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Invertebrate Paleoecology of High Paleo-latitude Carboniferous Strata of the Tepuel-Genoa Basin, Argentina

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INVERTEBRATE PALEOECOLOGY OF HIGH PALEO-LATITUDE CARBONIFEROUS STRATA OF THE TEPUEL-GENOA BASIN, ARGENTINA

by

Kate Gigstad

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May 2018

ABSTRACT

INVERTEBRATE PALEOECOLOGY OF HIGH PALEO-LATITUDE CARBONIFEROUS STRATA OF THE TEPUEL-GENOA BASIN, ARGENTINA

by

Kate Gigstad

The University of Wisconsin-Milwaukee, 2018
Under the Supervision of Professor Dr. Margaret Fraiser

The Late Paleozoic Ice Age (LPIA), which began in the latest Devonian and ended in the Late Permian, was a time of active environmental changes. During this time, glaciers waxed and waned over the ancient continent of Gondwana that was situated over the southern pole. This time of transition from icehouse to greenhouse in the Permian is our closest analogue to our current environmental conditions and increased knowledge of our planetary past will greatly influence our future. Much of the previous research on marine invertebrate paleoecology during the LPIA occurs in far-field or low paleolatitude localities, but less is known about the state of near-field invertebrate faunas of this time. The focus of this study is on the paleoecology of the high paleolatitude communities in the Tepuel-Genoa Basin in western Argentina in which the hypothesis that ice proximal, near-field paleocommunities differed significantly from those in far-field regions during glacial episodes is tested. Sedimentological and paleoecological data were collected and analyzed in two sections of the Pampa de Tepuel Formation (the lower and middle sections) in the Tepuel-Genoa Basin. In the lower Pampa de Tepuel Formation, diversity and fossil abundance was higher than in the middle section. These differences are accredited to changes in environmental factors attributed to the proximity to glacial sediment input at the time of deposition. Similar to low latitude studies, the effects of the LPIA glacial fluctuations differ by location. However, the changes in the high-latitude paleocommunities occur with fluctuations in the environment within the Pampa de Tepuel Formation.

To

my parents,

Jan and Barb Gigstad,

and to Michael Bryant

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1. Introduction

The late Paleozoic Ice Age (LPIA) ~374-256 Ma was a unique and environmentally dynamic time in Earth's history (e.g., Crowell and Frakes, 1970; Crowell, 1983; Caputo et al., 2008; Isaacson et al., 2008; Isbell et al., 2012; Frank, 2015). It was one of Earth's few "icehouse" environmental states, which comprise less than 25 percent of the planet's history (Montañez and Poulsen, 2013). The LPIA was the largest and longest icehouse interval to occur in the Phanerozoic (e.g., Fielding et al., 2008a; Montañez and Poulsen, 2013). It is presently the closest deep time analogue to modern climate change because its end marks the only icehouse to greenhouse transition that occurred when the planet had both complex fauna and flora, and evidence for high latitude glaciation, characteristics similar to the current state of the planet today (e.g., Gastaldo et al., 1996; Montañez and Soreghan, 2006; Isbell et al., 2008, 2012).

Gondwana, the landmass comprised of the modern continents of South America, Africa, Antarctica, India and Australia, was situated over the South Pole at the time of the LPIA (e.g., Crowel and Frakes, 1970; Crowell, 1983; González Bonorino, 1992; Isbell et al., 2003). There is overwhelming evidence for ice cover over the southern supercontinent during the late Paleozoic, but the presence of ice sheets and glaciers in the northern hemisphere is still under debate but unlikely (e.g., Crowell and Frakes, 1970; Crowell, 1983; Isbell et al. 2003 and 2016). Sedimentological data has shown evidence for glacial episodes comprising many small glaciers that waxed and waned over Gondwana during the LPIA (Fielding et al., 2008b; Lópes-Gamundí and Buatois, 2010; Isbell et al., 2012, 2016). Three glacial episodes have been identified from basins in Gondwana spanning times from the Late Devonian to the Early Mississippian (Glacial Episode I), Late Mississippian to Middle Pennsylvanian (Glacial Episode II), and finally Late

