to obtain a *p*-value, which was used to reject the null hypothesis that all beds are statistically similar (>0.05) or accept the null hypothesis (<0.05).

Trophic structures and modes of life of each individual within each sampling horizon were determined using information available on the Paleobiology Database

(Fossilworks.org) in the laboratory. Organisms were placed into guilds in order to analyze the distribution of the fossil assemblage. Taxa were also classified as either stenohaline or euryhaline in order to compare the overall population's relationship with salinity. This information aided in the reconstruction of paleocommunities in the Tepuel-Genoa Basin during the LPIA.

PAST, a free online software package used in quantitative paleontology, was used for multivariate data analysis and to generate rarefraction curves. The first multivariate tests used were a type of classification analysis known as a cluster analysis. This test identifies groups and subgroups based on a given distance of similarity measure (Hammer and Harper, 2006). The most similar clusters are then grouped into superclusters until all the clusters are joined, producing a tree called a dendrogram. Abundances of individuals of each genus from each sampling horizon were input into the PAST program in order to observe any distinct groupings. The strength of the groupings was then evaluated by investigating the different clustering levels (Hammer and Harper, 2006). Detrended correspondence analysis was another multivariate analysis used. This test attempts to group similar samples in similar positions on the ordination plot. The plot can help to determine how genera respond to an environmental gradient (Hammer and Harper, 2006). The two axes produced by detrended correspondence analysis were assessed by analyzing the groupings of taxa.

Rarefraction curves were generated with PAST in order to make sure results obtained were not due to a sampling bias in the field. The program randomly picked specimens from the original sample and counted the number of individuals obtained. This procedure was repeated in order to get a range of expected values. This repeated procedure revealed rarefraction curves with standard deviations and confidence intervals. If the rarefraction curve flattens out, we can infer that our original sample has recovered most of the species present in the population (Hammer and Harper, 2006).

4. RESULTS

4.1 Lithofacies Analysis

Two sections near the base of the Pampa de Tepuel Formation were measured in order to establish paleoenvironments during the height of the LPIA. A total of 246.8 meters with a dip of 70° (that decreases throughout a covered interval to 40°) and dip direction of 146° was measured and created the first stratigraphic section (Fig. 8). The second stratigraphic section (Fig. 9) was a total of 43.5 meters thick with a dip of 25° and a dip direction of 125°. The late Paleozoic rocks within this basin underlie Jurassic strata and were titled due to the uplift of the Andes during the Cenozoic (Pagani and Taboada, 2010). Strata from both sections were described and divided into seven different facies associations: 1) “Dispersed” fossil-bearing mudrock facies, 2) “Densely packed” fossil-bearing mudrock facies, 3) massive diamictite facies, 4) thin-bedded diamictite facies, 5) massive conglomerate facies, 6) rippled, cross laminated sandstone facies, and 7) massive sandstone facies (Table 1). Detailed stratigraphic columns are available in Appendix A.

4.1.1 “Dispersed” Fossil Bearing Mudrock Facies

This mudrock facies was common throughout the lower measured stratigraphic section. In stratigraphic section 1, the mudrock facies measured about 192 meters in thickness and is interrupted by multiple massive diamicite and massive sandstone facies intervals (Fig. 8). The first gradational contact occured at 60 meters between the mudrock facies and the massive sandstone. Between 90 and 183 meters was a fossiliferous interval in which sampling horizons 1-6 were located (lateral to the measured section). Some sampling horizons were vertically clustered together, such as sampling horizons 1, 2, and

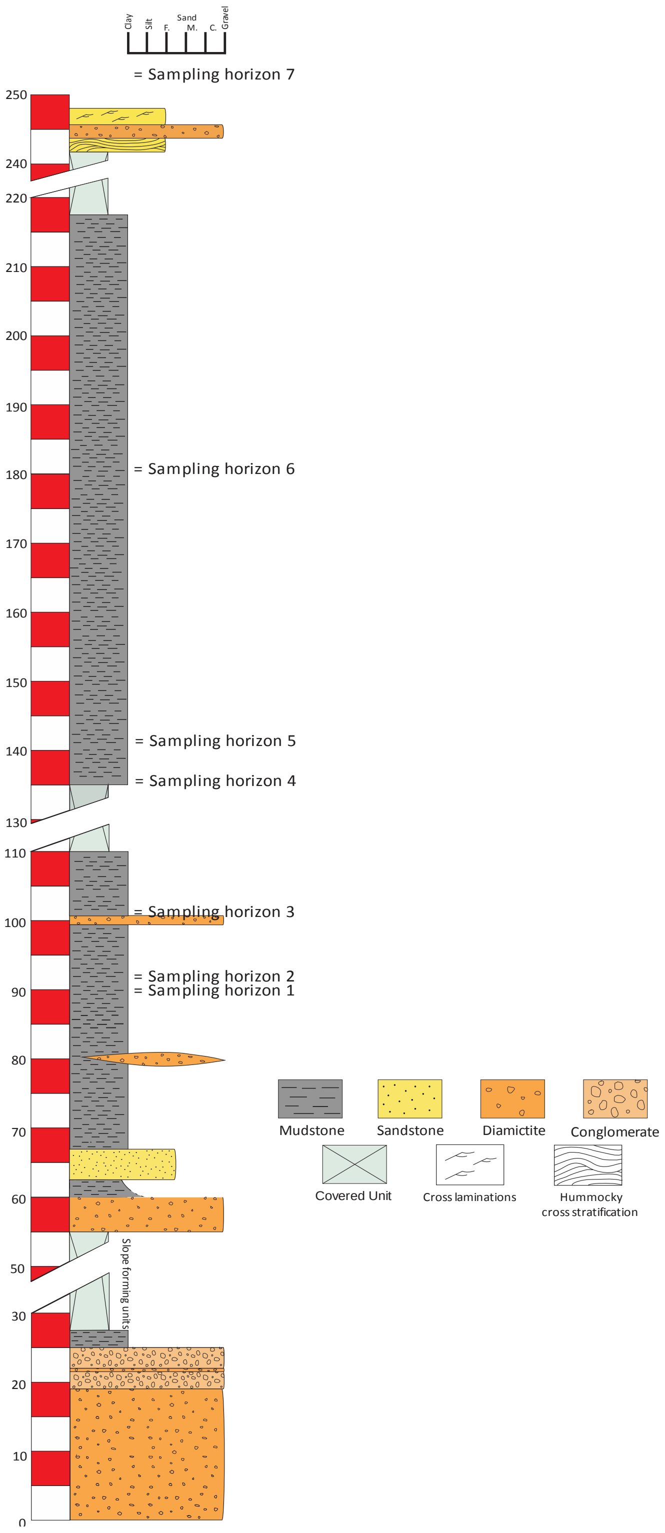


Figure 8. Generalized stratigraphic column (246.8 m) displaying identified and described lithofacies. Note that sampling horizon 7 does not reside in measured section, but is grouped with stratigraphic section 1 due to similarities in faunal composition.

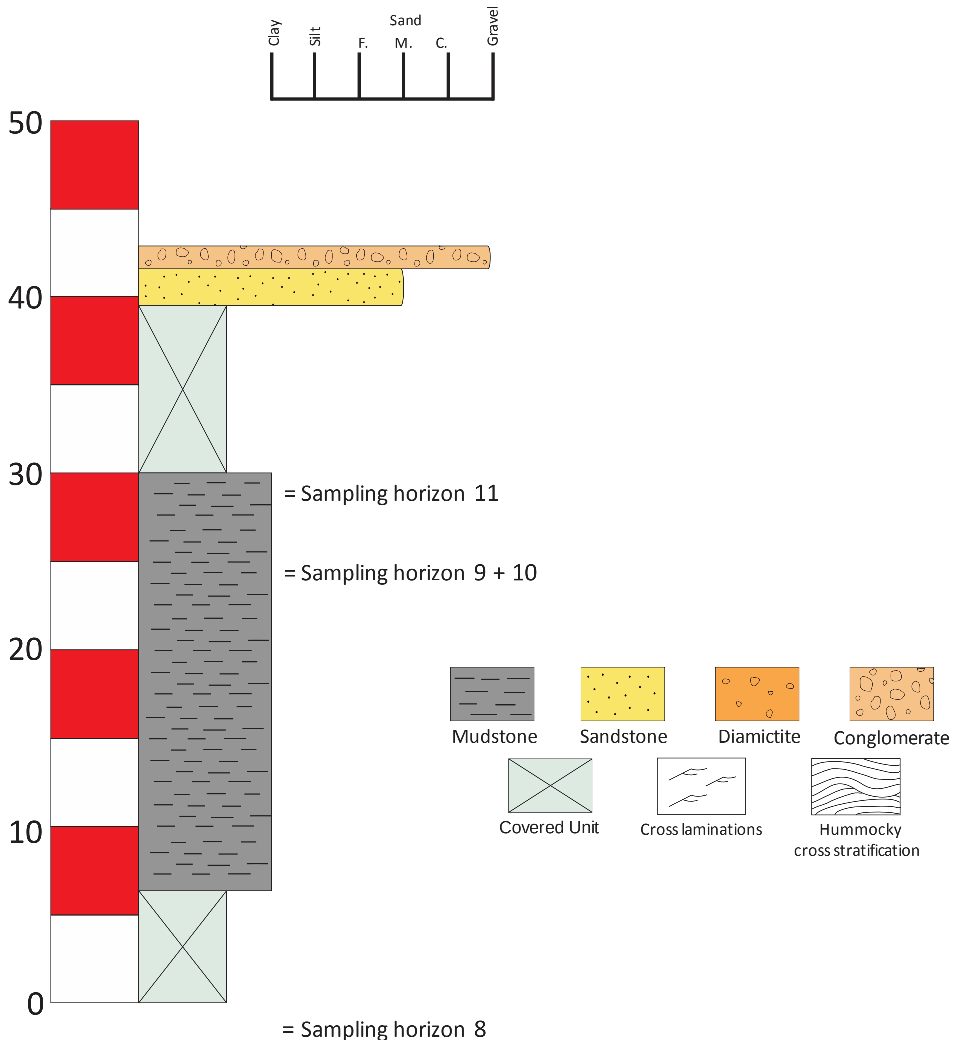


Figure 9. Generalized stratigraphic column (43.5 m) displaying identified and described lithofacies. Note that sampling horizon 8 does not reside in measured section, but is grouped with stratigraphic section 2 due to similarities in faunal composition.

3, and sampling horizons 4 and 5; sampling horizon 6 was located farther away from the clustered horizons. The stratigraphic positions of these sampling horizons were projected onto the respective stratigraphic columns. According to Kidwell's classification for bioclastic fabrics, the sampling horizons found in this facies contained "dispersed" fossil material. Marine invertebrate fossils found within these horizons include gastropods, bivalves, corals, crinoids, hyoliths, polyplacophorans, and ostrocodes. The observed grain-size in this facies consisted of very fine silt and clay-sized grains and appeared dark gray to black in color.

4.1.2 "Densely Packed" Fossil Bearing Mudrock Facies

In the shorter measured stratigraphic section 2, the fossil-bearing mudrock facies measured from 6 meters to 30 meters (Fig. 9). This facies contained sampling horizons 9-11, with sampling horizons 9 and 10 sampled laterally from one another. These rocks were classified as "densely packed" fossiliferous material according to Kidwell's classification for bioclastic fabrics. Marine invertebrate fossils found in these sampling horizons included bryozoans, brachiopods, crinoids, and bivalves. This facies consisted of greenish mudstone and contained characterstic wavy laminae and moldic porosity (possibly from crinoid fossils) (Fig. 10).

4.1.3 Massive Diamictite Facies

The clast-poor massive diamictite facies was observed only in stratigraphic section 1 and occurred at different intervals throughout the total measured unit (Fig. 8). The first diamictite measures 19.5 meters in thickness and consists of fine sand matrix with the maximum clast size measuring approximately 20 cm. Diamictite characterized by large clasts of granite and quartz and a few striated pebbles appeared again from 55 to 60 meters and formed a gradational contact with mudstone.

4.1.4 Thin-bedded Diamictite Facies

There were three thin-bedded diamictite units present in column 1: at 80 meters, 100 meters, and 244 meters (Fig. 8). The unit at 100 meters had fine laminations (Fig. 11) and contained lonestones that pierce stratification (Fig. 12). Also included in this section were striated pebbles found in the surrounding scree (Fig. 13). These lenses are different from the massive diamictite in that they are enclosed by mudrock. The thickness of these unitswass no more than 2 meters and they interrupted the fossil-bearing mudrock facies at this level in the section. They occurred as both beds and as discontinuous lenses (with lenses extending up to 4 meters). The last diamictite layer was 1.2 meters thick and occured at 244 meters. It resided above a fine-grained sandstone with hummocky cross-stratification and below a fine-grained sandstone with ripple marks.

4.1.5 Massive Conglomerate Facies

Massive conglomerate facies were found in both measured stratigraphic sections. The matrix of this unit consisted of fine-grained sand with interbedded pebble-sized clasts. No noticeable sedimentary structures were visible within the conglomerate facies due to heavy lichen cover. In stratigraphic section 1, the conglomerate facies measured approximately 3 to 4 meters in thickness (Fig. 8). In stratigraphic section 2, the conglomerate facies measured about 2 meters in thickness (Fig. 9).

Figure 10. Fossil-bearing mudrock facies in which sampling horizons 8-11 reside. Arrows show molded porosity interpreted to be caused by echinoderms.

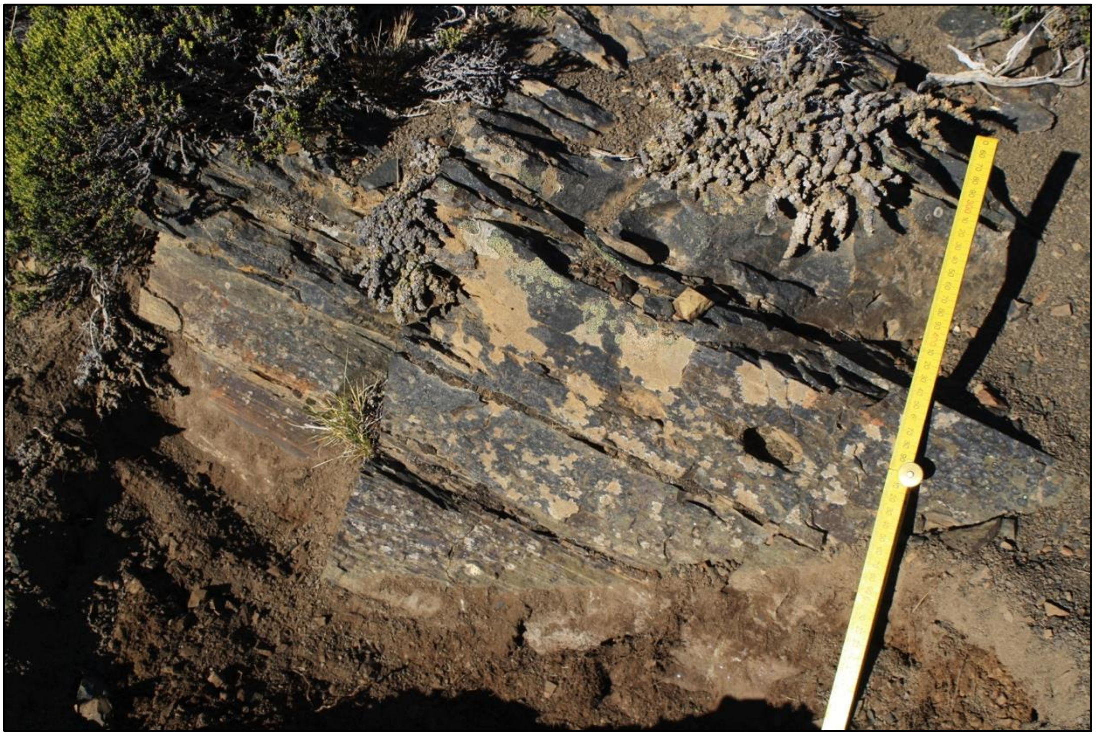


Figure 11. Laminations in diamictite facies.

Figure 12. Dropstone found in laminated diamictite. Photo credit John Isbell.

Figure 13. Striated pebble found in float material near thin-bedded diamictite.

4.1.6 Massive Sandstone Facies

Massive sandstone facies were found in both stratigraphic sections 1 and section 2. In stratigraphic section 1, the first observed fine- to medium-sized grained sandstone occurred at 65 m and measured about 4 meters in thickness (Fig. 8). This was the only massive sand that occured in the measured section. In stratigraphic section 2, a massive medium- grained sandstone overlies cover at 39 meters and measured 3 meters in thickness (Fig. 9). All bedding contacts were sharp, signifying an abrupt change in facies.

4.1.7 Rippled Cross-Laminated Sandstone Facies

This sandstone facies was observed as a ridge forming unit capping stratigraphic column 1 (Fig. 8). A fine-grained sandstone also containing hummocky cross stratification overlies cover at 243 meters and measured 2 meters in thickness. The fine-grained sandstone was interrupted by a 1.2 meter thick diamictite and returned to a fine-grained sandstone with ripple marks producing cross-laminations undulating just below the top of the section. Lateral to the measured section, where this sandstone was well-exposed, this facies was continuous, contained no mudstone interbeds, and was greater than 10 m thick. Where the basal contact was exposed, sandstone of this facies abruptly overlies the mudstone of the “dispersed” fossil-bearing mudrock facies.

4.2 Lithofacies Patterns

Stratigraphic column 1 was dominated by the fossiliferous mudstone facies, but also contained massive conglomerate, massive diamictite, and massive sandstone facies (Fig. 8). The section began with massive diamicite and transitioned between massive conglomerate and a thin diamictite for approximately 8 meters. The fossiliferous mudstone facies occurred at 20 meters before it was covered, indicating the presence of slope-forming units. At about 57 meters there was another diamictite that shared a gradational contact between a fossiliferous mudstone facies. A massive sandstone facies, a diamictite pod, and diamictite with laminations interrupted the fossiliferous mudstone facies between 63 and 100 meters. At 100 meters, a stratified diamictite with laminations and dropstones occured. A fine-grained sandstone with hummocky cross-bedding was observed from 242 to 244.1 meters, which is overlain by a 1.2 meter thick diamictite. The remaining layer, measuring from 242.5 meters to the top of the section at 246.8 meters, consisted of fine-grained sandstone with ripple marks.

Stratigraphic section 2 included fossiliferous mudstone facies, massive sandstone facies, and massive conglomerate facies (Fig. 9). The measured section began with cover underlying a fossiliferous mudstone facies. More covered interval began at 40 meters, and a massive conglomerate capped this sequence with no noticeable sedimentary structures due to the heavy lichen cover.

Facies Association	Lithologies	Sedimentary Structures	Bedding Characteristics	Interpreted Mechanisms
“Dispersed” fossil-bearing mudrock	Mudstone containing clay & silt, few small pebbles	None observed	Fine bedding, varied	Deposited in quiet waters below storm wave base.
“Densely packed” fossil- bearing mudrock	Mudstone containing clay & silt	Thin, wavy laminations with moldic porosity	Fine bedding, < 1 cm thick	Deposited in quiet waters below storm wave base.
Massive diamictite	Massive diamictite, matrix containing fine sand	None observed	No noticeable bedding	Deposited from glacial run-off in the form of meltwater plumes.
Massive conglomerate	Massive conglomerate, matrix containing fine sand	None observed, too lichen covered	0.5 m thick	Clastics from shelf/slope deposited by glacial run-off.
Rippled cross laminated sandstone	Mudstone containing clay & silt	Hummocky cross stratification, ripple marks & cross laminations	Bedding varied	Possible debri flow; progradation representing low stand sea-level.
Massive sandstone	Massive sandstone containing fine- to medium- grained sand	None observed	No noticeable bedding	Progradation of slope
Thin-bedded diamictite	Diamictite, matrix containing fine sand	Laminations	Very thin, < 1 cm thick	Small scale debri flows depositing small glacial material from shelf

Table 1. Facies descriptions and interpretations of the measured sections of the Pampa de Tepuel Formation in the Tepuel-Genoa Basin.