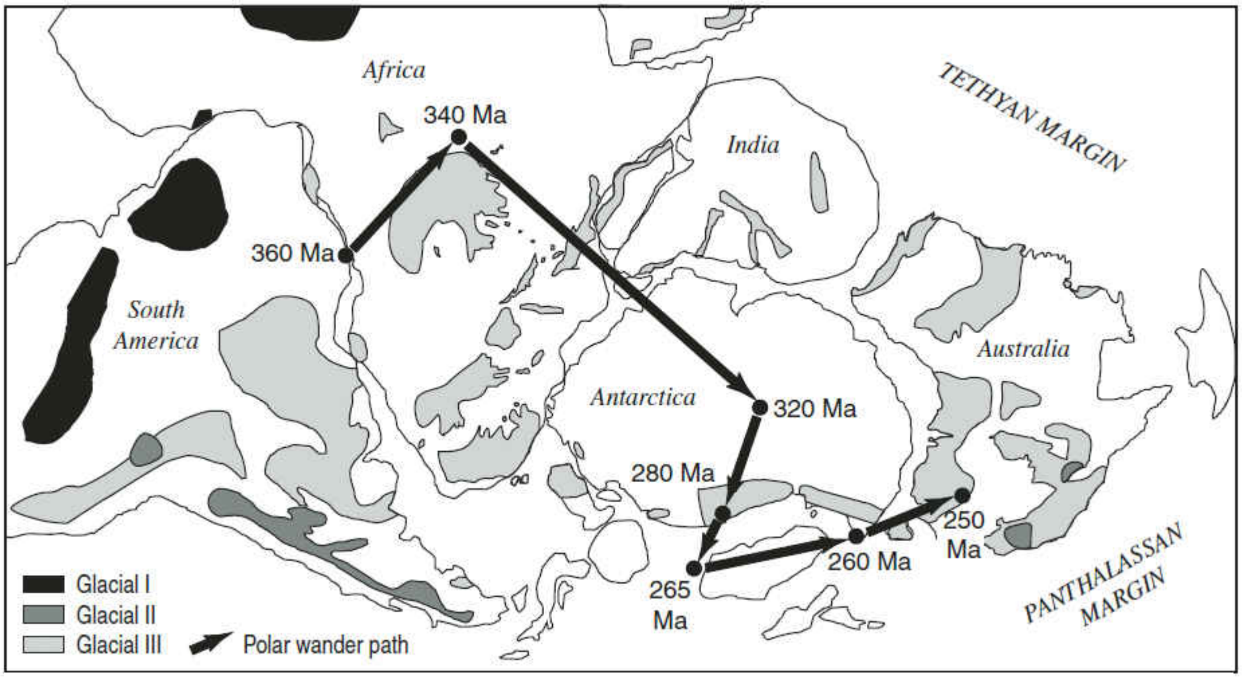


Figure 1. Path of the South Pole over Gondwana relative to Glacial Episodes. From Frank et al. 2008 (modified from Powell and Li, 1994 and Isbell et al., 2003).

Pennsylvanian to the Early Permian (Glacial Episode III) (Fig. 1; Lópes-Gamundí. 1997; Isbell et al. 2003).

The geochemical record reveals that the LPIA was a time of higher $\delta^{13}C$ and is hypothesized to have been due to organic carbon sequestration resulting to result in low CO_2 concentrations (Gastaldo et al. 1996; Veizer et al., 1999; Frank et al. 2008). High quantities of oxygen isotope $\delta^{18}O$ concentrations are interpreted as the result of increased ice expansion and drop in global temperatures causing high atmospheric O_2 due to the drawdown of CO_2 and decreased weathering (Gans et al., 1999; Veizer et al., 1999; Frank et al. 2008).

Much of the previous paleoecological research on the LPIA has focused on low paleo-latitude regions ('far-field'). For example, Heim (2009) found evidence for increased faunal turnover but no substantial decrease in ecological diversity in paleoequaitoral regions that are now the U.S. states of Arkansas and Oklahoma. In the Illinois Basin of the central United States, Bonelli and Patzkowsky (2008, 2011) found persistent faunal assemblages but less distinction between the near-shore and off-shore communities that were more greatly defined prior to the onset of the LPIA. Low paleolatitude research has also revealed that narrowly distributed brachiopod genera experienced extinctions due to low thermal tolerances (Stanley and Powell, 2003; Powell, 2005, 2007). Powell (2008) discovered a mass extinction of fauna in the low-latitude Central Appalachian Basin that specifically targeted genera with narrow latitudinal ranges in shallow near-shore areas.

Previous research on near-field paleocommunities hint at key similarities in ecosystem responses between low- and high-paleolatitudes. Research from western Argentina on high paleo-latitude brachiopods and bivalves revealed increases in taxonomic turnover, decreased diversity and restructuring within paleocommunities (Balseiro, 2016) in the Early Carboniferous attributed to glacial episodes (Sterren and Cisterna, 2010).

Still, more research is required for high paleo-latitude areas as little is known of the extent to which 'near-field' organisms responded similarly to 'far-field' organisms. The study herein, focuses on near-field paleocommunities from the western margin of Gondwana exposed in present-day Patagonia, Argentina which was located above a latitude of 60°S, and experienced at least one of the three LPIA glacial episodes (Fig. 1; Fig. 2; Veevers and Powell, 1987; López-Gamundí and Buatois, 2010). This study is a step towards filling that gap in our understanding of the effects on the high-latitude paleocommunities due to environmental fluctuations during the LPIA.

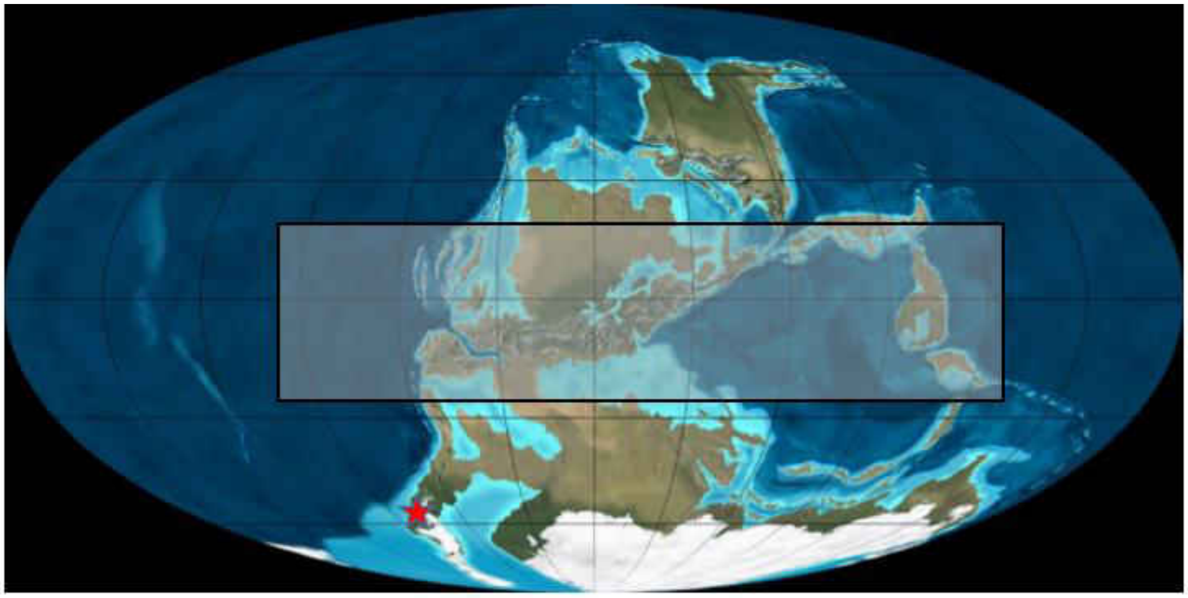


Figure 2. Earth during the Carboniferous. Shaded box shows the low-latitude region where most research during the LPIA has taken place. The red star denotes high-latitude research site in Argentina. Modified from Blakey, 2003.

1.1 Hypothesis

The purposes of this study are to 1) quantify the paleoecology of high paleolatitude near-field marine invertebrate fossil assemblages during the late Paleozoic Ice Age in the Tepuel-Genoa Basin in western Gondwana, and 2) compare these results to those of paleocommunities from lower and higher paleolatitudes. *I tested the over-arching hypothesis that the paleoecology of ice proximal, near-field paleocommunities differed significantly from those located distally in far-field regions during LPIA glacial episodes* (Fig. 2). Within this overarching hypothesis I also assessed how glaciers affected the marine invertebrate communities in near-field environmental settings via two *working hypotheses*: 1) Low diversity and low fossil abundance in the Tepuel-Genoa Basin occur as a result of proximity to glaciers,; and 2) faunal assemblages distal to glaciers in the Tepuel-Genoa Basin were more diverse and not adversely affected by glacial input.

2. Geologic Setting

The geologic origin of Patagonia and its relation to South America and Gondwana has a history of debate. Over the decades there have been two major hypothesis pertaining to Patagonia's origin. The first suggests evidence of Patagonia being autochthonous to South America (Forsythe, 1982; Dalla Salda et al. 1990), and the second suggests Patagonia as being an allocthonous terrane that was accreted to Gondwana in the Late Paleozoic (e.g., Pankhurst, 2006; Ramos, 1984; Rapelini et al., 2010). The second hypothesis would explain the lack of metamorphism in the Tepuel-Genoa Basin (the location of this study) but metamorphism to the east and the west of the Tepuel Basin due to accretionary processes (Fig. 3; Ramos, 2008). Recent age-dating studies on Patagonian basement rock suggest Patagonia was a para-autochthonous terrane (Pankhurst, 2006; Ramos, 2008; Pagani and Taboada, 2010).

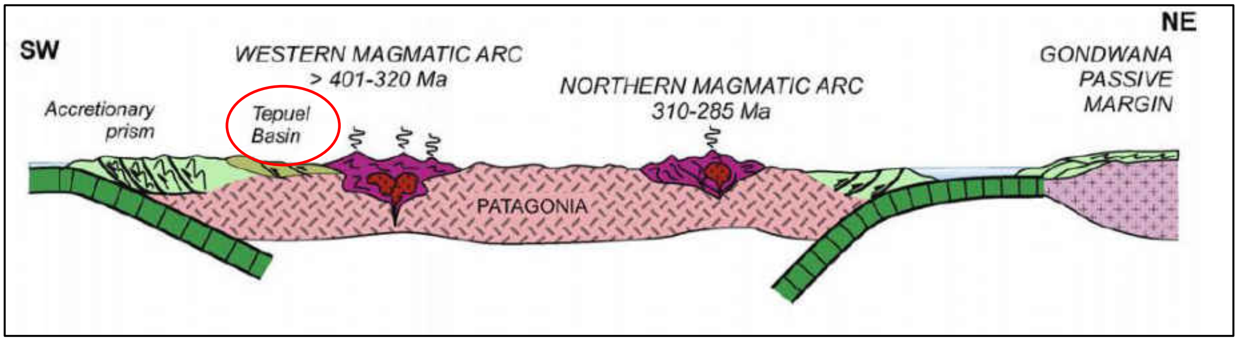


Figure 3. Cross section of Patagonia showing accretionary processes. Tepuel Basin is the location of this study Modified from Ramos, 2008.