4.3 Paleoecological Results

I examined 11 different sampling horizons near the base of the Pampa de Tepuel Formation, approximately 200 meters above a faulted contact with the Jaramillo Formation. Sampling horizons 1-6 were located within the first measured stratigraphic column and sampling horizons 9-11 were located within the second stratigraphic column; sampling horizons 7 and 8 did not fall within the measured columns. However, horizon 7 was grouped with the lower 6 horizons and horizon 8 was grouped with the upper 3 horizons due to similarities in lithology and taxonomic composition. Sampling horizons 1-7 resided in the “dispersed” fossil-bearing mudrock facies and contained scattered rounded, pebble-sized clasts with lignite fragments also present. The fauna was relatively small in size (5 mm – 10 mm) and contained primarily bivalves (*Nuculopsis*, Fig. 14, and *Phestia*, Fig. 15), crinoids, gastropods, ostracods, hyoliths, corals, and polyplacophora. Sampling horizons 8-11 resided in a wavy, laminated “densely packed” fossil-bearing mudrock with moldic porosity and an absence of clasts. Sampling horizons 8-11 were much more abundant in fossils than the lower sampling horizons and the fossils appeared to be slightly larger in size (10 mm -15 mm). Dominant taxa here included bryozoans (*Fenestella* and *Fistulamina*, Fig. 16), crinoids, brachiopods, and the bivalve *Paleolima*.

4.3.1 Multivariate Analysis

Two multivariate analyses were conducted in order to further understand community compositions and their response to the environment. Cluster analyses were used in order to observe any distinct groupings. All cluster analyses (including Bray-Curtis, Chord, Dice, Euclidean, and Rho) produced similar groupings of sampling horizons. Sampling horizons 1-7 were grouped together and sampling horizons 8-11 were

Figure 14. Nuculopsis (bivalve) specimens.

Figure 15. Phestia (bivalve) specimen.

Figure 16. *Fenestella* and *Fistulamina* (bryozoans) found in sampling horizons 8-11.

grouped together based on both similarity and distance. Groupings within sampling horizons 1-7 and 8-11 differed slightly depending on the cluster analysis used. The Dice cluster analysis of our data resulted in a high correlation coefficient of 0.99 and was used to determine the sub-group similarities (Fig. 17). Sampling horizon 6 was less similar than the rest of sampling horizons and horizons 2 and 7 are very similar in taxa. Sampling horizons 8 and 9 and horizons 10 and 11 shared similar compositions within their sub-groupings.

Multivariate data analysis (DCA) was also conducted in order to understand how genera responded to an environmental gradient. There was another distinct grouping between sampling horizons 1-7 and sampling horizons 8-11 (Fig. 18). Sampling horizons 1-7 grouped closely together based on both axes; however, sampling horizons 8-11 group together based on axis 1 while axis 2 caused them to spread out vertically.

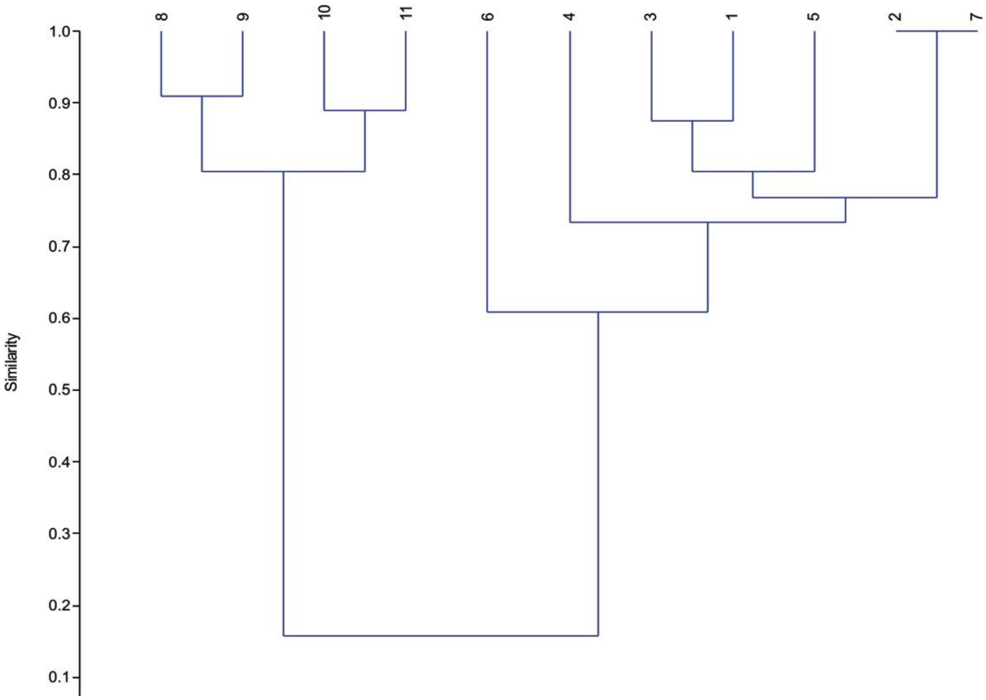


Figure 17. Cluster Analysis for sampling horizons 1-11 in the Pampa de Tepuel Formation using Dice cluster analysis based on similarity.

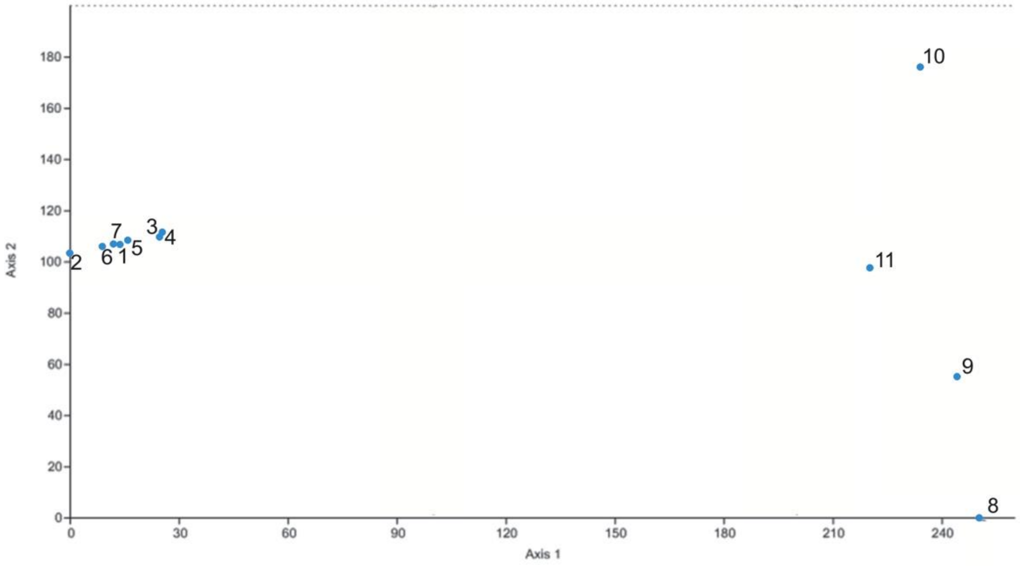


Figure 18. Multivariate Data Analysis for sampling horizons 1-11 in the Pampa de Tepuel Formation using Detrended Correspondence analysis (DCA) plot showing the relationship of all horizons based on two axes.

4.3.2 Diversity and Abundance

A total of 893 individual specimens were counted in the field. Alpha diversity within the sampling horizons ranged from 4 to 10 different genera within 12 different classes (Fig. 19). The alpha diversity remained relatively consistent throughout the first 5 sampling horizons with a value ranging between 6 and 8. In sampling horizon 6, diversity declined to an alpha value of 4 and then increased to 10 in sampling horizon 7. Sampling horizon 7 had the highest alpha diversity value of all the eleven sampling horizons. Alpha diversity for sampling horizons 8-11 remained consistent with values being either 4 or 5. There does not appear to be an overall trend in each stratigraphic section, as the majority of values remained between 4 and 8 with an exception of sampling horizon 7.

Crinoids were ranked 1st in overall abundance in sampling horizons 1-11, with a value of 2.3, followed by gastropods at 5.3 and bryozoans at 5.8 (Fig. 20). Crinoids were the only taxon that appeared in all eleven sampling horizons (Fig. 21). Bivalves were the 2nd most widely distributed group, appearing in eight of the eleven sampling horizons. Ostrocods, hyoliths, bryozoans, and brachiopods were more concentrated in a smaller number of horizons.

The total abundances of the organisms were tallied for each sampling horizon and are available in Appendix B. Crinoid, bivalve (specifically *Phestia* and *Nuculopsis*), and gastropod populations dominated sampling horizons 1-7 (Fig. 22). The abundance of crinoids remained consistent through out these beds, comprising about 50% of total taxa. Bivalves and gastropods comprised the next highest total abundances, yet they fluctuated from horizon to horizon. There was an absence of brachiopods, however, and one cephalopod and smaller populations of ostracods, hyoliths, polyplacophorans, and corals

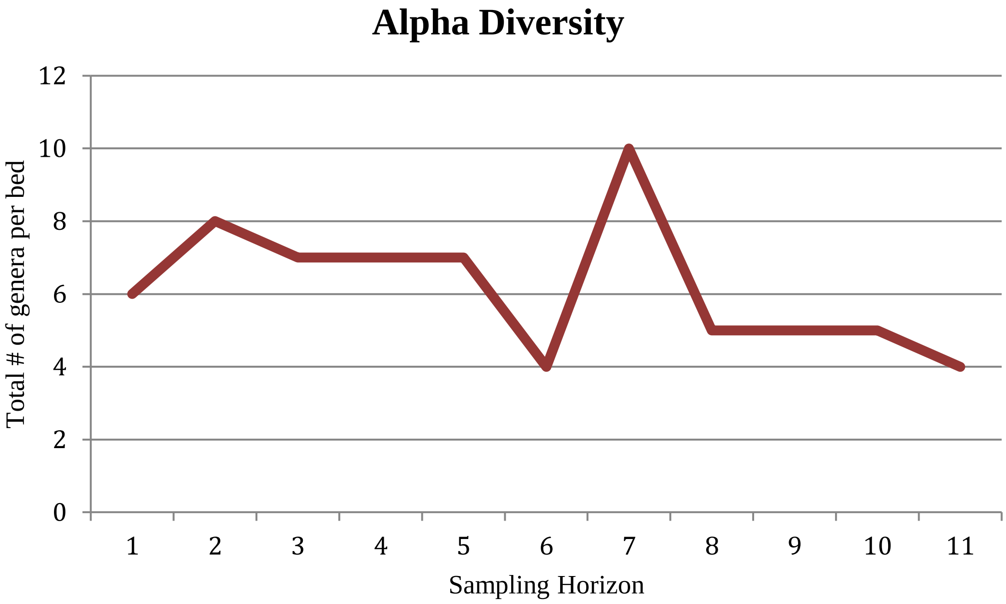


Figure 19. Alpha diversity of sampling horizons 1-11.

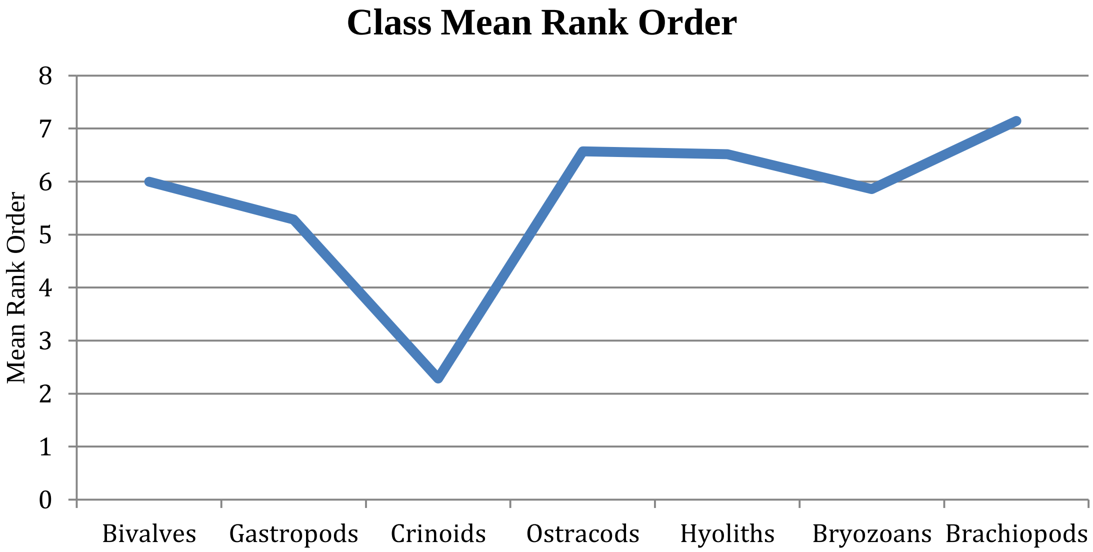


Figure 20. Mean rank order values of the different faunal classes recorded throughout sampling horizons 1-11 in the Pampa de Tepuel Formation. Values closer to 1 indicate the most abundant taxa.

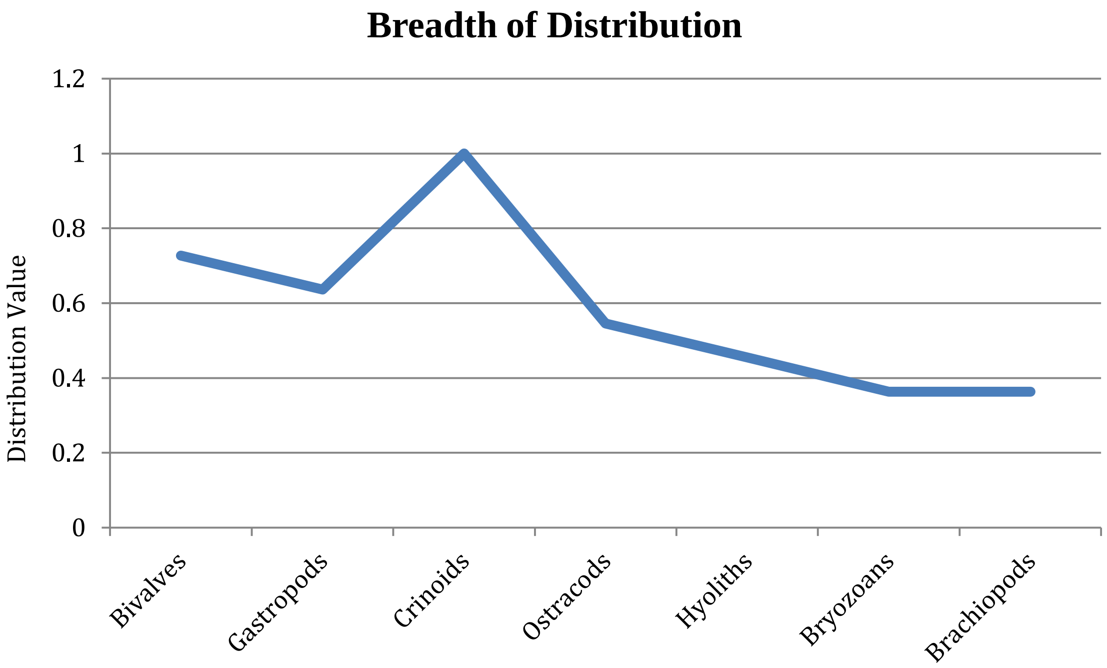


Figure 21. Breadth of Distribution of the different faunal classes recorded throughout sampling horizons 1-11 in the Pampa de Tepuel Formation. Values equal to 1 indicate the taxon was present in all sampling horizons.

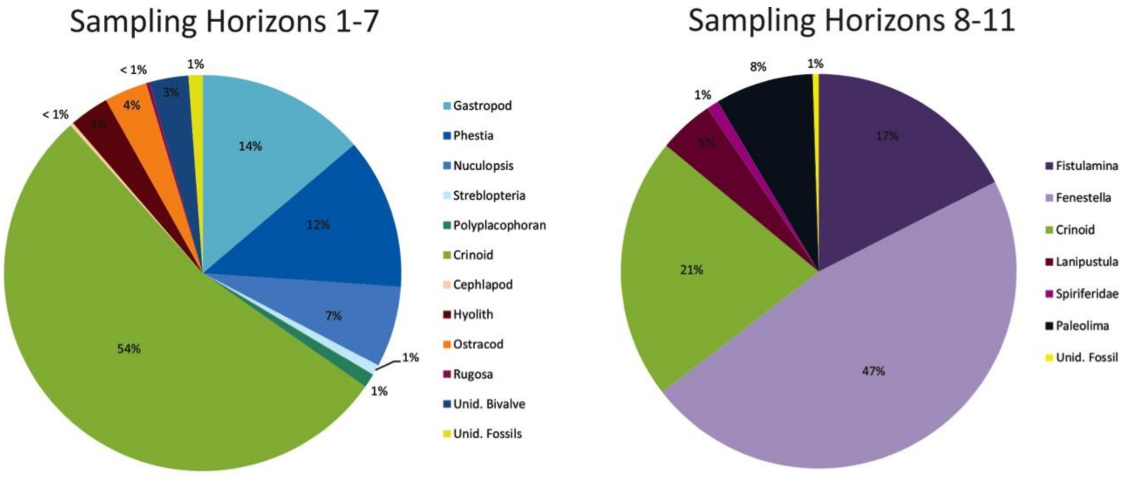


Figure 22. Comparison of the relative abundance of individuals in sampling horizons 1-7 and relative abundance of individuals in sampling horizons 8-11.

are represented. There are no noticeable trends throughout the sampling horizons 1-7. Sampling horizons 8-11 represented a different community composition, as they were dominated by bryozoans (specifically *Fistulamina* and *Fenestella*) and brachiopods (Fig. 22). The abundance of bryozoans remained consistent through out these horizons, comprising over 70% of total taxa. Small populations of crinoids are also represented, but there was an absence of gastropods, bivalves, and other taxa that were present and abundant in the sampling horizons 1-7 (with one exception; *Paleolima*, a bivalve, appeared abruptly in sampling horizon 11).

Rarefraction curves (e.g. an indication of how accurately a faunal survey actually represents the fauna in a particular area) were generated. Since the species accumulation curve eventually flattened out, the results showed that a reasonable number of individuals were collected and the samples collected in the field adequately represented the community (Appendix B).

Diversity indices were calculated in order to determine the richness of organisms throughout the sampling horizons. Shannon-Weiner index values (maximum value = ln(S), S=species richness) varied through the sampling horizons, ranging from higher diversity at 1.64 to lower diversity at 0.90 (Fig. 23). Diversity in sampling horizons 1-7 remained above 1.27, with a drop in diversity in sampling horizon 4. Diversity values remained around 1.2-1.4 in sampling horizons 8-11, but dropped below 1.0 in sampling horizon 10. Diversity values for Simpson's Diversity Index (values closer to 1 represent higher diversity) represented similar trends, with a slight drop in diversity in sampling horizons 4 and 10 (Fig. 23). The evenness values (e.g. measures how evenly distributed the composition of species is) for each sampling horizon also mimicked these results (Fig. 23). Certain genera were slightly more dominant in sampling horizons 4 and 10, which affected the diversity trends within stratigraphic sections. Calculated Z-Test values (Appendix B) showed no statistical difference between sampling horizons. However, it was important to not only rely on numerical statistics to make interpretations, but to also look at ecological differences in a community.

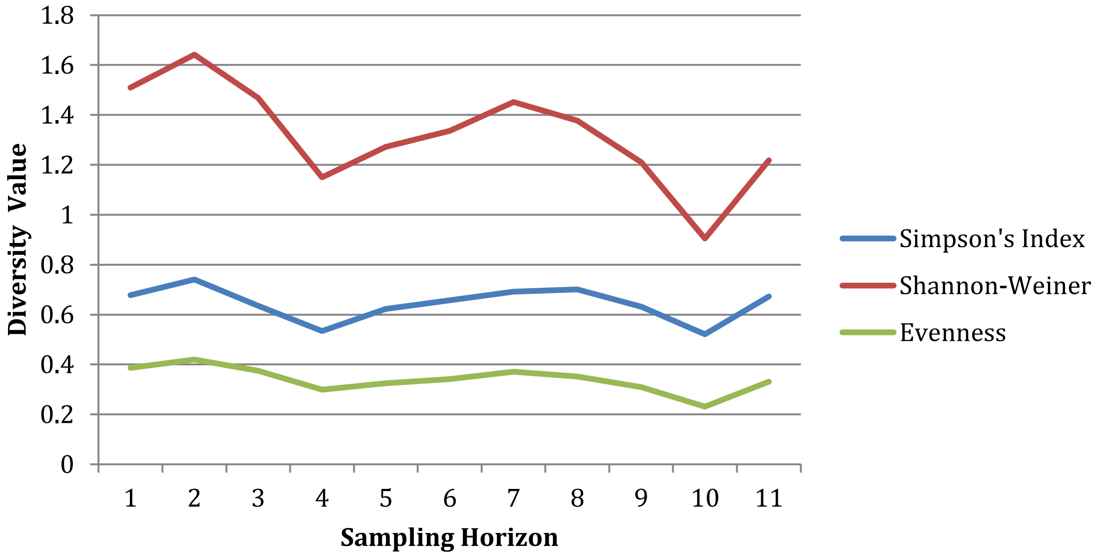


Figure 23. Comparison of different diversity indexes: Simpson’s Index, Shannon-Weiner Index, and evenness. In Simpson’s Index, values closer to 1 indicate higher diversity. In Shannon-Weiner Index, higher values indicate higher diversity ($H_{max} = \ln(S)$, S= species richness). In evenness, values closer to 1 indicate a more evenly distributed community with no one genus dominating.