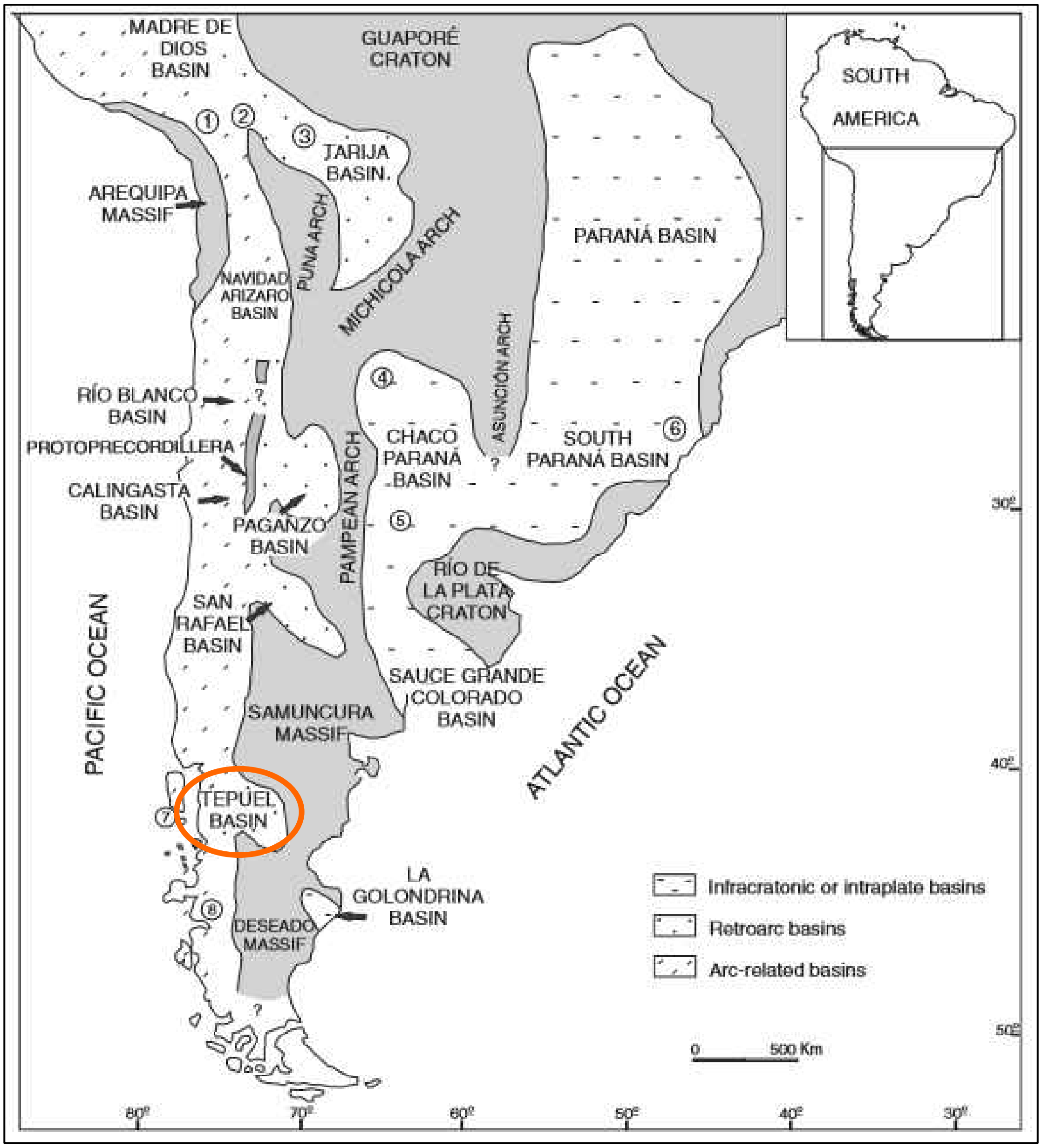


Figure 4. Orange circle indicates location of research in the Tepuel-Genoa basin in western Patagonia. Modified from Limarino and Spalletti, 2006.

The western boundary of Patagonia has several basins formed during the Upper Paleozoic that provide an almost complete succession of the stratigraphic record of Carboniferous age strata (Limarino and Spalletti, 2006). The Tepuel-Genoa Basin is surrounded by the Samuncura and Deseado mastiffs and was formed in the Late Mississippian around 330

Mya (Fig. 4; Isbell, 2003; Limarinio and Spalletti, 2006). It is considered to be a retroarc basin showing only minor metamorphic deformation (Fig. 3; Limarino and Spalletti, 2006; Ramos, 2008). Evidence also shows that the Carboniferous age strata of the Tepuel-Genoa Basin to be glaciomarine providing both glacial evidence and an extensive fossil record making this a model area for this study (e.g; López Gamuni, 1987).

The specific area of this study is the Pampa de Tepuel Formation in the Tepuel Hills locality near the town of Tecka around 22 km to the North (Fig. 5). The Pampa de Tepuel Formation lies between the Jaramillo and Mojón de Hierro Formations; together these make up the three formations in the Tepuel-Genoa Basin at Tepuel Hills. The Pampa de Tepuel Formation was deposited from the middle Mississippian to the early Permian, is almost 3000 meters thick, and was determined to have been deposited in a marine slope setting (Andreis and Cuneo, 1989; Fielding et al., 2008; Isbell et al. 2003, 2012; González and Saravia, 2010). The Pampa de Tepuel Formation contains course-grained sediment within deep marine mudrocks, which is mostly produced through rainout and subglacial till showing evidence for glacial influence (González-Bonorino, 1992). Possible glacial pavements have

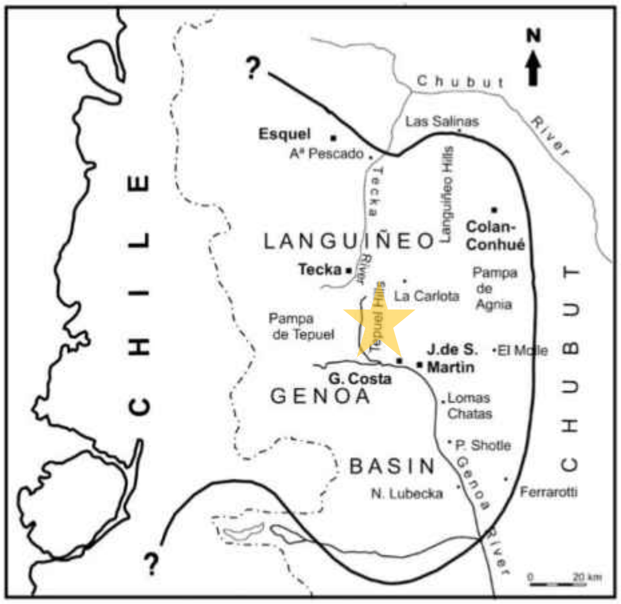


Figure 5. Yellow star denotes location of research within the Tepuel-Genoa Basin. Modified from González and Saravia, 2010.

also been identified (e.g., González, 2003; Limarino and Spalletti, 2006) although they have more recently been debated (Isbell 2013; Pauls, 2014). There is also non-glacially influenced marine deposits such as dark siltstone and fine-grained sandstone where the fossil assemblages in the Tepuel Hills are preserved (e.g., Pagani and Taboada, 2010; Pauls, 2014; Braun et al., 2015). The alternating deposition of glacial sediment and dark siltstone has been interpreted to indicate that up to six glacial episodes occurred in this region (e.g.; González and Saravia, 2010; Taboada, 2010).

The biostratigraphy of this region is based mainly on brachiopod and mollusk faunas that has been revised many times since the first faunal zonations were established (e.g., Amos and Rolleri, 1965; Pagani and Taboada, 2010). In the Pampa de Tepuel Formation, at least two biozones have been identified: *Lanipustula* biozone (named for brachiopod *Lanipustula patagoniensis)* and *Costatumulus* biozone (named for brachiopod *Costatumulus amosi*) (e.g. Taboada, 2010; Pagani and Taboada, 2010). The focus of this study is on the *Lanipustula* biozone, formally the Levipustula Zone (Amos and Rolleri, 1965) which has a time frame of Late Mississippian to Late Pennsylvanian (Fig. 6; Pagani and Taboada, 2010).

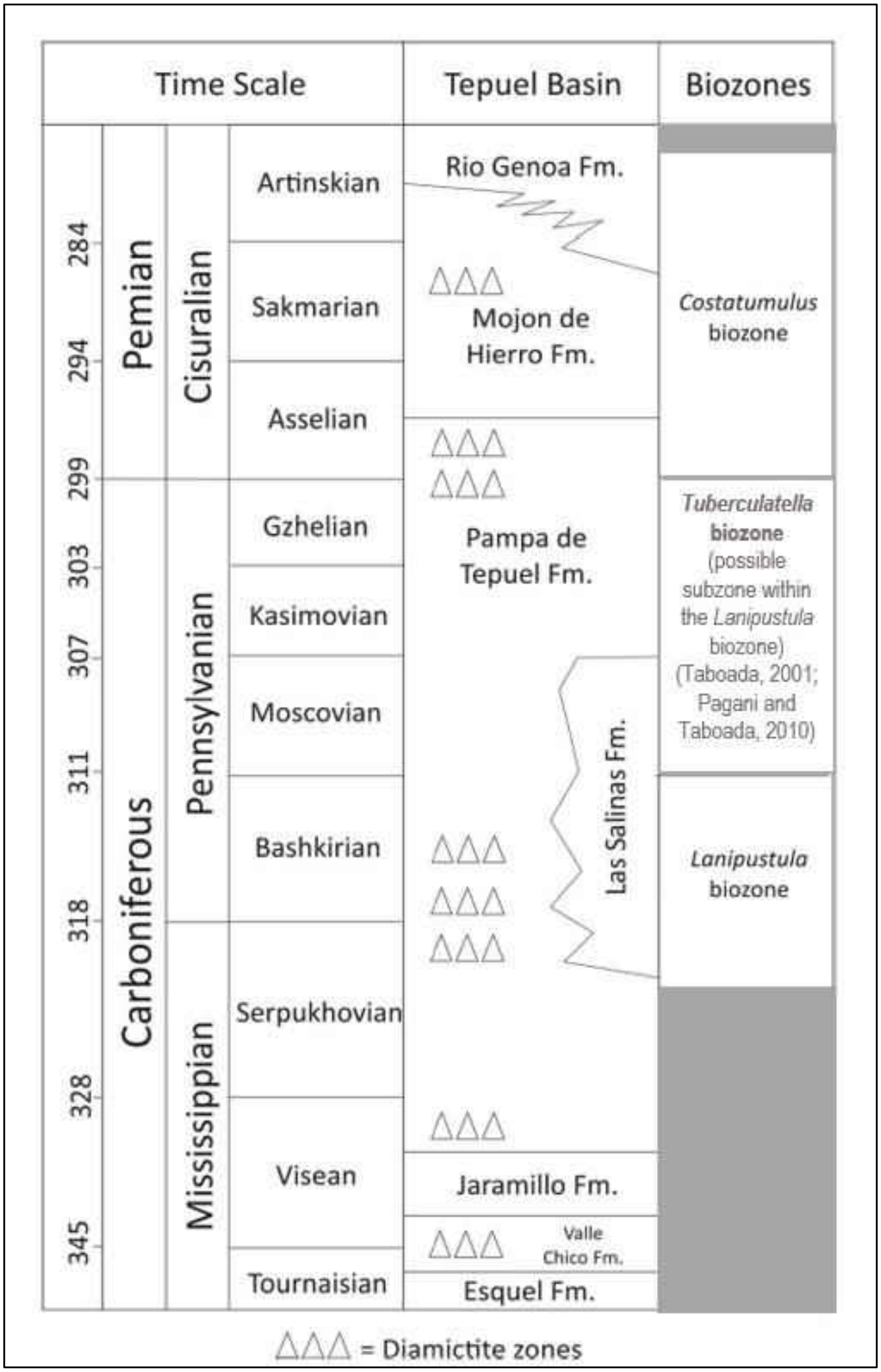


Figure 6. Lithostratigraphy and biostratigraphy of the Late Paleozoic in the Tepuel-Genoa Basin. Modified from Taboada, 2008, 2010; Cesari et al., 2011. Modified from Taboada, 2008, 2010; Pagani and Taboada, 2010; Pauls et al., 2014; Braun et al. 2015.