4.3.2 Ecological Analysis

The lower sampling horizons showed a numerical dominance in sessile, epifaunal, suspension feeders that represented over 50% of the community (Fig. 24). There was a small proportion of faculatitvely mobile, infaunal and epifaunal suspension feeders (33%). The upper sampling horizons were dominated by sessile, epifaunal, suspension feeders comprising 91% of the community. Modes of life throughout the lower sampling horizons were more diverse than those in the upper sampling horizons, with a small percentage of detrital feeders (sampling horizons 1, 2, 3, 5, and 7) and a nektonic carnivore (sampling horizon 4). Salinity relationships among the groups of sampling horizons were also compared. Stenohaline organisms dominated both sampling horizons 1-7 and sampling horizons 8-11 (Fig. 25). However, there were more euryhaline organisms present in sampling horizons 1-7 at 37%, whereas euryhaline organisms represented less than 10% of the community in sampling horizons 8-11.

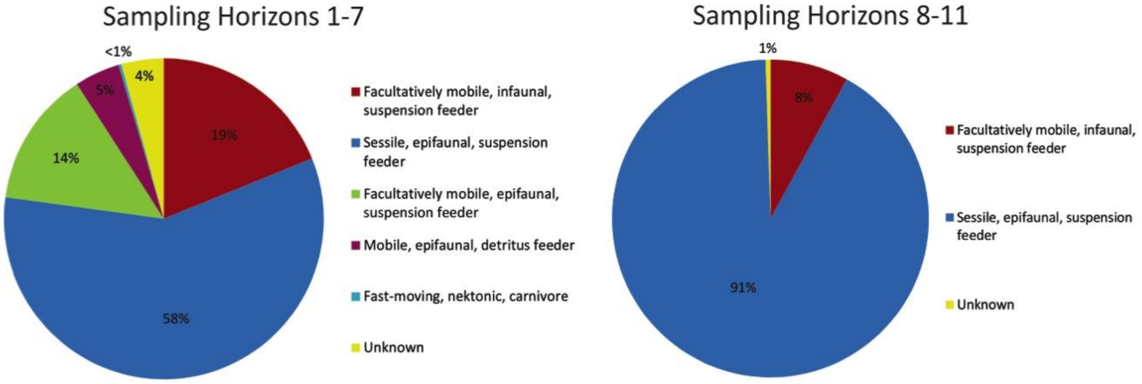


Figure 24. Comparison of the relative abundance of the individuals in sampling horizons 1-7 and sampling horizons 8-11, displaying various life modes as a potential indicator for overall environmental change throughout the Pampa de Tepuel Formation.

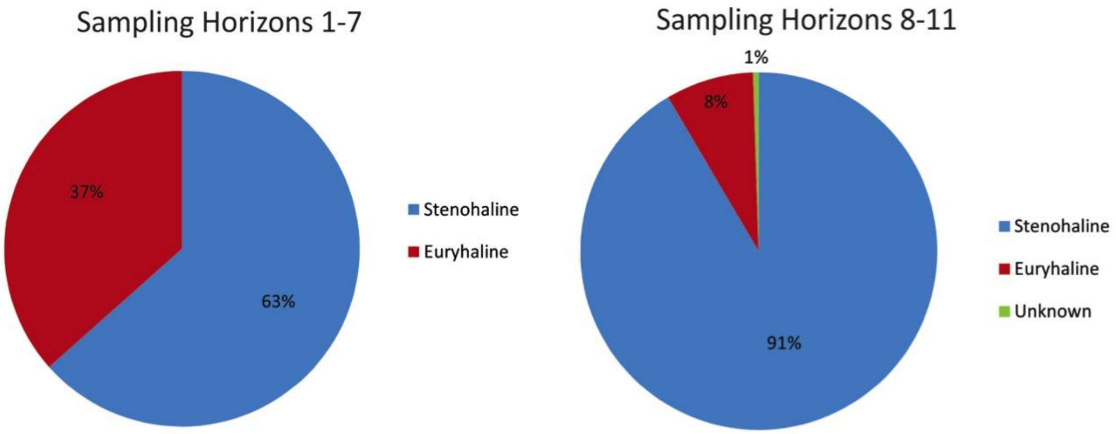


Figure 25. Comparison of the relative abundance of the individuals in sampling horizons 1-7 and sampling horizons 8-11, displaying various salinity tolerances as a potential indicator for water salinity change throughout the Pampa de Tepuel Formation.

5. DISCUSSION

5.1 Environmental Interpretations

Results presented here suggest that the base of the Pampa de Tepuel Formation is comprised of glacially-influenced marine strata deposited on a basinal slope beyond the shelf-slope break (Pauls, 2014). First, a possible glacial signature is interpreted throughout the lower stratigraphic section (Fig. 8) within the diamictite lithofacies. Near the base of this measured section, a thick diamictite (approximately 28 meters) contained quartzite and granite clasts, with striated clasts present in the surrounding scree. The diamictite at 55 meters in stratigraphic section 1 contained pebbles with striations oriented in all directions; interpreted here as ice-rafted debris. The stratified diamictite just below sampling horizon 3 contained dropstones that pierce stratification. These diamictites were deposited either as rain out from meltwater plumes and deposition of pebbles as iceberg rafted debris, or as resedimented (debris flow) deposits. Regardless, the occurrence of striated clasts and “dropstones” indicated a contemporaneous glacial signal within this glacially-influenced marine deposit. These characteristics indicated an active clastic depositional setting (movement and deposition of sediments by small debris flows, meltwater plumes, and iceberg rafted debris) that likely would have impacted the benthic fauna living there.

The fossiliferous mudstone lithofacies dominated stratigraphic section 1, indicating more of an inactive or quiet, calm marine environment below storm wave base. These intervals of diamictite, conglomerate, sandstone, and mudstone, suggested a fluctuation between an active and inactive glaciomarine environment. While the strata from stratigraphic section 1 seem to have been influenced by glaciation, the paleocommunities were likely located tens of kilometers away from an active glacier that would have been located somewhere on the shelf (Fig. 26). Hummocky cross stratification and wave-ripple cross-stratified sandstones at the top of section 1 indicated deposition above storm wave base. Thick wave-ripple cross-stratified sandstone better exposed elsewhere along the ridge capping this section indicated deposition on a shoreface above normal wave base. These sandstones represented progradation of the shelf across slope mudstones in this area. Although not enough evidence was collected to determine whether seaward extension of the shelf was the result of normal regression or progradation of the shelf edge during a relative sea-level fall, the abrupt change from shelf mudstone to wave-reworked sandstones containing an absence of mudstone interbeds was suggestive of a forced regression (cf. Plint, 1988; Posamentier and Allen, 1999; Clifton, 2006).

Stratigraphic section 2 was deposited several hundred meters higher stratigraphically than section 1. Due to the absence of diamictite and striated lonestones, no glacial indicators were found in this section. It is interpreted that strata in stratigraphic section 1 were deposited slightly closer to glacial influences in the region and therefore more likely to have been affected by meltwater plumes, whereas stratigraphic section 2 was deposited in calmer, clearer water farther from glacial influences and other stressful physical processes (Fig. 26). The sandstone and conglomerate facies deposited near the top are interpreted as another abrupt change from shelf mudstone to a coarse clastic facies, suggesting a possible forced regression (cf. Plint, 1988; Posamentier and Allen, 1999; Clifton, 2006).

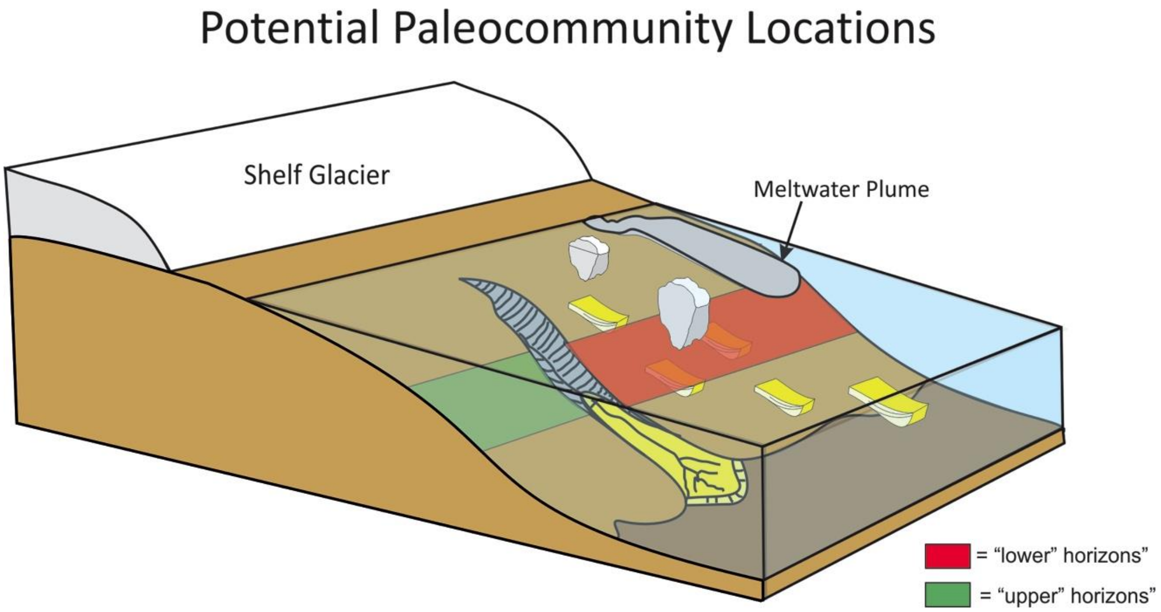


Figure 26. Comparison model of the potential paleocommunity location of the lower horizons (red) and the upper horizons (green). Modified from Isbell.

5.2 Paleoecological Interpretations

Multivariate data analysis suggested two groupings of the sampling horizons. All cluster analyses performed grouped sampling horizons 1-7 and sampling horizons 8-11 together based on similarity (Fig. 17). Taxonomic composition was similar among sampling horizons grouped in the same cluster of the dendrograms, implying that the "upper sampling horizons" (8-11) were dissimilar in taxa compared to the "lower sampling horizons" (1-7). The detrended correspondence analysis also implied a separation between the upper and lower sampling horizons. The lower horizons were clustered closely together based on axis 2, and slightly spread apart based on axis 1. The upper horizons were grouped closely together based on axis 1, but were spread a great distance apart based on axis 2 (Fig. 18). Axis 1 may account for a paleoenvironmental gradient; the lower sampling horizons had been influenced by indirect glacial effects and sedimentation due to debris flows, whereas the upper horizons were isolated from those effects. Axis 2 may represent the similarity of genera composition; the lower seven sampling horizons were more similar in terms of generic composition and were clustered close to one another, whereas the upper four sampling horizons are dissimilar and have a greater distance between them.

Differences in the lower and upper sampling horizons can be explored by first evaluating the limiting factors in an environment. Factors such as water temperature, oxygen concentrations, water salinity, substrate, turbidity, and nutrients affect organisms' interactions within a community, as well as their physiological processes (Anderson, 1983; Dayton, 1990; Carey, 1991; Clarke, 1993; Brenchley and Harper, 1998) (Fig. 27). If any environmental factor shifts, it becomes a stressor and can affect community diversity. The presence of stenohaline groups (taxa that cannot tolerate a large range of salinities), such as brachiopods, corals, echnioderms, ammonoids, and larger benthic forminifera, represent normal marine waters (Brenchley and Harper, 1998; Pagani and Taboada, 2010). In stressful marine environments, there can be an increase in eurytopic (taxa able to tolerate a large range of environments) (Brenchley and Harper, 1998) and opportunistic taxa (taxa able to exploit vacant niches, quickly achieve high abundances, and invade unstable faunas) (e.g. Levinton, 1970; Hallam and Wignall, 1997; Rodland and Bottjer, 2001). Comparing feeding, mobility, substrate, and salinity preferences of dominant genera in the upper and lower sampling horizons can provide further insight to these paleoecological differences.

Salinity is the first limiting factor to assess in these communities. Neither brachiopods, ammonoids, nor forminifera (stenohaline taxa that are characteristic of normal marine communities) (Brenchley and Harper, 1998) were observed in the lower sampling horizons. The fauna represented a community with 63% stenohaline organisms and 37% euryhaline organisms (Fig. 25). This euryhaline percentage is due to the large abundance of bivalves observed throughout the first 7 sampling horizons. The presence of euryhaline taxa suggested that there may have been fluctuating environmental conditions, causing an increase in organisms that are better equipped to tolerate salinity changes. On the contrary, the upper sampling horizons had over 90% stenohaline organism and very few euryhaline organisms (8%). The abundance of euryahline organisms in the lower horizons compared to the upper horizons was statistically significant (z-value: 7.2, p-value = <0.0001). This data suggesed that salinity was potentially more stable in the upper sampling horizons than it had been in the lower sampling horizons.

Freshwater influxes from glacial melt often decrease ocean salinity, while the formation of sea ice can release brine and increase ocean salinity (Eicken, 1992). Glacial meltwater into a deep water basin may have had little influence on bottom waters as it would be more buoyant than the sea water. The paleocommunities in this study were deposited below storm wave base and the influx of meltwater in a surface plume probably had little mixing with water below the pycnocline (depths less than 10-30 m) (Cottier et al., 2010; Inall and Gillibrand, 2010). If there were fluctuations in salinity within these communities, a more probable explanation would be due to the formation of sea ice. The formation of sea ice releases brine that sinks into colder waters potentially raising the salinity of basin bottom waters and influencing the fauna living there (Cottier et al., 2010).

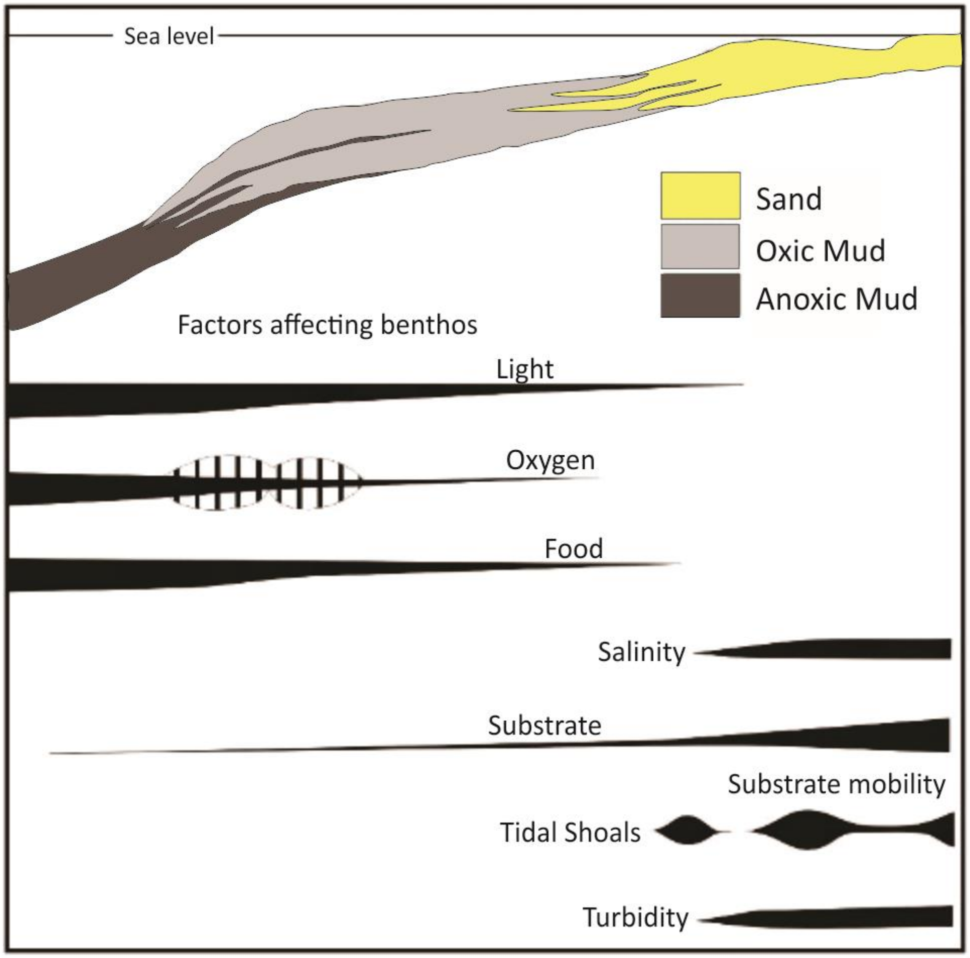


Figure 27. Various environmental factors that affect benthic organisms based on where they reside beneath sea level. Modified from Brenchley and Harper, 1998.

Colder ocean temperatures often accompany this glacial regime and are coupled with high nutrient supply due to increased mixing within the water column (e.g. Kirchman et al., 2009). A higher nutrient supply can appear beneficial to the productivity of the organisms; however, the episodic conditions often produce low diversity (e.g. Brenchley and Harper, 1998; Kirchman et al, 2009). Lower water temperatures, influxes in ocean salinity, and fluctuations in nutrient supply could have potentially attributed to the low biodiversity observed throughout the base of the Pampa de Tepuel Formation.

The most diverse and abundant fossil groups found within the Tepuel-Genoa Basin are brachiopods, bryozoans, gastropods, and bivalves (Pagani and Taboada, 2010). However, this composition was not observed throughout the paleocommunities near the base of the Pampa de Tepuel Formation in this study. For example, there was an absence of brachiopods and bryozoans within lower sampling horizon communities. *Lanipustula* brachiopods were expected within sampling horizons 1-7, but were not observed. This environment may not have been preferable for *Lanipustla* or immigration of these brachiopods into this region may not have taken place yet. While *Lanipusutla* brachiopods were absent, other organisms included in the biozone, such as bivalves (*Phestia* and *Nuculopsis*), crinoids (*Camptocrinus*), and gastropods, dominated these horizons (Fig. 22). However, diversity was low and the fauna seemed relatively impoverished for paleocommunities within the Pampa de Tepuel Formation. These characteristics, including the small body size of fauna, were likely a function of fluctuations and stressors in environments located on basinal slopes beyond the shelf slope break during both an interval that was glacially influenced and an interval when glacial signatures were absent (e.g. Gutt, 2001; Wlodarska-Kowalczek et al., 2005).

Bivalves are more diverse than brachiopods in central Argentina (Sterren and Cisterna, 2010). This diversification of bivalves was generally reflected in the lower seven sampling horizons of the Pampa de Tepuel Formation. Nuculoids, whom often inhabit slightly dysaerobic, organic rich substrates, and *Phestia*, often associated with stress conditions and found in opportunistic assemblages (Sterren, 2000; Simanauskas and Cisterna, 2000; Lebold and Kammer, 2006; Sterren and Cisterna, 2010), were the dominant bivalve groups within the lower sampling horizons. The presence of an opportunistic assemblage could further indicate highly stressed and unstable ecological conditions for these paleoecommunities. Glacial sedimentary records in the Paganzo, Río Blanco, and Calingasta-Uspallata basins in western Argentina are associated with low diversity faunas and extreme temperature fluctuations, further facilitating the dominance of bivalves compared to brachiopods (Sterren and Cisterna, 2010). Even though bivalves and brachiopods exhibit a large number of morphological similarities, they often have different metabolic demands; bivalves have the ability to withstand a wider range of environmental conditions and exploit a greater number of habitats than brachiopods (e.g. Steele-Petrovic, 1977; Sterren and Cisterna, 2010). These conditions may explain why bivalves dominated the lower seven sampling horizons and brachiopods remained absent throughout the base of the Pampa de Tepuel Formation.