Previous paleoecological research conducted in the Pampa de Tepuel Formation has indicated environmental fluctuations and diversity variations in paleocommunities during the LPIA. Pauls et al. (2014) and Dineen et al. (2010) found relatively high alpha diversity in the middle of the Pampa de Tepuel Formation while Braun et al. (2015) found that many of the fossil assemblages in the lower Pampa de Tepuel Formation were diminished and low in alpha diversity.

There were two sections in the Tepuel Hill where data were collected for this study, both belonging to the Pampa de Tepuel Formation. One measured section for the study herein was in the lower part of the Pampa de Tepuel Formation which is situated between those of Braun et al. (2015) (where it slightly overlaps based on GPS data) and Dineen et al. (2013). The other section measured in this study is in the middle of the Pampa de Tepuel Formation and lies above all previous studies including that of Pauls et al. (2014). The addition of my data will create a more complete analysis from the bottom to the upper middle of the Pampa de Tepuel Formation (Fig. 7).

Figure 7. Aerial view image from Google Earth of the Pampa de Tepuel Formation near Tecka, Argentina in stratigraphic order. Blue tacs represent previously sampled areas and yellow tacs represent areas sampled in this study.

3. Methods

Within the Pampa de Tepuel Formation, two sections were measured to study the sedimentology and paleoecology of the Carboniferous strata of the Tepuel-Genoa Basin in western Argentina deposited during LPIA. The lower Pampa de Tepuel (LPDT) section began near the base of the Pampa de Tepuel Formation (S43° 41’ 00.2”, W70° 44’ 55.8”) and 88 m were measured there. The middle Pampa de Tepuel section (MPDT) (S43° 41’ 13.0”, W70° 42’ 59.8”) was measured for 312 m near the upper middle portion of the Pampa de Tepuel Formation. The two sections were measured using a Jacob staff and an Abney level. Sedimentological evaluation in the field included determining lithology, grain size, diagenesis, and sedimentary structures. These data were used to construct stratigraphic columns using Adobe Illustrator, a vector graphics editor.

Fossils were identified in the field to the genus level. Brachiopods and bivalves were tallied for full articulated specimens and tallied for pedicle and brachial or left and right valves. Only the whole specimen and largest number of either of the valves were counted which is referred to as the minimum number of individuals method (Gillinsky and Bennington, 1994). Crinoid ossicles were measured and counted individually in the field. There are no reliable methods for using the number of ossicles to calculate abundances of individual crinoids (Moore and Jefords, 1968) so numbers were calculated using modern crinoid ossicles counts of a maximum of 350 (Roux et al., 2002). Since all the counts in this study were less than 350, a total of one individual crinoid was counted for each fossil assemblage unless there were different size ossicles and then two individuals were counted. In the LPDT bryozoans were numerous and overlapping. They were only counted if the taper toward the bottom of the colony was visible because of the need to decrease the possibility of counting a colony more than once due to breakage. The tapered area was visible on many of the colonies.

In each fossil assemblage, a minimum of 25 fossils were collected, when available, to ensure statistical significance (Forcino, 2012). This number included bryozoan colonies, disarticulated valves and crinoid ossicles. Some beds in the MPDT were not able to meet this criterion. A rarefaction curve was used to rule out sampling biases and to assure that enough data was collected to infer accurate results (Hammer and Harper, 2006). In a rarefaction analysis the expected number of individuals or taxa is computed when a sample is drawn at random from a sample that represents the fossil assemblage (Gotelli and Colwell, 2010). The curve is plotted with number of sample location on the y-axis and number of genera or number of individual fossils from each sample on the x-axis. If the curve flattens out, enough data has been collected to create reliable results.

In each fossil assemblage, genera were totaled and given a mean rank order which gives each genera a rank based on the abundance (1 being most abundant) in each fossil assemblage. Breadth of distribution coefficient was also established to show the number of fossil assemblages in which each genus was found (Clapham et al., 2006). Diversity and evenness indices such as the Simpson diversity index for dominance (1-D), the Shannon-Weiner index of diversity (H’), and evenness (E) were run on the fossil data to evaluate diversity in the invertebrate communities (Hammer and Harper, 2006). The Simpson diversity index calculates the probability that two randomly selected individuals are from the same group or genera (Hammer and Harper, 2006). The result will be closer to one if there is one group that is more dominant. The Shannon-Weiner diversity index calculates the probability to predict the next selected individual from a group and is based on relative abundance as well as total number of taxa (Hammer and Harper, 2006). A higher number (closer to one) will signify a higher diversity. Evenness is calculated to show how even the counts of genera are within each fossil assemblages. Statistical Z-tests were conducted to determine if the most abundant genus in each section (LPDT and MPDT) had significantly larger numbers than the rest of the genera in each section.

Multivariate statistics used in this study are cluster analysis (Euclidian, Chord, Bray-Curtis, Dice, and Rho), rarefaction, and detrended correspondence analysis (DCA) using the PAST (Paleontological Statistics) computer program (free to download from and online source) to analyze for multivariate statistics (Hammer et al., 2001). Cluster analysis groups fossil assemblages by likeness or similarities and displays them on a graph called a dendrogram (Hammer and Harper, 2006). The farther the fossil assemblages are on the dendrogram the less alike they are interpreted to be. DCA is another way to show relationships between data in a 3D plot meaning that it is plotted on 3 axes. Clusters of data closer together are more similar than those farther away (Hammer and Harper, 2006).

The functional groups in the community were also evaluated to help understand the community structure and modes of life such as feeding methods and locomotion (Clapham et al, 2006). This data was collected from the Paleobiology database (fossilworks.org).

4. Results

4.1 Sedimentology

In the two sections of the Pampa de Tepuel Formation examined herein, seven facies were identified: 1) Very fine- to medium-grained sandstone with lonestones, 2) clast-rich sandy conglomerate, 3) fossil-rich muddy siltstone, 4) fossil-poor sandy siltstone, 5) sandy siltstone with lonestones 6) fine-grained sandstone, and 7) clast-poor medium diamictite.

4.1.1 Lower Pampa de Tepuel Formation (LPDT)

The LPDT section herein begins approximately 450 m after the boundary of the Jaramillo Formation and above fossil horizons 1 through 8 measured by Braun et al. (2015). My measured section overlaps with Braun's (2015) fossil horizons 9 through 11. The LPDT contained three of the identified lithofacies: very fine- to medium-grained sandstone, clast-rich sandy conglomerate, and fossil-rich muddy siltstone. Almost 70 percent of this measured section is covered by vegetation and scree from above, and exposure to dangerous weather conditions limited our time on the outcrop. Nevertheless, 88 m were measured (Fig. 8).

4.1.1.1 Very Fine- to Medium-Grained Sandstone with Lonestones Facies

The very fine- to medium-grained sandstone with lonestones facies marks the base of the measured LPDT section and has an average strike of 30° and average dip of 31°. The sandstone is massive, orange in color, and contains discontinuous lenses (between 10 and 40 cm) of a medium-grained, green sandstone (Table 1-1; Fig. 10-A). The very fine- to medium-grained sandstone with lonestones facies containing rounded to subrounded gravel- and cobble- sized lonestones that increases in abundance up the section for approximately 20 m until it transitions into the clast-rich sandy conglomerate facies (described below) (Fig. 8). The transition between these two facies is not visible due to scree from above. The very fine- to medium-grained sandstone with lonestones facies includes possible slump structures that are often associated near the medium-grained, green sandstone lenses as well as some mineral filled fractures. However, much of the sandstone outcrop is lichen-covered and badly weathered. No body fossils were found in this facies.

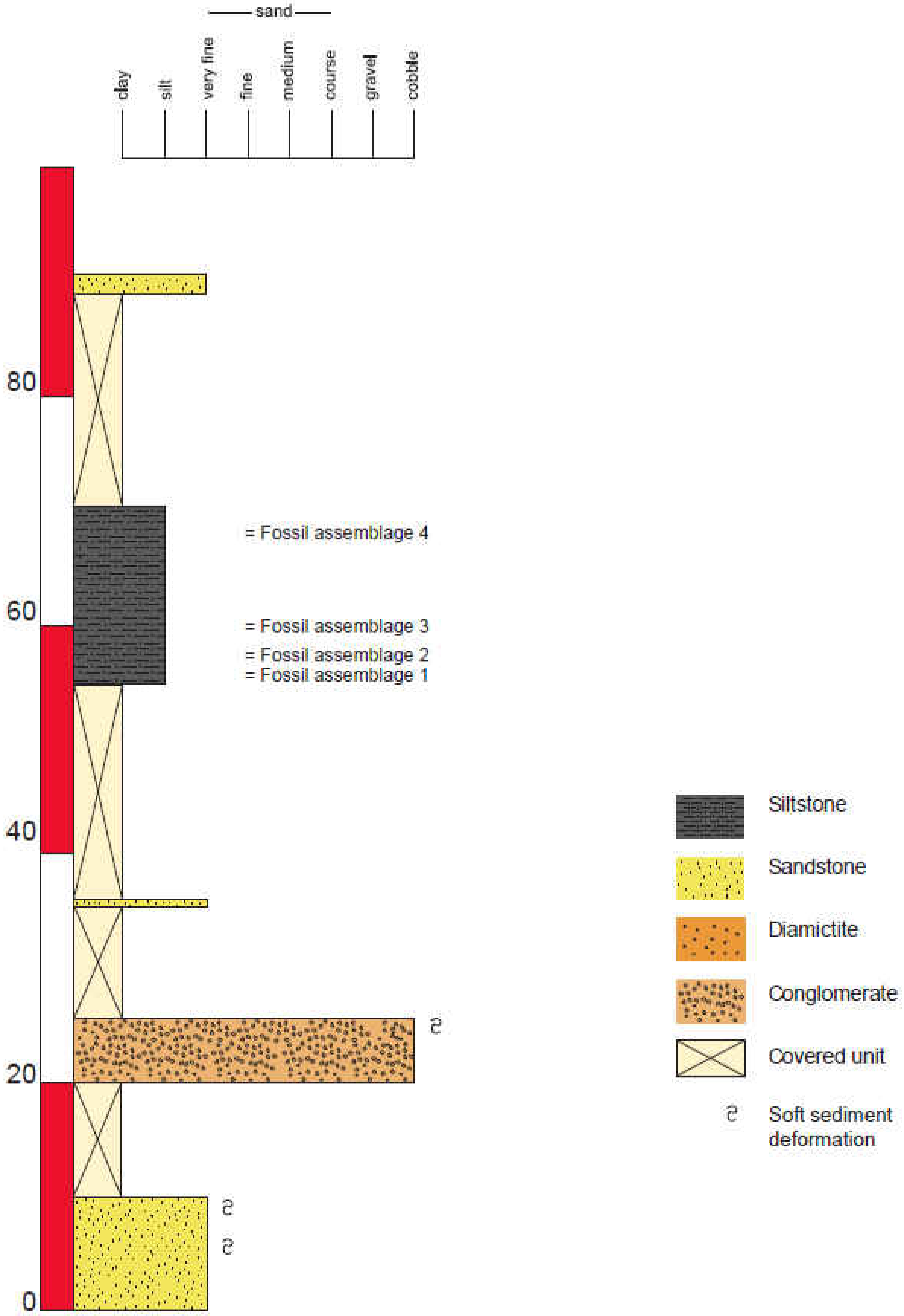
4.1.1.2 Clast-Rich Sandy Conglomerate Facies