It has also been suggested that along with salinity, turbidity affected the lower sampling horizons greater than the upper sampling horizons. The lower sampling horizons contained higher abundances of facultatively mobile or mobile taxa, whereas the upper horizons were dominated by sessile, epifaunal, suspension feeders (Fig. 24). The occurrence of mobile organisms could further suggest more active, stressful physical processes in the lower horizons. Since these organisms have the ability to move, they could have potentially adapted better to their shifting habitats (e.g. Reynolds and Casterlin, 1985; Hirzel, 2004).

Bryozoans, crinoids, and brachiopods dominated the upper sampling horizons horizons, while bivalves remained absent (excluding sampling horizon 11) (Fig. 24). Bryozoan genera are sensitive to particular environments; they are not common in areas of high sedimentation and prefer calm, clear waters for attachment and feeding purposes (Schopf, 1969; Taylor, 2005). Their presence would have indicated a calm, quiet marine depositional environment. The return of the highly productive *Lanipustula* brachiopods in the upper sampling horizons may have indicated the transition to the *Lanipustula* biozone that dominated the Pampa de Tepuel Formation. The bivalve *Paleolima* appeared in the uppermost sampling horizon. The arrival of this epifaunal, facultatively mobile bivalve could have suggested migration to this environment due to changes in climate; a biostratigraphic study on *Paleolima* would be necessary in order to support latitudinal migration. However, these upper sampling horizons appeared to have been more stable than the lower sampling horizons and resided in a more productive paleoenvironment with fewer stressors and no glacial influences. A paleoecological reconstruction of the lower paleocommunity (Fig. 28) and upper paleocommunity (Fig. 29) showed differences in benthic ecological organization.

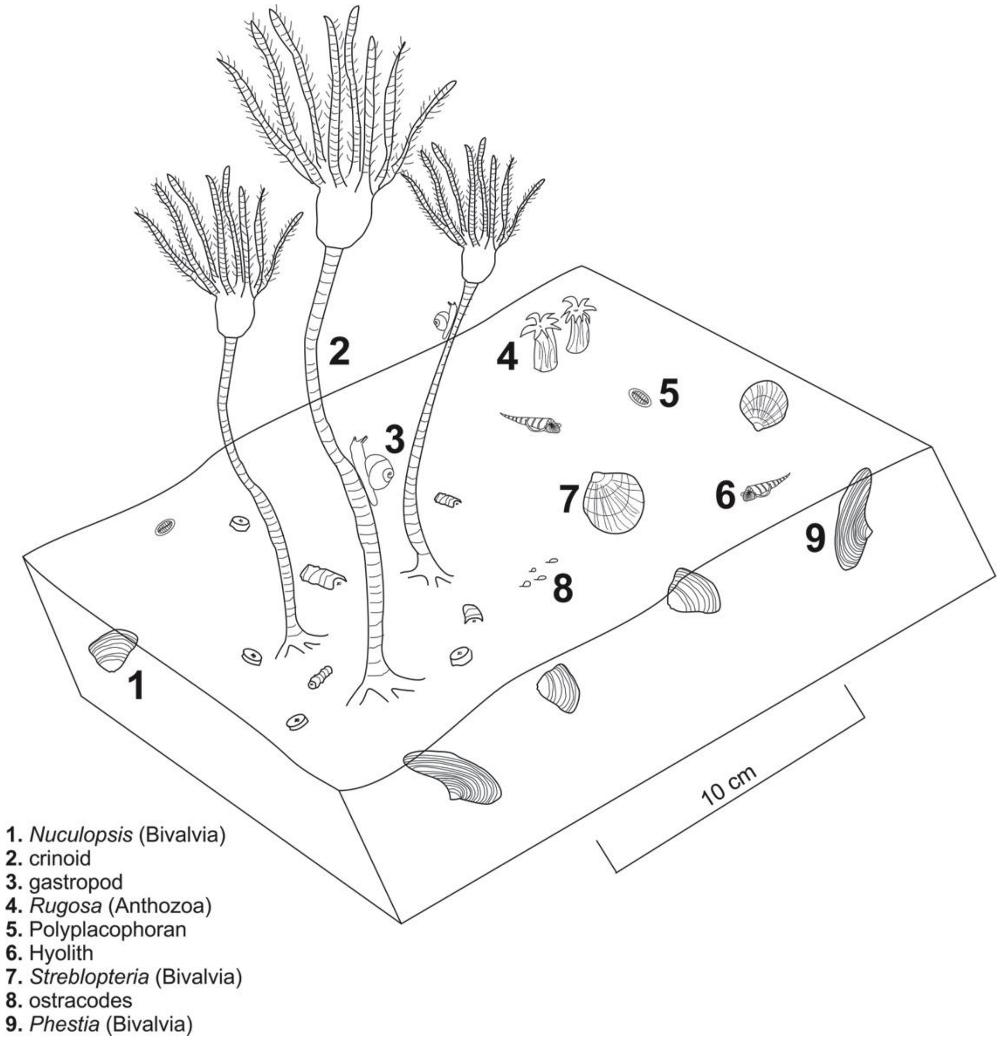


Figure 28. Paleoecological reconstruction of lower sampling horizons during the LPIA.

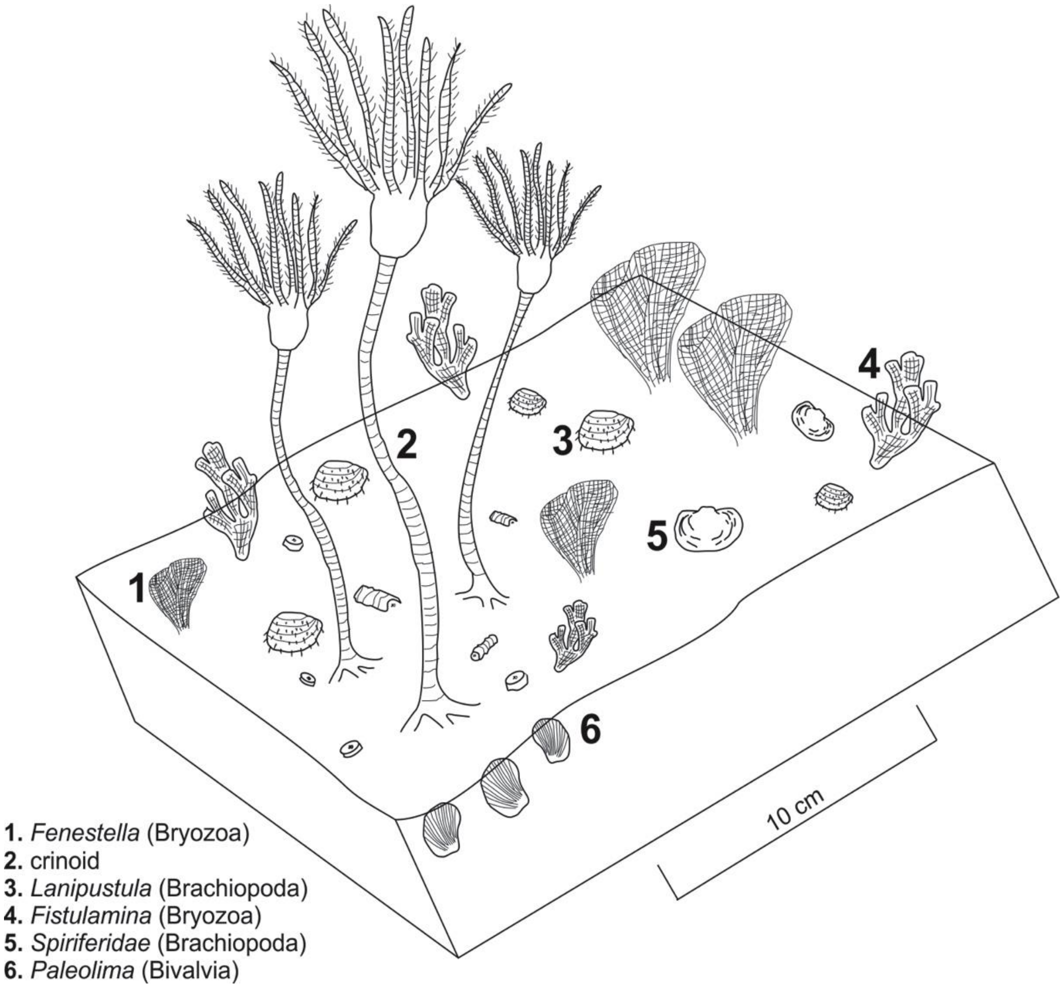


Figure 29. Paleoecological reconstruction of upper sampling horizons during the LPIA.

5.3 Tepuel-Genoa Basin Study Comparisons

Two additional paleoecological studies were completed in the Tepuel-Genoa Basin by Dineen in 2010 and Pauls in 2014. The relative abundances of shelled marine invertebrates varied among all studies, with different organisms dominating the sampling horizons (Fig. 30). Paleoecommunities from this study had lower evenness than previous studies conducted by Dineen and Pauls (Fig. 31). Communities sampled by Paul and Dineen had higher evenness, but also stronger variation throughout their sampling horizons.

Dineen's (2010) study in the Tepuel-Genoa Basin focused on the lower member of the Pampa de Tepuel Formation, where deposition also took place in a deep marine environment, possibly on a basin slope or basin floor setting. She interpreted the environment to have been very distal to the glacial margin due to the absence of glacial structures in sediments. The paleoecology of these communities varied from the results in this study: rhynchonelliform brachiopods were overwhelming dominant, followed by bryozoans, bivalves, crinoids, and corals. The only mode of life present in Dineen's (2010) succession was sessile, epifaunal suspension feeders, indicating a stable environment with little turbidity and slow sedimentation rates. Opportunistic fauna were not present in the sampled locations in this study, suggesting the fauna were not likely suffering from stressful conditions.

The paleoecology of the faunas reported on by Dineen (2010) is similar in composition to the upper sampling horizons in this study. Environments observed in the upper sampling horizons in this study and in Dineen's (2010) sampling horizons are interpreted to have been stable, deep marine with a lack of wave ripples and hummocky cross-bedding.

The alpha diversity values in the study herein were lower than those recorded from horizons sampled in Pauls' (2014) study (Fig. 32). Pauls' (2014) sampling horizons were likely located in the upper portion of the *Lanipustula* biozone higher in the Pampa de Tepuel Formation and represented a diverse faunal composition. Her established communities were interpreted to have been in a stable, lower slope and basin floor environment. Pauls' (2012) results consisted of taxa that were absent from sampling horizons near the base of the formation including ostracods, which accounted for over 50% of organisms in 4 of the 6 sampling horizons. The upper sampling horizons in Pauls' (2014) study included opportunistic and mobile fauna, including the ostracod *Graphiadactylloids* and the bivalves *Phestia* and *Nuculopsis*. Pauls' (2014) fauna was also larger in size (mean size = 20-25 mm) than the fauna observed in this study (mean size = 5-15 mm), suggested that environment had an influence on physiological growth. Paleoecological results differed throughout the Tepuel-Genoa Basin, suggesting a possible shift in marine environments and glacial influences.

Paleocommunities from the lower sampling horizons within this study have a more impoverished, opportunistic fauna with environmental stressors (possibly due to distal glacial influences and or due to growth in a more active environment with higher sediment fluxes) than studies previously conducted by Dineen and Pauls in different parts of the Tepuel-Genoa Basin. These results suggested that the near-field fauna had different ecological responses to physical processes throughout the formation.

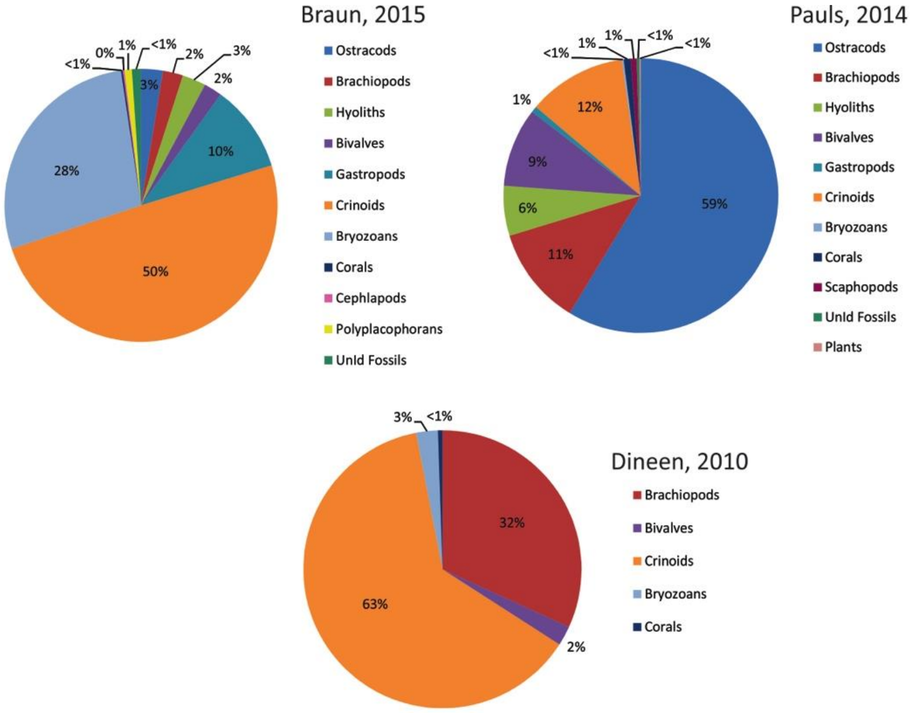


Figure 30. Comparison of relative abundances in Braun, Pauls, and Dineen's studies in the Pampa de Tepuel Formation.

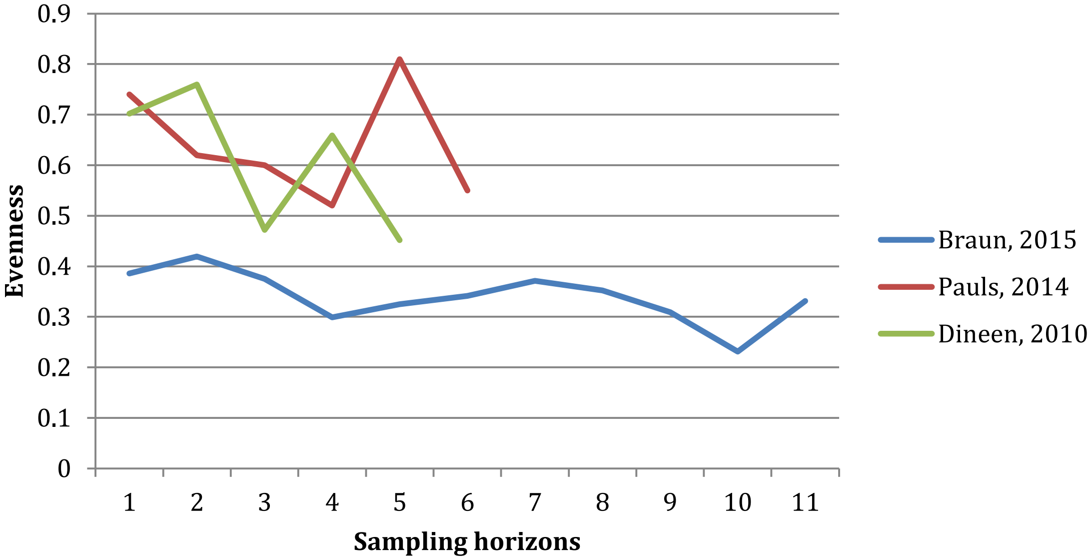


Figure 31. Comparison of evenness between Tepuel-Genoa Basin studies by Dineen (2010), Pauls (2014) and Braun (2015).

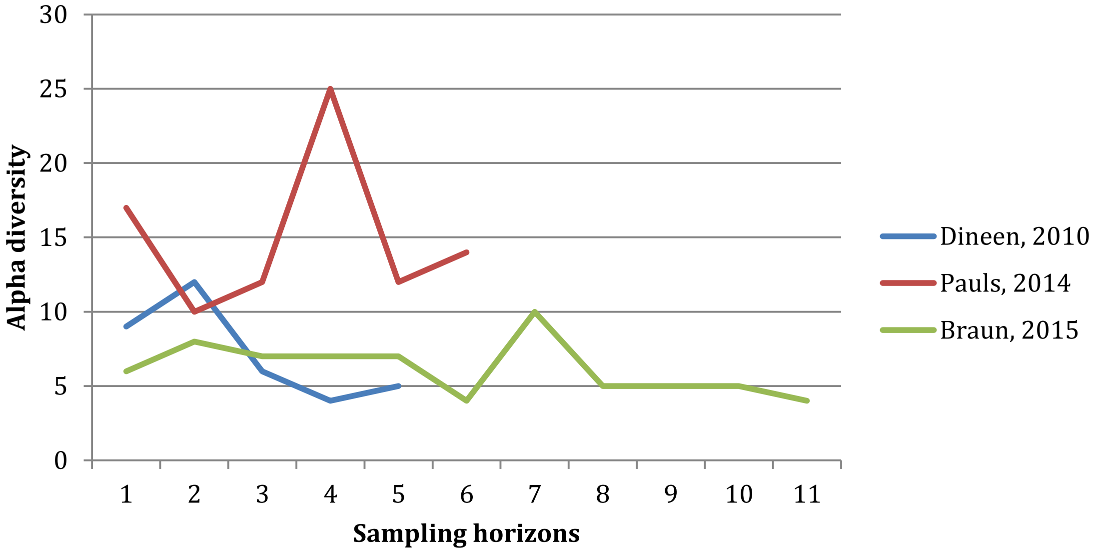


Figure 32. Comparison of alpha diversity between Tepuel-Genoa Basin studies by Dineen (2010), Pauls (2014) and Braun (2015).

5.4 Regional Comparisons

Regional studies on the LPIA are necessary because regional diversity and ecological patterns do not always parallel global diversity (Heim, 2009; Waterhouse and Shi, 2010). The results of this near-field study compared with results from previous far-field studies suggest that the effects of the LPIA on taxonomic abundance varied with latitude. In Upper Mississippian strata from the Illinois Basin, USA (a far-field locality), it was concluded that eurytopes (broadly-adapted taxa) increased in abundance following the onset of the LPIA (Bonelli and Patzkowsky, 2008, 2011). It was hypothesized that, due to the increase in eurytopy, high levels of faunal persistence (taxa that endured and survived times of environmental hardship) occurred in low latitude regions throughout the LPIA (Holterhoff, 1996; Olszewski and Patzkowsky, 2001b). Other results at the

Mississippian/Pennsylvanian boundary in southwestern Arkansas and northeastern Oklahoma, USA suggest that although there was a taxonomic turnover event resulting from brachiopod taxa shifting their latitudinal ranges, there was statistically no decrease in total diversity. This turnover event was driven by extirpation (the removal of a certain brachiopod genera), followed by latitudinal range shifts of taxa to the equator (Heim, 2009).

Overall global biotic responses during the LPIA are comparable to the Illinois Basin results, indicating that the onset of glaciation in the late Mississippian weakened latitudinal diversity gradients, with little faunal differentiation among depositional environments and an increase in overall eurytopic taxa abundance (Powell, 2005, 2007). This may have been due to the loss of stenotopic taxa that may have not been adapted to fluctuations in sea level and climate (Powell, 2005, 2007).

Converse to the results from far-field basins, the paleoecological near-field study herein combined with other previous studies from the Tepuel-Genoa Basin, indicated a change occurred in faunal diversity and evenness over a paleoenvironmental gradient. Alpha diversity remained relatively low near the base of the Pampa de Tepuel Formation, with the presence of many opportunistic fauna (Nuculoids), suggesting a dynamic, stressful paleoenvironment (Sterren, 2000; Simanauskas and Cisterna, 2000; Lebold and Kammer, 2006; Sterren and Cisterna, 2010). These observations indicated that there are direct and indirect environmental effects (i.e. debris flows and glacial influences) at both the community level and individual level. The shift in diversity throughout the Tepuel-Genoa Basin differed from Heim's (2009) far-field study in North America, in which total diversity remained relatively constant during the LPIA. It can be concluded that due to the changes in diversity and faunal composition throughout the Pampa de Tepuel Formation, near-field ecosystems from this study responded differently to physical processes experienced during the LPIA than previously studied far-field ecosystems. It is suggested that near-field ecosystems are more sensitive to the physical environments, whereas far-field ecosystems may have responded more to global changes in temperature.

5.5 Modern Global Comparisons

Antarctic marine invertebrate communities have many characteristics that distinguish them from temperate and tropical communities. Antarctic benthic shelf faunas are about five times slower in growth and metabolic rates compared to temperate ones (e.g. Pearse et al., 1991; Brey and Clarke, 1993; Arntz et al., 1994, Peck and Robinson, 1994; Chapelle and Peck, 1995; Peck et al., 2000; Peck, 2002; McClintock et al., 2008a). Invertebrates in this polar region are also highly stenothermal (exhibiting extreme temperature sensitivity) (Peck, 1989; Peck et al., 2002; Peck et al., 2004b) and studies suggest that an increase in global ocean temperatures will inhibit invertebrates to perform essential biological functions for survival (Kidawa and Janecki, 2011). Southernmost high latitude faunas were also observed to be less diverse than lower latitude faunas, with possible reduced rates of speciation and extinction (Gutt, 2001; Clarke et al., 2004). It has also been proposed that the waxing and waning of the Antarctic ice cap may influence benthic species distributions and may have already fragmented populations and forced them down the continental slope (Clarke and Crame, 1989, 1992). The Southern Ocean surrounding Antarctica also contains low phytoplankton productivity, restricted to 2-3 months a year, causing a decrease in food availability (Barnes and Clarke, 1995b; Peck, 2005). This seasonality indirectly restricts glacially-influenced communities' physiological development. Ultimately, it is suggested that the communities of the Antarctic reflect an ecological response to the glacial-marine environment, combined with an evolutionary response to lack of predators (Clarke et al., 2004).

Modern Antarctic communities are currently experiencing effects from recent climate change on the phenology, composition, distribution, and of species (Walther et al., 2002; Parmesan, 2006). Global seawater has warmed by approximately 0.6°C over the past 100 years (Levitus et al., 2000) and the projected increase in sea level will rise by 18-59 cm by the end of the 21st century (IPCC, 2014). Numerous Antarctic plants and invertebrates have exhibited a latitudinal distribution change due to increased ocean temperatures (Walther et al., 2002).

It has been suggested that modern Antarctic benthic shelf faunas resemble the Paleozoic Fauna with their lack of several primary predator groups, the dominance of suspension feeders, and abundant crinoid populations (Dell 1972, Aronson et al. 1997). Communities within the Pampa de Tepuel Formation exhibited these key characteristics, along with small body sizes and low taxonomic diversity. While ammonoids were commonly found in far-field LPIA studies (e.g. Veevers and Powell, 1987; Bahrami, et al., 2014), large populations of these organisms were absent from the Pampa de Tepuel Formation, as well as in other near-field studies (Clapham and James, 2008). Sessile, epifaunal, suspension feeders dominated the communities near the base of the formation, possibly reflecting a lack of large durophagous predation populations due to cold ocean temperatures (Aronson and Blake, 2001). A decrease in overall temperatures during this time is suggested by studies from Henry et al. 2008, Marenssi et al., 2005, and Gulbranson et al. 2010 that record glaciation in northwest Argentina during the latest

Mississippian and earliest Pennsylvanian, well documented by similarly U-Pb calibrated low-eusastic reconstructions (Bishop et al., 2009; Eros et al., 2012). It is also observed that glacial-marine environments become more stable with increasing depth (Gutt, 2001), possibly providing an explanation on why the upper sampling horizon community is dominated by stenohaline communities and turbidity-sensitive bryozoan populations. Glacial retreats and advances could also explain why a more stenohaline community existed on the slope; the communities were driven to deeper waters from the continental shelf from environmental perturbations.

Not only are these Carboniferous communities similar to Antarctic communities, they also parallel modern Arctic benthic communities off the coast of Kongsfjord, Norway (Wlodarska-Kowalczuk et al., 2005). Communities found near glacial bays are also dominated by small-bodied, deposit feeders with low species diversity and richness (Wlodarska-Kowalczuk et al., 2005). From this study in the Tepuel-Genoa Basin, it is suggested that Paleozoic marine invertebrate communities in a near-field region during the LPIA are sensitive to paleoenvironmental conditions in contrast to time-equivalent far-field ecosystems, and thus provides a way to assess global-scale comparisons of high- and low-paleolatitude ecologic change. It is also important to consider regional differences when using the late Paleozoic communities in Gondwana as an analogue for modern Antarctic ecosystems. Factors such as ocean circulation patterns, differences in latitude, and glacier characteristics must also be considered.

6. CONCLUSION

The climatic and environmental perturbations during the LPIA had different impacts on the ecosystem and differed between regions. Previous studies on far-field faunas have been used as a global proxy for paleocommunities during the duration of the LPIA. Since regional patterns do not always parallel global patterns (Heim, 2009; Waterhouse and Shi, 2010), the Tepuel-Genoa Basin provides an excellent opportunity to evaluate Mississippian to Permian depositional history and paleoecological records from a near-field region. High paleo-latitude studies coupled with low paleo-latitude studies can be used to produce a more robust understanding of the overall ecological impacts of the LPIA.

Paleocommunities observed in this study differed from one another. The lower sampling horizons are hypothesized to be more glacially-influenced than the upper sampling horizons, yet still deposited distally to the ice center on a lower shelf/slope setting. Stratigraphic evidence for these inferences was the diamictite strata containing dropstones and the occurrence of striated pebbles. It was hypothesized that the upper sampling horizons were deposited in a calmer, clearer marine slope setting due to the high abundance of bryozoan populations and absence of hummocky cross stratification and wave ripples.

The paleocommunities studied herein were interpreted as somewhat impoverished and less diverse compared to previous studies conducted in the Pampa de Tepuel Formation. Crinoids and bivalves dominated the lower paleocommunities, but other key members of the Paleozoic Fauna, such as brachiopods and bryozoans, were absent. This composition suggests that these horizons were undergoing more active environmental changes (such as meltwater plume rain-out and small debris flows) than the upper horizons were experiencing. There was also a statistically significant difference of euryhaline organisms present between the upper and lower sampling horizons, suggesting the upper sampling horizons experience less fluctuations in ocean salinity. The presence of key opportunistic bivalves, such as *Nuculopsis* and *Phestia*, were also abundant in the lower sampling horizons suggesting vacant niche invasion during times of environmental stress. These communities were interpreted to be less stable than other communities studied by Dineen (2010) and Pauls (2014), as their communities were higher in alpha diversity, more even, and larger in overall body size.

From this study, it is inferred that far-field faunas during the LPIA responded differently to climate change than near-field faunas. Far-field studies concluded that there was little change in overall diversity throughout the LPIA and that there were high levels of faunal persistence in the form of eurytopic communities. The near-field communities in the Tepuel-Genoa Basin changed in taxonomic composition throughout the Pampa de Tepuel Formation, with certain genera disappearing and reappearing depending on the environment. The communities observed in this study were also compared to modern Antarctic fauna due to the presence of abundant suspension feeding populations (specifically crinoids), low diversity, and lack of primary predators (Dell 1972, Aronson et al. 1997). It is suggested that these communities could potentially aid us in understanding the biotic responses from modern Antarctic communities undergoing modern climate change.

The conclusions from this paleoecological study help to further understand the biotic responses of near-field faunas in Gondwana during the LPIA. Communities that are glacially influenced seem to be less stable and suffer greater ecological effects, at least temporarily, than those located farther from ice centers. This study also aids in our global understanding of how biotic responses to climate fluctuations differ between regions. The paleoecology of communities during the LPIA is most strongly influenced by changes in ocean temperatures, salinity, turbidity, and nutrient availability.

7. REFERENCES

ANDERSON, F.E., 1983, The northern muddy intertidal: seasonal factors controlling erosion and deposition – a review. Canadian Journal of Fisheries and Aquatic Sciences 40, 143-159.

ANDREIS, R.R., ARCHANGELSKY, S., GONZÁLEZ, C.R., LÓPEZ GAMUNDI, O., SABATTINI, N., 1987, Cuenca Tepuel–Genoa. In: Archangelsky, S. (Ed.), El Sistema Carbonífero en la República Argentina. Academia Nacional de Ciencias, Córdoba 169–196.

ANDREIS, R.R., CÚNEO, R., LÓPEZ GAMUNDI, O., SABATTINI, N., GONZÁLEZ, C.R., 1996, Cuenca Tepuel–Genoa. In: Archangelsky, S. (Ed.), El Sistema Pérmico en la República Argentina y en la República Oriental del Uruguay. Academia Nacional de Ciencias, Córdoba 65–92.

ARNTZ, W.E., BREY, T., GALLARDO, V.A., 1994, Antarctic zoobenthos. Marine Biology Oceanographic Annual Review, 241-303.

ARONSON, R.B., BLAKE, D.B., OJI, T., 1997, Retrograde community structure of the late Eocene of Antarctica. Geology 25, 903-906.

ARONSON, B.R., and BLAKE, D.B., 2001, Global climate change and origin of modern benthic communities in Antarctica. American Zoologist 41: 27–39.

BAHRAMI, A., BONCHEVA, I., KÖNGISHOF, P., YAZDI, M., KHAN-ABADI, A.E., 2014, Conodonts of the Mississippian/Pennsylvanian boundary interval in Central Iran. Journal of Asian Earth Sciences. *In Press.*

BARNES, D.K.A., CLARKE, A., 1995b, Seasonality of feeding activity in Antarctic Suspension feeders. Polar Biology 15, 335-340.

BONELLI, J.R., and PATZKOWSKY, M.E., 2008, How are global patterns of faunal turnover expressed at regional scales? Evidence from the Upper Mississippian (Chesterian Series), Illinois Basin, USA. PALAIOS 23, 760-772.

BONELLI, J.R., and PATZKOWSKY, M.E., 2011, Taxonomic and ecologic persistence across the onset of the late Paleozoic ice age: evidence from the upper Mississippian (Chesterian Series), Illinois Basin, United States. PALAIOS 26, 5-17.

BRENCHLEY, P.J., and HARPER, D., 1998, Palaeoecology: ecosystems, environments and evolution. Chapman & Hall, New York.

BREY, T., and CLARKE, A, 1993, Population dynamics of marine benthic invertebrates in Antarctic and subantarctic environments: are there unique adaptations? Antarctic Science 5, 253-266.

CAREY, A.G., 1991, Ecology of North America Arctic continental shelf benthos: a review. Continental Shelf Research 1, 865-883.

Césaria, S.N.,. Limarino, C.O., Gulbranson, E.L., 2011, An Upper Paleozoic bio-chronostratigraphic sheme for the western margin of Gondwana. Earth Science Reviews 106, 149-160.

CHAPELLE, G., and PECK, L. S., 1995, The influence of acclimation and substratum on the metabolism of the Antarctic amphipods *Waldeckia obesa* (Chevreux, 1905) and *Bovallia gigantea* (Pfeffer, 1888). Polar Biology 15: 225-232.

CLAPHAM, M.E., BOTTJER, D.J., POWERS, C.M., BONUSO, N., FRAISER, M.L., MARENCO, P.J., DORNBOS, S.Q., PRUSS, S.B., 2006, Assessing the ecological dominance of Phanerozoic marine invertebrates. PALAIOS 21, 431-441.

CLAPHAM, M.E., and JAMES, N.P., 2008, Paleoecology of early–middle Permian marine communities in eastern Australia: response to global climate change in the aftermath of the late Paleozoic ice age. PALAIOS 23, 738-750.

CLARKE, A., and CRAME J.A., 1989, The origin of the Southern Ocean marine fauna. In: Carme, J.A. (Ed.), Origins and evolution of the Antarctic Biota. Geological Society Special Publication 46, 253–268.

CLARKE, A., and CRAME J.A., 1992. The Southern Ocean benthic fauna and climate change: a historical perspective. Philosophical Transactions of the Royal Society B 338, 299–309

CLARKE, A., 1993. Temperature and extinction in the sea: A physiologist's view. Paleobiology 19, 499-518.

CLARKE, A., ARONSON, R.B., CRAME, J.A., GILI, J., BLAKE, D.B., 2004, Evolution and diversity of the benthic fauna of the southern ocean continental shelf. Antarctic Science 16, 559-568.

CLIFTON, H. E., 2006, A reexamination of facies models for clastic shorelines. Special Publication - Society for Sedimentary Geology 84, 293-337.

COTTIER, F. R., NILSEN, F., SKOGSETH, R., TVERBERG, V., SKARDHAMAR, J., AND SVENDSEN, H., 2010, Arctic fjords; a review of the oceanographic environment and dominant physical processes. Geological Society Special Publications 344, 35-50.

CROWELL, J.C., and FRAKES, L.A., 1970, Ancient Gondwana glaciations. In: Haughton, S.H., (Ed.), Proceedings and Papers of the Second Gondwana Symposium, South Africa, Pretoria, CSIR, 469-76.

DALLA SALDA, L., CINGOLANI, C., VARELA, R., 1990, The origin of Patagonia. Comunicaciones 41, 55-61.

DAYTON, P.K., 1990, Polar benthos. In: Smith W.O. Jr (Ed.), Polar oceanography, part B chemistry, biology, and geology. Academic Press, San Diego, CA.

DELL, R.K., 1972, Antarctic benthos. Advances in Marine Biology 10, 1-216.

DINEEN, A.A., 2010, Regional Paleoecology of near-field marine faunas during the late Paleozoic Ice Age, western Argentina. M.S. thesis, University of Wisconsin-Milwaukee.

DINEEN, A.A., FRAISER, M.L., ISBELL, J.L., 2012, Palaeoecology and sedimentology of carboniferous glacial and post-glacial successions in the Paganzo and Río Blanco basins of northwestern Argentina: Geological Society, London, Special Publications 376, 109-140.

EICKEN, H, (1992), Salinity profiles of Antarctic sea ice: Field data and model results. Journal of Geophysical Research 97, 15545–15557.

EROS, J.M., MONTAÑEZ, I.P., DAVYDOV, V.I., OSLEGER, D.A., NEMYROVSKA, T.I., 2012, Sequence stratigraphy and onlap history of the Donets Basin, Ukraine: insight into Carboniferous icehouse dynamics. Palaeogeography, Palaeoclimatology, Palaeoecology 313-314, 1-25.

FIELDING, C.R., FRANK, T.D., BIRGENHEIER, L.P., RYGEL, M.C., JONES, A.T., ROBERTS, J., 2008a, Stratigraphic imprint of the Late Paleozoic Ice Age in eastern Australia: a record of alternating glacial and nonglacial climate regime. Journal of the Geological Society of London 165, 129–140.

FIELDING, C.R., FRANK, T.D., ISBELL, J.L., 2008b, The Late Paeozoic ice age – a review of current understanding and synthesis of global climate patterns. In: Fielding, C.R., Frank, T.D., Isbell, J.L., (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space: Geological Society of America Special Paper 441, 343-354.

FORCINO, F.L., 2012, Multivariate assessment of the required sample size for community paleoecological research: Palaeogeography, Palaeoclimatology, Palaeoecology, 315-316, 134-141.

FORCINO, F.L., BARCLAY, K., SCHNEIDER, C.L., LINGE-JOHNSEN, S., LEIGHTON, L.R., 2013, The influence of dataset decisions on paleocommunity results: Comparison of different categorizations of two datasets from Devonian carbonate units. Paleogeography, Paleoclimatology, Palaeoecology, 386, 479-491.

FORSYTHE, R., 1982, The late Paleozoic to early Mesozoic evolution of southern South America: a plate tectonic interpretation: Journal Geological Society, 139, 671-682.

FRANK, T.D., SHULTIS, A.I., FIELDING, C.R., 2015, Acme and demise of the late Palaeozoic ice age: A view from the southeastern margin of Gondwana. Palaeogeoraphy, Palaeoclimatology, Palaeoecology 418, 176-192.

FRAKES, L.A., and CROWELL, J.C., 1969, Late Paleozoic glaciation: I, South America: Geological Society of America Bulletin, 80, 1007-1042.

FRAKES, L.A., FRANCIS, J.E., SYKTUS, J.I., 1992, Climate modes of the Phanerozoic. The history of the earth's climate over the Past 600 Million Years. Cambridge University Press, Cambridge.

GASTALDO, R.A., DIMICHELLE, W.A., PFEFFERKORN, H.W., 1996, Out of the icehouse into the greenhouse; a late Paleozoic analog for modern global vegetational change. GSA Today 6, 1-7.

GILINSKI, N.L., and BENNINGTON, J.B., 1994, Estimating numbers of whole individuals from collections of body parts: a taphonomic limitation of the paleontological record. Paleobiology 20, 245-258.

GONZÁLEZ, C.R., 2003, Additional comments on the Upper Paleozoic glaciations in Argentina. Newsletter on Carboniferous Stratigraphy 21, 25-28.

GONZÁLEZ, C.R., AND GLASSER, N.F., 2008, Carboniferous glacial erosional and depositional features in Argentina: Geologica et Palaeontologica 42, 9-54.

GULBRANSON, E.L., MONTAÑEZ, I.P., SCHMITZ, M.D., LIMARINO, C.O., ISBELL, J.L., MARENSSI, S.A., CROWLEY, J.L., 2010, High-precision U-Pb calibration of Carboniferous glaciation and climate history, Paganzo Group, NW Argentina. Geological Society of America Bulletin 122, 1480-1498.

GULBRANSON, E.L., MONTAÑEZ, I.P., TABOR, N.J., LIMARINO, C.O., 2015, Late Pennsylvanian aridification on the southwestern margin of Gondwana (Paganzo Basin, NW Argentina): A regional expression of a global climate perturbation. Palaeogeography, Palaeoclimatology, Palaeoecology 417, 220-235.

GUTT, J., 2001, On the direct impact of ice on marine benthic communities, a review. Polar Biology 24, 553-564.

HALLAM, A., and WIGNALL, P.B., 1997, Mass Extinctions and Their Aftermath. Oxford University Press, Oxford.

Hammer, O., and Harper, D., 2006, Paleontological Data Analysis. Blackwell Publishing, Malden, MA.

Harrington, H.J., 1962, Paleogeographic development of South America. American Association of Petroleum Geologists Bulletin 46, 1773–1814.

Harris, J.A., Hobbs, R.J., Higgs, E., Aronson, J., 2006, Ecological restoration and global climate change. Restoration Ecology 14, 170-176.

Heckel, P.H, 2008, Pennsylvanian cyclothems in Midcontinent North America as far-field effects of waxing and waning of Gondwana ice sheets. In: Fielding, C.R., Frank, T.D., and Isbell, J.L., (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space: Geological Society of America Special Paper 441, 275-289.

Heim, N.A., 2009, Stability of regional brachiopod diversity structure across the Mississippian/Pennsylvanian boundary. Paleobiology 35, 393-412.

Henry, L.C., Isbell, J.L., Limarino, C.O., 2008, Carboniferous glaciogenic deposits of the proto-Precordillera of west-central Argentina. In: Fielding, C.R., Frank, T.D., and Isbell, J.L., (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space: Geological Society of America Special Paper 441, 131-142.

Henry, L.C., Isbell, J.L., and Limarino, C.O., 2014, The late Paleozoic El Imperial Formation, western Argentina: glacial to post-glacial transition and stratigraphic correlation with arc-related basins. Gondwana Research 25, 1380-1395.

Henry, L.C., Isbell, J.L., Limarino, C.O., McHenry, L.J., Fraiser, M.L., 2010, Mid-Carboniferous deglaciation of the Protoprecordillera, Argentina recorded in the Agua de Jagüel palaeovalley. Palaeogeography, Palaeoclimatology, Palaeoecology 298, 112-129.

Hizel, A.H., Posse, B., Oggier, P.A., Crettenand, Y., Glenz, C., Arlettaz, R., 2004, Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. Journal of Applied Ecology 41, 1103-1116.

Holterhoff, P.F., 1999, Filtration models, guilds, and biofacies: Crinoid paleoecology of the Stanton Formation (Upper Pennsylvanian), midcontinent, North America. Palaeogeography, Palaeoclimatology, Palaecology 130, 177-208.

Inall, M. E., and Gillibrand, P. A., 2010, The physics of mid-latitude fjords; a review: Geological Society Special Publications 344, 17-33.

IPCC, 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L., (Eds.), Cambridge University Press, Cambridge, United Kingdom and New York, NY.

ISBELL, J.L., MILLER, M.F., WOLFE, K.L., LENAKER, P.A., 2003, Timing of late Paleozoic glaciation in Gondwana: Was glaciation responsible for the development of northern hemisphere cyclothems? In: Chan, M.A., Archer, A.W., (Eds.), Extreme Depositional Environments: Mega End-Members in Geological Time. Geological Society of America Special Paper 370, 5–24.

ISBELL, J.L., FRAISER, M.L., HENRY, L.C., 2008, Examining the complexity of environmental change during the late Paleozoic and early Mesozoic, PALAIOS 23, 267-269.

ISBELL, J.L., HENRY, L.C., GULBRANSON, E.L., LIMARINO, C.O., FRAISER, M.L., KOCH, Z.J., CICCIOLI, P.L., DINEEN, A.A., 2012, Glacial paradoxes during the late Paleozoic ice age: Evaluating the equilibrium line altitude (ELA) as a control on glaciation. Gondwana Research 22, 1-19.

ISBELL, J.L., HENRY, L., REID, C. & FRAISER, M.L., 2013, Sedimentology and palaeoecology of lonestone-bearing mixed clastic rocks and cold-water carbonates of the lower Permian basal beds at Fossil Cliffs, Maria Island, Tasmania (Australia): Insight into the initial decline of the late Palaeozoic ice age. Geological Society, London, Special Publications Geological Society 376, 307-341.

KASER, G., HARDY, D.R., MÖLG, T., BRADLEY, R.S., HYERA, T.M., 2004, Modern glacier retreat on kilimanjaro as evidence of climate change: observations and facts. International Journal of Climatology 24, 329-339.

KIDAWA, A., and JANECKI, T., 2011, Antarctic benthic fauna in the global climate change. Papers of Global Change 18, 71-86.

KIDWELL, S.M., 1991, The stratigraphy of shell concentrations: Taphonomy: Releasing the Data Locked in the Fossil Record 9, 211-290.

KIRHCMAN, D.L., MORÁN, X.G., DUCKLOW, H., 2009, Microbial growth in the polar oceans– role of temperature and potential impact of climate change. Nature Reviews Microbiology 7, 451-459.

LEANZA, A.F., 1958, Geologica Regional. In: Pueser (Ed.), La Argentina, Suma de Geografia: Buenos Aires 1, 217-349.

Lebold, J.G., and Kammer, T.W., 1970, Gradient analysis of faunal distributions associated with rapid transgressions and low accommodation space in a Late Pennsylvanian marine embayment: Biofacies of the Andes Member (Glenshaw Formation, Conemaugh Group) in the northern Appalachian Basin, USA. Palaeogeography, Palaeoclimatology, Palaecology 231, 291-314.

Levinton, J.S., 1970, The paleoecological significance of opportunistic species. Lethaia 3, 69-78.

Levitus, S., Antonov, J.I., Boyer, T.P., Stephens, C., 2000,Warming of the World Ocean. Science 24, 2225-2229.

Limarino, C.O., and Spalletti, L.A., 2006, Paleogeography of the upper Paleozoic basins of southern South America: an overview. Journal of South American Earth Sciences 22, 134-155.

Limarino, C.O., Césaria, S.N., Spalletti, L.A., Taboada, A.C., Isbell, J.L., Geuna, S., Gulbranson, E.L., 2014, A paleoclimatic review of Southern America during the Late Paleozoic: a record from icehouse to extreme greenhouse conditions. Gondwana Research 25, 1396-1421.

López-Gamundí, O.R., 1989, Postglacial transgressions in late Paleozoic basins of western Argentina; a record of glacioeustatic sea level rose. Paleogeography, Paleoclimatology, Palaeoecology 71, 257-270.

López-Gamundí, O.R., 1997, Glacial-postglacial transition in the late Paleozoic basins of southern South America. In: Martini, I.P., (Ed.), Late Glacial and Postglacial Environmental Changes: Quaternary, Carboniferous-Permian and Proterozoic. Oxford University Press, Oxford, UK.

López-Gamundí, O.R., and Buatois, L.A., 2010, Introduction: Late Paleozoic glacial events and postglacial transgressions in Gondwana. Geological Society of America Special Papers 468, v-viii.

Marenssi, S.A., Tripaldi, A., Limarino, C.O., Caselli, A.T., 2005, Facies and Architecture of a Carboniferous Grounding-line System From the Guandacol Formation, Paganzo Basin, Northwestern Argentina. Gondwana Research 8, 187-202.

McClintock, J. B., Ducklow, H.,Fraser, B., 2008a. Ecological impacts of climate change on the Antarctic Peninsula. American Scientist 96, 302-310

Moore, R.C., and Jeffords, R.M., 1968, Classification and nomenclature of fossil crinoids based on studies of dissociated parts of their columns: University of Kansas Paleontological Contributions, Echinodermata 9, 1-114.

MONTAÑEZ, I.P., and SOREGHAN, G.S., 2006, Earth’s fickle climate: Lessons learned from deep- time ice ages. Geotimes, 51, 24-27.

MONTAÑEZ, I.P., and POULSEN, C.J., 2013, The late Paleozoic ice age: an evolving paradigm. Annual Review of Earth & Planetary Sciences 41, 1-28.

OLSZEWSKI, T.D., and M.E., PATZKOWSKY, 2001b, Measuring recurrence of marine biotic gradients: A case study from the Pennsylvanian-Permian midcontinent. Palaios 16, 444-460.

PAGANI, M.A., and TABOADA, A.C., 2010, The marine upper Paleozoic in Patagonia (Tepuel-Geona Basin, Chubut Province, Argentina): 85 years of work and future prospects. Palaeogeography, Palaeclimatology, Palaeoecology 298, 130-151.

PANKHURST, R.J., RAPELA, C.W., FANNING, C.M., MÁRQUEZ, M., 2006, Gonwanide continental collision and the origin of Patagonia. Earth-Science Reviews 76, 235–257.

PARMESAN, C., 2006, Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37, 637–669.

PAULS, K.N., 2014, Sedimentology and Paleoecology of fossil-bearing, high-latitude marine and glacially-influenced deposits in the Tepuel Basin, Patagonia, Argentina. M.S. thesis, University of Wisconsin-Milwaukee.

PAZOS, P.J., 2002a, The Late Carboniferous Glacial to Postglacial Transition: Facies and Sequence Stratigraphy, Western Paganzo Basin, Argentina. Gondwana Research 5, 467-487.

PAZOS, P.J., 2002b, Palaeoenvironmental Framework of the Glacial-Postglacial Transition (Late Paleozoic) in the Paganzo-Calingasta Basin (Southern South America) and the Great Karoo-Kalahari Basin (Southern Africa): Inchnological Implications. Gondwana Research 5, 619-640.

PEARSE, J.S., MCCLINTOCK, J.B., BOSCH, I., 1991, Reproduction of Antarctic benthic marine invertebrates: tempos, modes, and timing. American Zoology 31, 65-80.

PECK, L.S., 1989, Temperature and basal metabolism in two Antarctic marine herbivores. Journal of Experimental Marine Biology Ecology 127, 1-12.

PECK, L.S., and ROBINSON, K., 1994. Pelagic larval development in the brooding Antarctic brachiopod Liothyrella uva. Marine Biology 120, 279-286.

PECK, L.S., COLMAN, J.G., MURRAY, A.W.A., 2000, Growth and tissue mass cycles in the infaunal bivalve Yoldia eightsi at Signy Island, Antarctica. Polar Biology 23, 420-429.

PECK, L.S., 2002, Ecophysiology of Antarctic marine ectotherms: limits to life. Polar Biology 25, 31-40

PECK, L.S., PÖRTNER, H.O., AND HARDEWIG, I., 2002, Metabolic demand, oxygen supply and critical temperatures in the Antarctic bivalve Laternula elliptica. Physiological and Biochemical Zoology 75, 123-133.

PECK, L.S., WEBB, K.E., BAILEY, D.M., 2004b. Extreme sensitivity of biological function to temperature in Antarctic marine species. Functional Ecology 18, 625-630.

PECK, L.S., 2005, Prospects for survival in the Southern Ocean: vulnerability of benthic species to temperature change. Antarctic Science 17, 497-507.

Plint, A. G., 1988, Sharp-based shoreface sequences and "offshore bars' in the Cardium Formation of Alberta: their relationship to relative changes in sea level. In: Wilgus, C. K., (Ed.), Sea-level changes: an integrated approach: Special Publication 42, 357-370.

POSAMENTIER, H.W., AND ALLEN, G.P., 1999, Siliciclastic sequence stratigraphy: concepts and applications. SEPM Concepts in Sedimentology and Paleontology 7.

POWELL, M.G., 2005, Climate basis for sluggish macroevolution during Late Paleozoic ice age. Geology 33, 381-384.

POWELL, M.G., 2007, Latitudinal diversity gradient for brachiopod genera during late Palaeozoic time: links between climate, biogeography and evolutionary rates. Global Ecology and Biogeography 16, 519-528.

RAMOS, V.A., 1984, Patagonia: un continente paleozoico a la deriva? Actas, 9° Congreso Geológico Argentino, S.C. Bariloche 2, 311-325.

RAMOS, V.A., 2008, Patagonia: a Paleozoic continent adrift?. Journal of South American Earth Sciences 26, 235-251.

RAPALINI, A.E., LÓPEZ DE LUCHI, M., MARTÍNEZ DPOICO, C., LINCE KLINGER, F. GIMÉNEZ, MARTÍNEZ, P., 2010, Did Patagonia collide with Gondwana in the Late Paleozoic? Some insights from a multidisciplinary study of magmatic units of the North Patagonian Massif. Geologica Acta 8, 349-371.

RAYMOND, A., and METZ, C., 2004, Ice and its consequences: glaciation in the Late Ordivician, Late Devonian, Pennsylvanian-Permian, and Cenozoic compared. Journal of Geology 112, 655-70.

Reynolds, W.W., and Casterlin, M.E., 1985, Vagile macrofauna and the hydrographic environment of the Saco River Estuary and adjacent waters of the Gulf of Maine. Hydrobiologia 128, 207-215.

RODLAND, D.L., and BOTTJER, D.J., 2001, Biotic recovery from the end-Permian mass extinction: behavior of the inarticulate brachiopod lingula as a disaster taxon. PALAIOS 16, 95-101.

SCHOPF, T.J.M., 1969, Paleoecology of ectoprocts (bryozoans). Journal of Paleontology 43, 234-244.

SCOTESE, C.R., BOUCOT, A.J., MCKERROW, W.S., 1999, Gondwanan palaeogeography and palaeoclimatology. Journal of African Earth Sciences 28, 99-114.

SIMANAUSKAS, T., and SABATTINI, N., 1997, Bioestratigrafía del Paleozoico superior marino de la Cuence Tepuel-Genoa, Provincia del Chubut, Argentina. Ameghiniana 34, 49-60.

SIMANAUSKAS, T., and CISTERNA., 2000, A palaeo-opportunistic brachiopod from the Early Permian of Argentina. Alcheringa 24, 45-53.

STOLLHOFEN, H., WERNER, M., STANISTREET, I.G., ARMSTRONG, R.A., 2008, Single-zircon UPb dating of Carboniferous–Permian tuffs, Namibia, and the intercontinental deglaciation cycle framework. In: Fielding, C.R., Frank, T.D., Isbell, J.L. (Eds.), Resolving the late Paleozoic ice age in time and space: Geological Society of America Special Paper 441, 83–96.

STANLEY, S.M. and POWELL, M.G., 2003, Depressed rates of origination and extinction during the late Paleozoic ice age: a new state for the global marine ecosystem. Geology 31, 877–880.

STEELE-PETROVIC, M., 1977, The physiological differences between articulate brachiopods and filter-feeding bivalves as a factor in the evolution of marine level-bottom communities. Palaeontology 22, 101-134.

STERREN, A.F., 2000, Paleoecologíca, tafonomía y taxonomía de los moluscos bivalvos del Carbonífero-Pérmico en las cuencas de Río Blanco y Calingasta-Uspallata. Doctoral Thesis. Córdoba, Universidad Nacional de Córdoba, p. 230.

STERREN, A.F., and CISTERNA, G.A., 2006, La fauna de Levipustula en la Formación Hoyada Verde: control paleocológico versus resolución bioestratigráfica. Córdoba, 9th Congresso Argentino de Paleontologíca y Bioestratigrafía, Resúmenes, p. 192.

STERREN, A.F., and CISTERNA, G.A., 2010. Bivalves and brachiopods in the Carboniferous- Early Permian of Argentine Precordillera: Diversification and faunal turnover in Southwestern Gondwana. Geologica Acta 8, 501-517.

TABOADA, A.C., 2008, First record of the Late Palaeozoic brachiopod Verchojania Abramov in Patagonia, Argentina. Proceedings of the Royal Society of Victoria 120, 305–319.

TABOADA, A.C., 2010, Mississippian-Early Permian brachiopods from western Argentina: Tools for middle- to high-latitude correlation, paleobiogeographic and paleoclimatic reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 298, 152-73.

TABOADA, A.C., and PAGANI, M.A., 2010, The coupled occurrence of Cimmeriella-Jakutoproductus (Brachiopoda: Productidina) in Patagonia: implications for Early Permian high to middle paleolatitudinal correlations and paleoclimatic reconstruction. Geologica Acta 8, 513-534.

TAYLOR, P.D., 2005, Bryozoans and palaeoenvironmental interpretation. Journal of the Palaeontological Society of India 50, 1-11.

VEEVERS, J.J., POWELL, C.M., 1987, Late Paleozoic glacial episodes in Gondwanaland reflected in transgressive-regressive depositional sequences in Euramerica. Geological Society of America Bulletin 98, 475–487.

VISSER, J.N., 1997, Deglaciation sequences in the Permo-Carboniferous Karoo and Kalahari basins of southern Africa: a tool in the analysis of cyclic glaciomarine basin fills. Sedimentology 44, 507-521.

WALTHER, G., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T.J., FROMENTIN, J., HOEGH-GULDBERG, O., BAIRLEIN, F., 2002, Ecological responses to recent climate change. Nature 416, 389-95.

WATERHOUSE, J.B., and SHI, G.R., 2010, Evolution in a cold climate. Palaeogeography, Palaeoclimatology, Palaeoecology 298, 17-30.

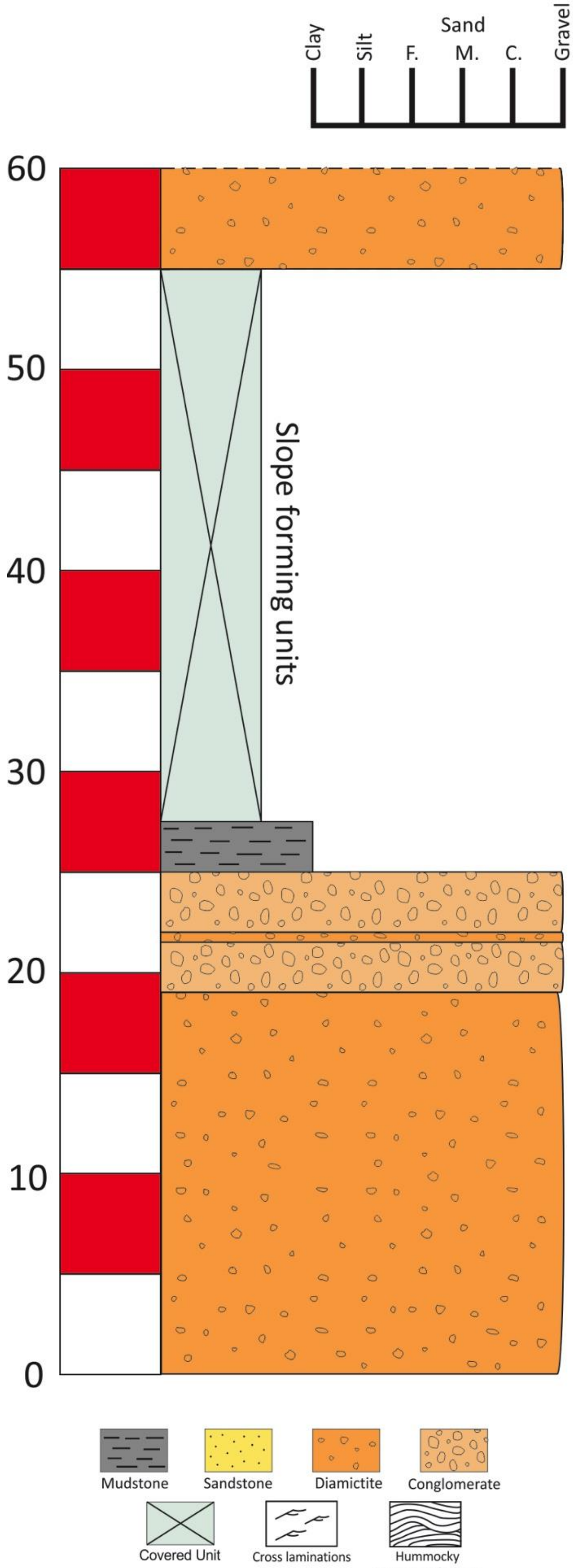
WHITLOCK, M.C., and SCHLUTER, D., 2009, The Analysis of Biological Data. Roberts and Company Publishers, Greenwood Village, CO.

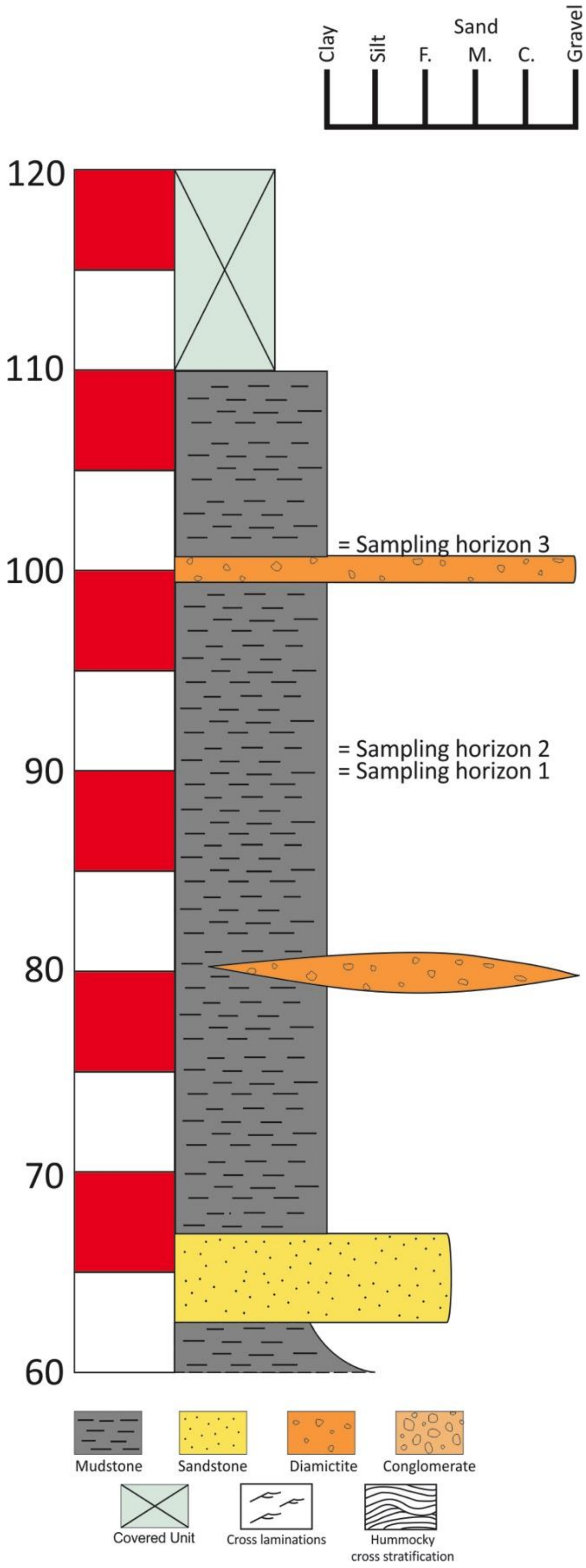
WLODARSKA-KOWALCZEK,M., PEARSON, T.H., and KENDALL, M.A., 2005, Benthic response to chronic natural physical disturbance by glacial sedimentation in an Arctic fjord. Marine Ecology Progress Series 303, 31-41.

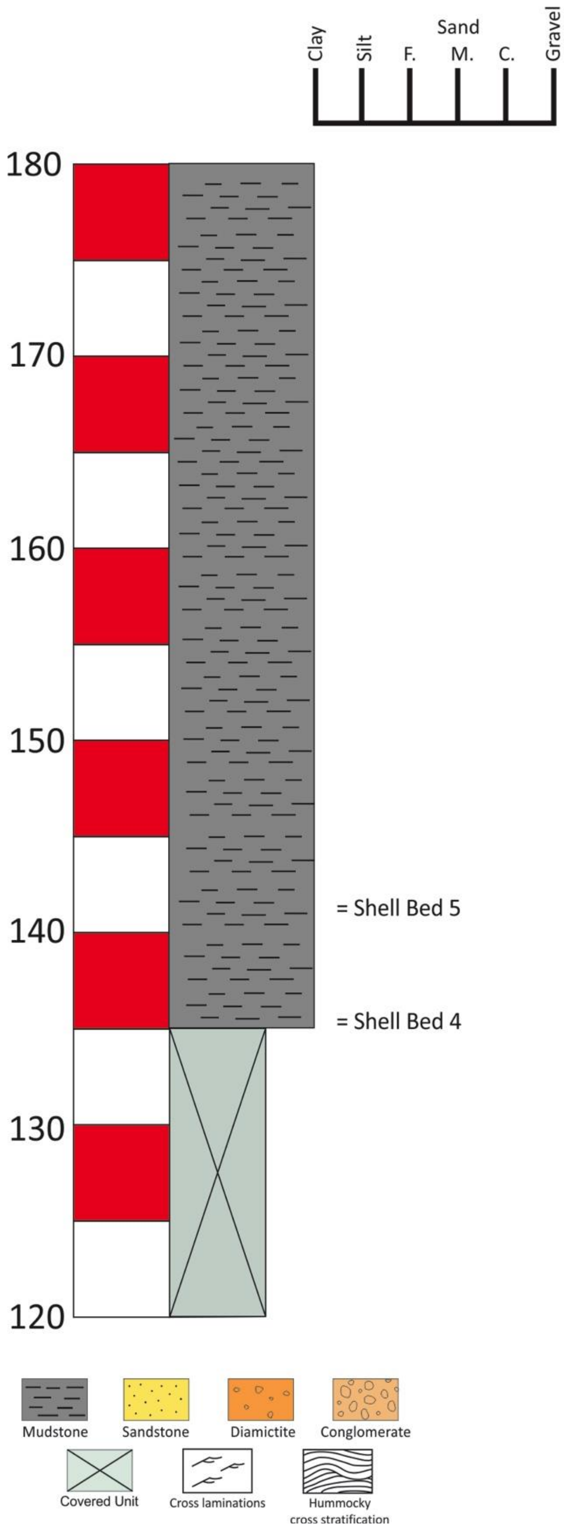
Appendix A

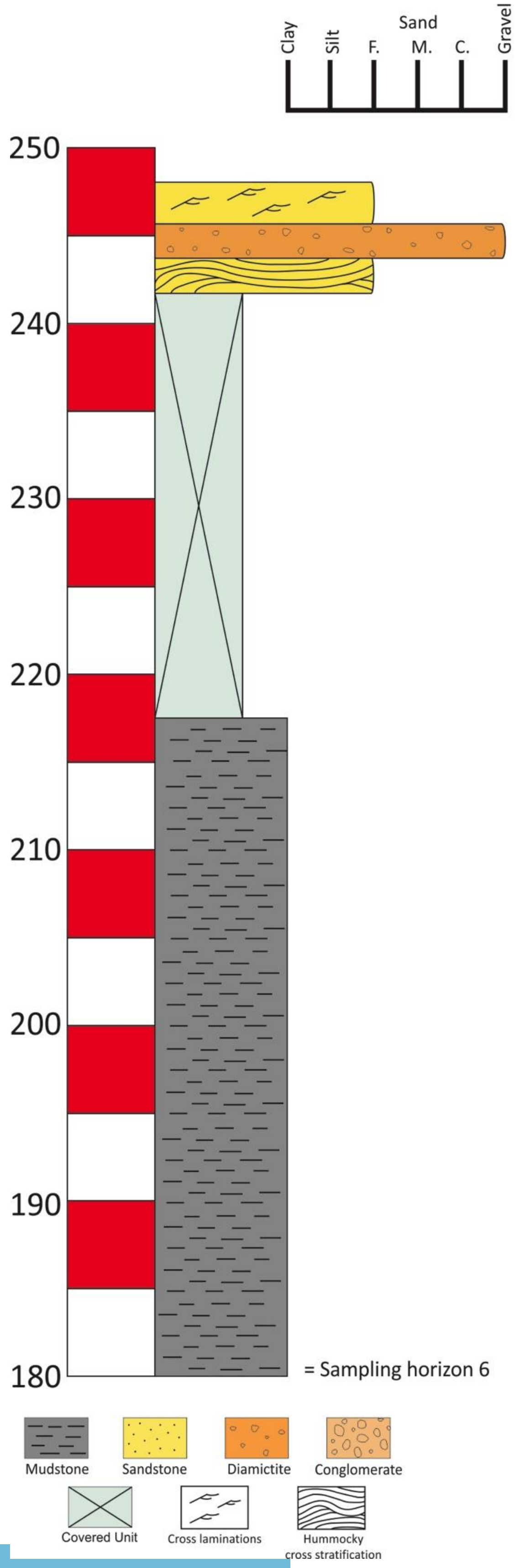
Pampa de Tepuel Formation

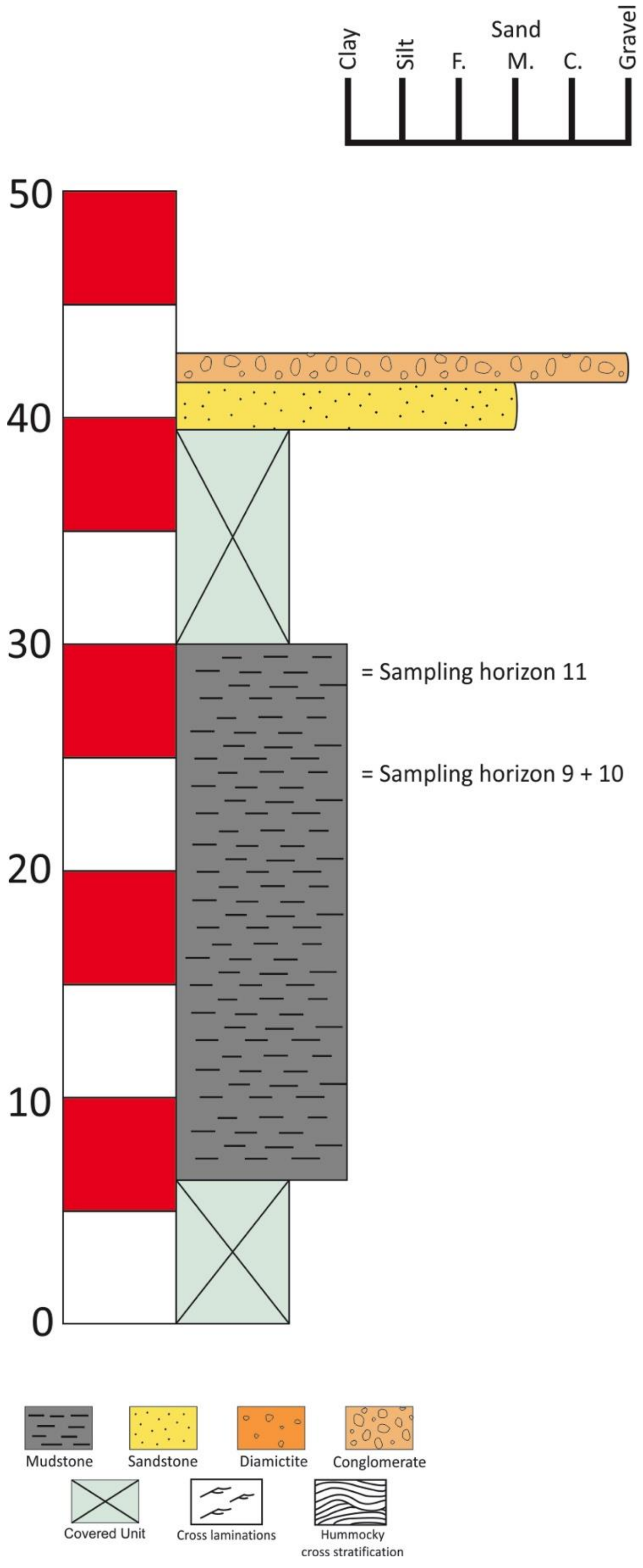
Stratigraphic Columns


Clay
Silt
Sand
F.
M.
C.
Gravel
60
50
40
30
20
10
0
Slope forming units
Mudstone
Sandstone
Diamictite
Conglomerate
Covered Unit
Cross laminations
Hummocky cross stratification


Clay
Silt
Sand
F.
M.
C.
Gravel
120
110
100
90
80
70
60
= Sampling horizon 3
= Sampling horizon 2
= Sampling horizon 1
Mudstone
Sandstone
Diamictite
Conglomerate
Covered Unit
Cross laminations
Hummocky cross stratification


Sand
Clay
Silt
F.
M.
C.
Gravel
180
170
160
150
140
130
120
= Shell Bed 5
= Shell Bed 4
Mudstone
Sandstone
Diamictite
Conglomerate
Covered Unit
Cross laminations
Hummocky cross stratification

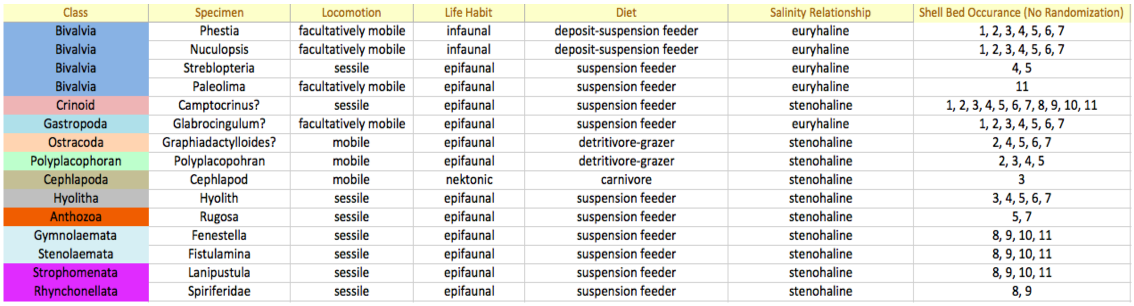

Sand
Clay
Silt
F.
M.
C.
Gravel
250
240
230
220
210
200
190
180
= Sampling horizon 6
Mudstone
Sandstone
Diamictite
Conglomerate
Covered Unit
Cross laminations
Hummocky cross stratification


Clay
Silt
Sand
F.
M.
C.
Gravel
50
40
30
20
10
0
= Sampling horizon 11
= Sampling horizon 9 + 10
Mudstone
Sandstone
Diamictite
Conglomerate
Covered Unit
Cross laminations
Hummocky cross stratification

Appendix B

Pampa de Tepuel Formation

Paleoecological Data



Class	Specimen	Locomotion	Life Habit	Diet	Salinity Relationship	Shell Bed Occurance (No Randomization)
Bivalvia	Phestia	facultatively mobile	infaunal	deposit-suspension feeder	euryhaline	1, 2, 3, 4, 5, 6, 7
Bivalvia	Nuculopsis	facultatively mobile	infaunal	deposit-suspension feeder	euryhaline	1, 2, 3, 4, 5, 6, 7
Bivalvia	Streblopteria	sessile	epifaunal	suspension feeder	euryhaline	4, 5
Bivalvia	Paleolima	facultatively mobile	epifaunal	suspension feeder	euryhaline	11
Crinoid	Camptocrinus?	sessile	epifaunal	suspension feeder	stenohaline	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11
Gastropoda	Glabrocingulum?	facultatively mobile	epifaunal	suspension feeder	euryhaline	1, 2, 3, 4, 5, 6, 7
Ostracoda	Graphiadactylloides?	mobile	epifaunal	detritivore-grazer	stenohaline	2, 4, 5, 6, 7
Polyplacophoran	Polyplacopohran	mobile	epifaunal	detritivore-grazer	stenohaline	2, 3, 4, 5
Cephlapoda	Cephlapod	mobile	nektonic	carnivore	stenohaline	3
Hyolitha	Hyolith	sessile	epifaunal	suspension feeder	stenohaline	3, 4, 5, 6, 7
Anthozoa	Rugosa	sessile	epifaunal	suspension feeder	stenohaline	5, 7
Gymnolaemata	Fenestella	sessile	epifaunal	suspension feeder	stenohaline	8, 9, 10, 11
Stenolaemata	Fistulamina	sessile	epifaunal	suspension feeder	stenohaline	8, 9, 10, 11
Strophomenata	Lanipustula	sessile	epifaunal	suspension feeder	stenohaline	8, 9, 10, 11
Rhynchonellata	Spiriferidae	sessile	epifaunal	suspension feeder	stenohaline	8, 9

Sampling Horizon 1		
Taxa (Genera)		#
Gastropod		6
Phestia		8
Crinoid		27
Ostracod		1
Nuculopsis		1
Hyolith		1
Unid. Fossil #1		1
Unid. Fossil #2		1
Unid. Bivalve		5
	Total	51
Randomized		#
Gastropod		6
Phestia		8
Crinoid		26
Ostracod		1
Nuculopsis		1
Hyolith		1
Unid. Fossil #1		1
Unid. Fossil #2		1
Unid. Bivalve		5
	Total	50

Sampling Horizon 2		
Taxa (Genera)		*#*
Gastropod		11
Ostracod		4
Nuculopsis		7
Phestia		6
Crinoid		22
Unid. Bivalve		1
Polyplacophoran		2
Hyolith		1
Streblopteria		1
	Total	55
Randomized		*#*
Gastropod		9
Ostracod		4
Nuculopsis		6
Phestia		5
Crinoid		22
Unid. Bivalve		0
Polyplacophoran		2
Hyolith		1
Streblopteria		1
	Total	50

Sampling Horizon 3		
Taxa (Genera)		*#*
Gastropod		5
Crinoid		29
Ostracod		3
Nuculopsis		3
Phestia		3
Hyolith		3
Cnidarian- Rugosa		1
Unid. Bivalve		3
	Total	50
Randomized		*#*
Gastropod		5
Crinoid		29
Ostracod		3
Nuculopsis		3
Phestia		3
Hyolith		3
Cnidarian- Rugosa		1
Unid. Bivalve		3
	Total	50

Sampling Horizon 4		
Taxa (Genera)		*#*
Gastropod		19
Phestia		8
Nuculopsis		3
Crinoid		48
Fenetalus		1
Unid. Bivalve		2
Cephlapod		1
Hyolith		3
Polyplacophoran		1
	Total	86
Randomized		*#*
Gastropod		7
Phestia		5
Nuculopsis		1
Crinoid		32
Polyplacophoran		0
Unid. Bivalve		0
Cephlapod		1
Hyolith		4
	Total	50

Sampling Horizon 5		
Taxa (Genera)		#
Gastropod		15
Crinoid		27
Phestia		3
Ostracod		1
Unid. Bivalve		2
Nuculopsis		3
Polyplacophoran		1
	Total	52
Randomized		#
Gastropod		14
Crinoid		27
Phestia		3
Ostracod		1
Unid. Bivalve		2
Nuculopsis		2
Polyplacophoran		1
	Total	50

Sampling Horizon 6		
Taxa (Genera)		#
Phestia		15
Gastropod		3
Nuculopsis		6
Crinoid		26
Unid. Fossil #1		1
Unid. Fossil #2		1
Unid. Bivalve		1
	Total	53
Randomized		#
Phestia		14
Gastropod		3
Nuculopsis		5
Crinoid		25
Unid. Fossil #1		1
Unid. Fossil #2		1
Unid. Bivalve		1
	Total	50

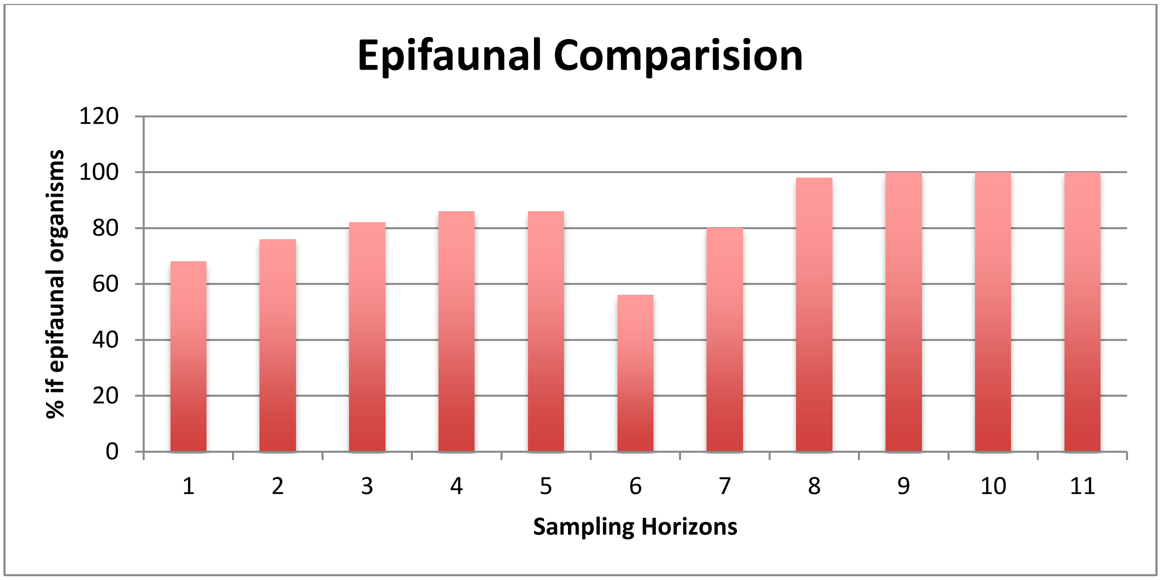
Sampling Horizon 7		
Taxa (Genera)		#
Polyplacophoran		1
Nuculopsis		8
Crinoid		45
Gastropod		8
Cnidarian (Rugosa?)		1
Streblopteria		2
Hyolith		3
Phestia		8
Fenetalus		3
Coleolus		1
Ostracod		6
Unid. Bivalve		3
	Total	89
Randomized		#
Polyplacophoran		1
Nuculopsis		5
Crinoid		26
Gastropod		4
Cnidarian (Rugosa?)		0
Streblopteria		2
Hyolith		4
Phestia		5
Unid. Bivalve		0
Coleolus		0
Ostracod		3
	Total	50

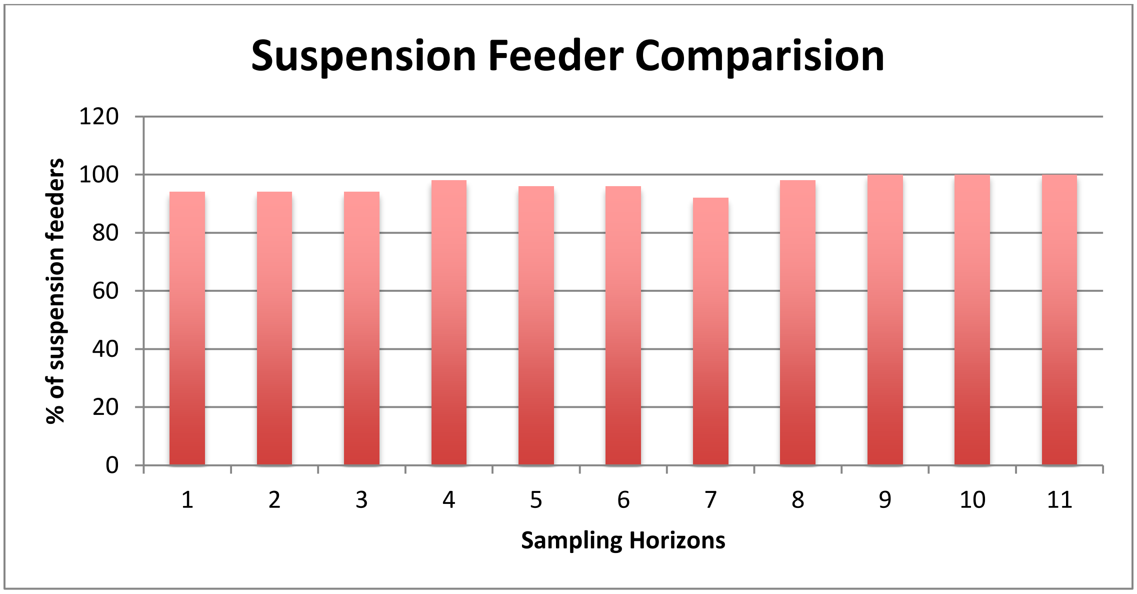
Sampling Horizon 8		
Taxa (Genera)		#
Fistulamina bifurcata		39
Fenestella		41
Crinoid		21
Lanipustula		7
Spiriferidae		1
Unid. Fossil		1
	Total	110
Randomized		#
Fistulamina bifurcata		21
Fenestella		15
Crinoid		8
Lanipustula		4
Spiriferidae		1
Unid. Fossil		1
	Total	50

Sampling Horizon 9		
Taxa (Genera)		#
Fistulamina bifurcata		22
Fenestella		66
Crinoid		19
Spiriferidae		1
Lanipustula		6
Fenestella penniretepora		1
	Total	115
Randomized		#
Fistulamina bifurcata		10
Fenestella		27
Crinoid		9
Spiriferidae		1
Lanipustula		3
Fenestella penniretepora		0
	Total	50

Sampling Horizon 10		
Taxa (Genera)		#
Crinoid		41
Fenestella		69
Fistulamina		12
Lanipustula		3
	Total	125
Randomized		#
Crinoid		15
Fenestella		31
Fistulamina		3
Lanipustula		1
	Total	50

Sampling Horizon 11		
Taxa (Genera)		*#*
Lanipustula		4
Crinoid		26
Paleolima		28
Fenestella		45
Fistulamina		4
	Total	107
Randomized		*#*
Lanipustula		1
Crinoid		11
Paleolima		16
Fenestella		21
Fistulamina		1
	Total	50


Epifaunal Comparision
% if epifaunal organisms
120
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
10
11
Sampling Horizons


Suspension Feeder Comparision
% of suspension feeders
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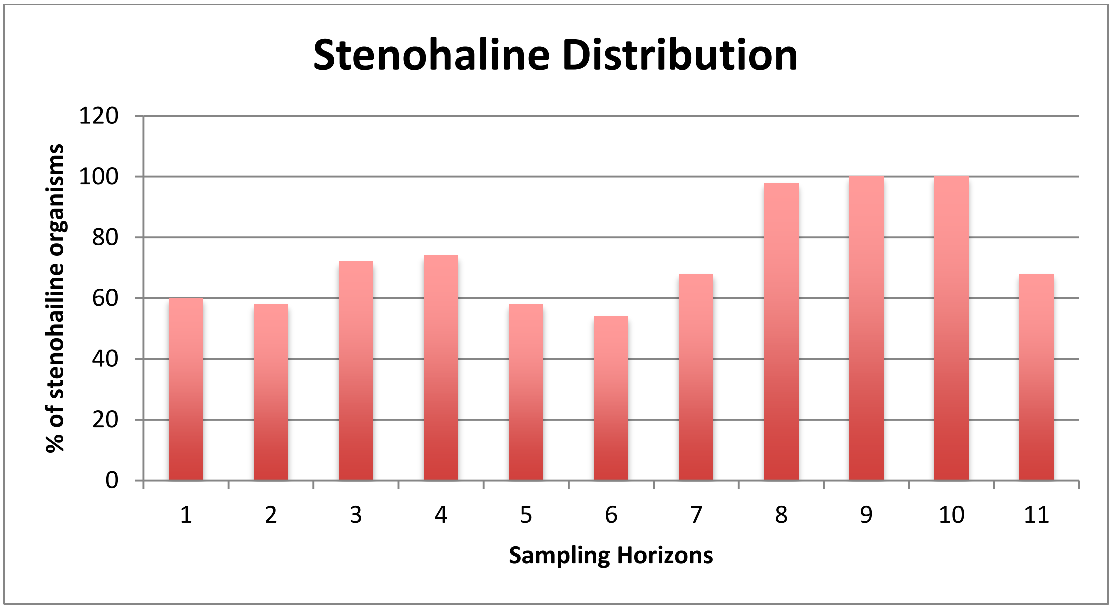
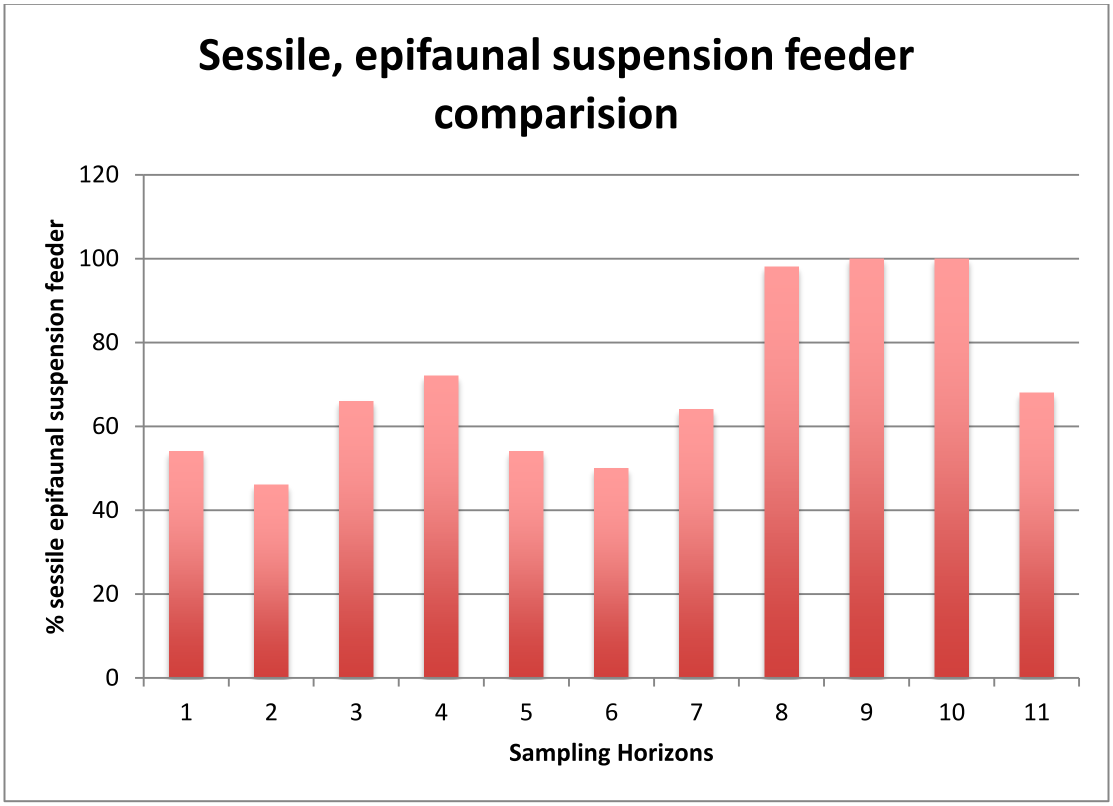
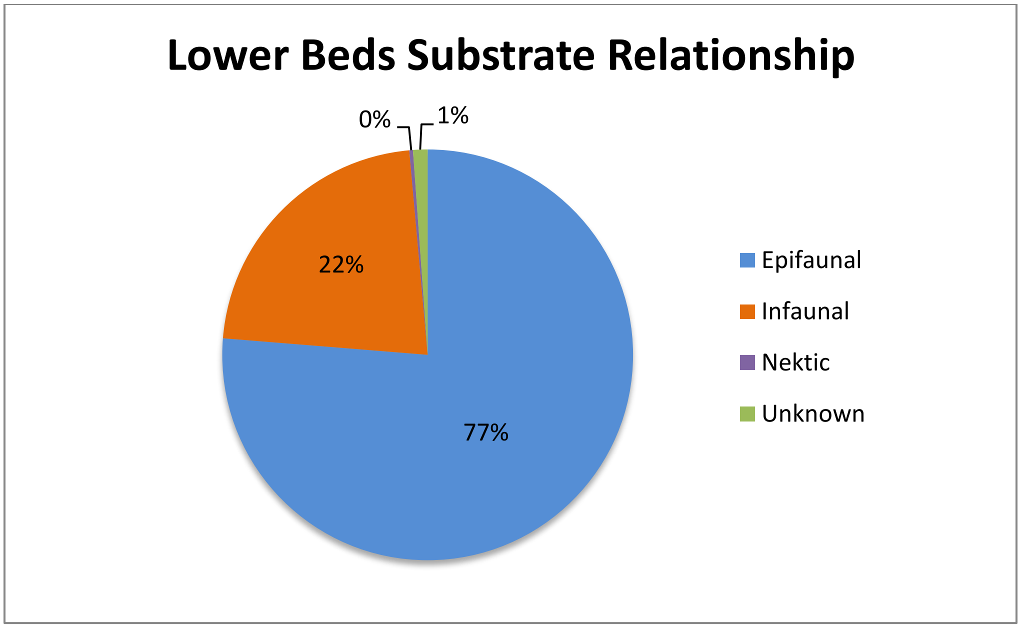
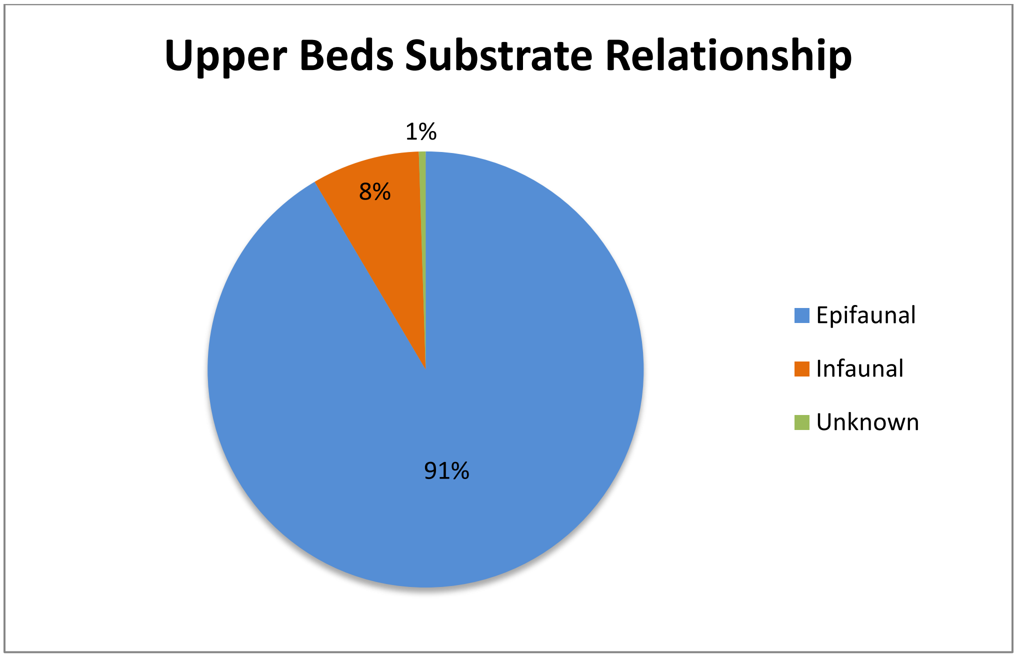
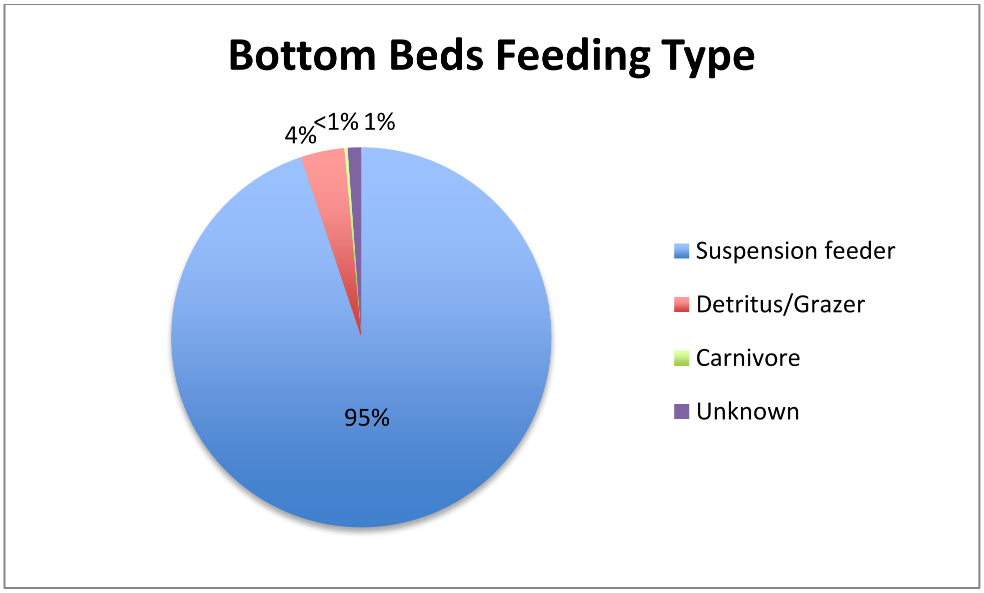
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
10
11
Sampling Horizons

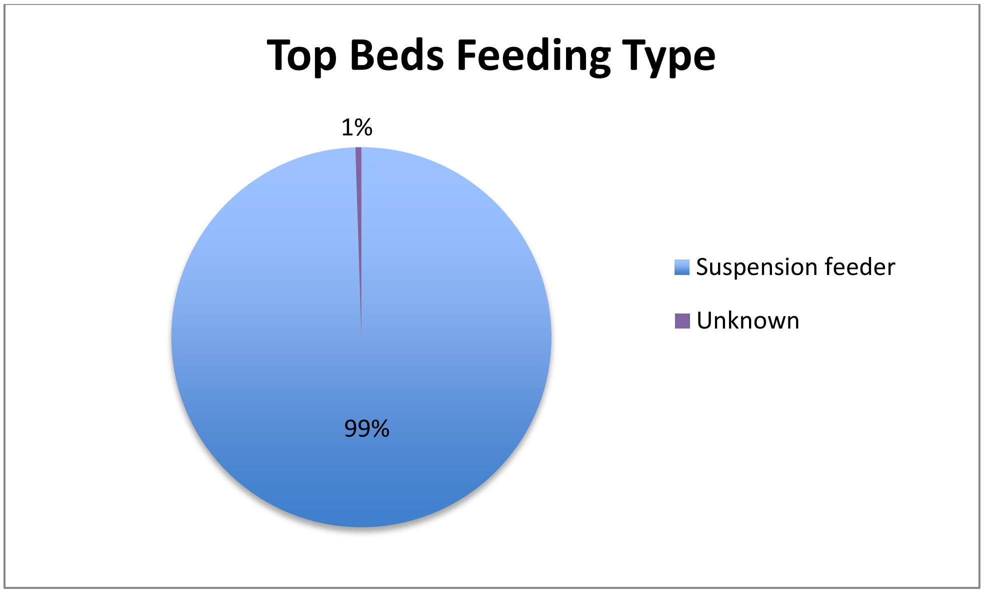

Stenohaline Distribution
% of stenohailine organisms
120
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
10
11
Sampling Horizons


Sessile, epifaunal suspension feeder comparision
% sessile epifaunal suspension feeder
120
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
10
11
Sampling Horizons


Lower Beds Substrate Relationship
0%
1%
22%
77%
Epifaunal
Infaunal
Nektic
Unknown


Upper Beds Substrate Relationship
1%
8%
91%
Epifaunal
Infaunal
Unknown


Bottom Beds Feeding Type
4%
<1%
1%
95%
Suspension feeder
Detritus/Grazer
Carnivore
Unknown


Top Beds Feeding Type
1%
99%
Suspension feeder
Unknown

Z-Test	*p1*	*p2*	*p*	*(1-p)*	*(1/n1)+(1/n2)*	*Z*
Bed 1 vs. Bed 2	0.12	0.16	0.14	0.86	0.04	-0.576390418
Bed 1 vs. Bed 3	0.12	0.14	0.13	0.87	0.04	-0.297350517
Bed 1 vs. Bed 4	0.12	0.14	0.13	0.87	0.04	-0.297350517
Bed 1 vs. Bed 5	0.12	0.12	0.12	0.88	0.04	0
Bed 1 vs. Bed 6	0.12	0.08	0.1	0.9	0.04	0.666666667
Bed 1 vs. Bed 7	0.12	0.16	0.14	0.86	0.04	-0.576390418
Bed 1 vs. Bed 8	0.12	0.1	0.11	0.89	0.04	0.319601386
Bed 1 vs. Bed 9	0.12	0.1	0.11	0.89	0.04	0.319601386
Bed 1 vs. Bed 10	0.12	0.1	0.11	0.89	0.04	0.319601386
Bed 1 vs. Bed 11	0.12	0.08	0.1	0.9	0.04	0.666666667
Bed 2 v. Bed 3	0.16	0.14	0.15	0.85	0.04	0.280056017
Bed 2 v. Bed 4	0.16	0.14	0.15	0.85	0.04	0.280056017
Bed 2 v. Bed 5	0.16	0.12	0.14	0.86	0.04	0.576390418
Bed 2 v. Bed 6	0.16	0.08	0.12	0.88	0.04	1.23091491
Bed 2 v. Bed 7	0.16	0.16	0.16	0.84	0.04	0
Bed 2 v. Bed 8	0.16	0.1	0.13	0.87	0.04	0.89205155
Bed 2 v. Bed 9	0.16	0.1	0.13	0.87	0.04	0.89205155
Bed 2 v. Bed 10	0.16	0.1	0.13	0.87	0.04	0.89205155
Bed 2 v. Bed 11	0.16	0.08	0.12	0.88	0.04	1.23091491
Bed 3 v. Bed 4	0.14	0.14	0.14	0.86	0.04	0
Bed 3 v. Bed 5	0.14	0.12	0.13	0.87	0.04	0.297350517
Bed 3 v. Bed 6	0.14	0.08	0.11	0.89	0.04	0.958804158
Bed 3 v. Bed 7	0.14	0.16	0.15	0.85	0.04	-0.280056017
Bed 3 v. Bed 8	0.14	0.1	0.12	0.88	0.04	0.615457455
Bed 3 v. Bed 9	0.14	0.1	0.12	0.88	0.04	0.615457455
Bed 3 v. Bed 10	0.14	0.1	0.12	0.88	0.04	0.615457455
Bed 3 v. Bed 11	0.14	0.08	0.11	0.89	0.04	0.958804158
Bed 4 v. Bed 5	0.14	0.12	0.13	0.87	0.04	0.297350517
Bed 4 v. Bed 6	0.14	0.08	0.11	0.89	0.04	0.958804158
Bed 4 v. Bed 7	0.14	0.16	0.15	0.85	0.04	-0.280056017
Bed 4 v. Bed 8	0.14	0.1	0.12	0.88	0.04	0.615457455
Bed 4 v. Bed 9	0.14	0.1	0.12	0.88	0.04	0.615457455
Bed 4 v. Bed 10	0.14	0.1	0.12	0.88	0.04	0.615457455
Bed 4 v. Bed 11	0.14	0.08	0.11	0.89	0.04	0.958804158
Bed 5 v. Bed 6	0.12	0.08	0.1	0.9	0.04	0.666666667

Bed 5 v. Bed 7	0.12	0.16	0.14	0.86	0.04	-0.576390418
Bed 5 v. Bed 8	0.12	0.1	0.11	0.89	0.04	0.319601386
Bed 5 v. Bed 9	0.12	0.1	0.11	0.89	0.04	0.319601386
Bed 5 v. Bed 10	0.12	0.1	0.11	0.89	0.04	0.319601386
Bed 5 v. Bed 11	0.12	0.08	0.1	0.9	0.04	0.666666667
Bed 6 v. Bed 7	0.08	0.16	0.12	0.88	0.04	-1.23091491
Bed 6 v. Bed 8	0.08	0.1	0.09	0.91	0.04	-0.349428279
Bed 6 v. Bed 9	0.08	0.1	0.09	0.91	0.04	-0.349428279
Bed 6 v. Bed 10	0.08	0.1	0.09	0.91	0.04	-0.349428279
Bed 6 v. Bed 11	0.08	0.08	0.08	0.92	0.04	0
Bed 7 v. Bed 8	0.16	0.1	0.13	0.87	0.04	0.89205155
Bed 7 v. Bed 9	0.16	0.1	0.13	0.87	0.04	0.89205155
Bed 7 v. Bed 10	0.16	0.1	0.13	0.87	0.04	0.89205155
Bed 7 v. Bed 11	0.16	0.08	0.12	0.88	0.04	1.23091491
Bed 8 v. Bed 9	0.1	0.1	0.1	0.9	0.04	0
Bed 8 v. Bed 10	0.1	0.1	0.1	0.9	0.04	0
Bed 8 v. Bed 11	0.1	0.08	0.09	0.91	0.04	0.349428279
Bed 9 v. Bed 10	0.1	0.1	0.1	0.9	0.04	0
Bed 9 v. Bed 11	0.1	0.08	0.09	0.91	0.04	0.349428279
Bed 10 v. Bed 11	0.1	0.08	0.09	0.91	0.04	0.349428279