The very fine- to medium-grained sandstone with lonestones facies transitions into a clast-rich sandy conglomerate facies containing cobble-sized, rounded clasts as well as angular interclasts of sedimentary and igneous origins (Table 1-2; Fig. 8; Fig. 10-B). This facies is massive and has a very fine-grained sand matrix. It also contains very course-grained sand grains that are subangular (Fig. 10-C). The clast-rich sandy conglomerate is approximately 5 to 6 m thick and also did not contain body fossils. The very fine- to medium-grained sandstone and clast-rich sandy conglomerate were only seen from 0 to 45 meters in the LPDT. Above the clast-rich sandy conglomerate facies there about 10 m of scree before there is a thin outcrop of very fine- to medium grained sandstone with lonestones facies (fig. 8).

4.1.1.3 Fossil-Rich Muddy Siltstone Facies

Eighteen meters of scree covers the area between the clast-rich sandy conglomerate facies and the fossil-rich muddy siltstone facies (Fig. 8). Strike and dip changes in these beds on the outcrop to 50° and 23° respectively. The fossil-rich muddy siltstone facies is dark gray in color (Table 1-3). This facies outcrops from 54 meters to 70 meters and contains all the fossil specimens from this section of the LPDT examined in this study (Fig. 8). Bedding varied with laminations that are 1 mm to 4 cm in thickness (Fig. 10-D). Fossils were deposited in layers of 1 to 5 mm and the layers are 5 mm to 3 cm apart (Fig. 10-E).

Figure 8. Stratigraphic representation of the LPDT section.



4.1.2 Middle Pampa de Tepuel Formation (MPDT)

The analysis of the sedimentology in the MPDT indicated four facies: fossil-poor sandy siltstone, fossil-barren sandy siltstone with lonestones, fine-grained sandstone, and clast-poor intermediate diamictite. Almost a third of this section is covered by vegetation and scree from above (Fig. 9).

4.1.2.1 Fossil-Poor Sandy Siltstone Facies

Outcrops of this facies have an average strike of 27° and an average dip of 25°. Throughout this MPDT, the fossil-poor sandy siltstone facies has color ranges from medium gray to brown. Some thin layers of very fine sand are found interbedded with the fossil-poor sandy siltstone facies near the base of the section. Only this facies of the MPDT examined in this study, contain fossils. Fossil abundances drop to zero when lonestones and sedimentary structures became abundant (Fig. 9). Much of the fossil-poor sandy siltstone facies shows signs of oxidation and the formation of concretions (Fig. 10-F; Table 1-4). Bedding varies from laminated to thin, between 3 mm to 5 cm, and is often fissile. Secondary fracturing was found throughout the siltstone that often cross cut beds. Interclasts of a darker gray siltstone are visible in the sandy siltstone around 115 m, and small patches of course sand and granules (1-4 mm in diameter) are dispersed in the siltstone beginning around 125 m.

4.1.2.2 Fossil-Barren Sandy Siltstone with Lonestones Facies

This facies is demarcated at 140 m where no invertebrate body fossils were found (Table 1-5; Fig. 9). However, some small, horizontal unidentified trace fossils occur around 164 m. Bedding in this facies is laminar to thin and varied from 1 mm to 7 cm. Soft sediment deformation, including slumping and folding, is present at around 160 m and again at 240 m (Fig. 10-G). The siltstone also dips more severely to about 40° around 160 m. Cobble size, rounded lonestones are found in the fossil-barren sandy siltstone layers at 237 m (Fig. 10-H). Lenses of course-grained sand and pebble-sized sediments were also found within this facies (Fig. 10-I). Slight metamorphism is indicated by mineral filled fractures and possible slicken sides around 150 m.

4.1.2.3 Fine-Grained Sandstone Facies

The fine-grained sandstone facies is interbedded with the fossil-barren, sandy siltstone facies from 156 m to 190 m and again between 240 and 247 m (Table 1-6; Fig. 9). Bedding is think to medium and ranged between 1.5 cm and 24 cm. Most of this fine-grained sandstone facies has a yellow-orange coloration. At 169 m, the fine-grained sandstone facies contained ripple structures and crossbedding, and at 240 m wave ripple structures are visible with mud draping (Fig. 9; Fig. 10-J). The fine-grained sandstone also contained soft sediment deformation in the form of slump and fold structures. Low-grade metamorphism can also be seen in the fine-grained sandstone in the form of fracturing. Between 241 and 244 m there are larger beds (averaging 21 cm) of fine-grained sandstone with sharp contacts interbedded with the siltstone (Fig. 10-K).

4.1.2.4 Clast-Poor Intermediate Diamictite Facies

At 262 m, a clast-poor intermediate diamictite interbeds with finely laminated fossil-barren, sandy siltstone facies (Table 1-7; Fig.9; Fig. 10-L). Two beds of this diamictite facies are visible and about 20 cm thick. They contain large cobble- to pebble-sized clasts of an unknown (due to time constraints) darker lithology, as well as angular very course sand, silt and mud-sized grains.

Figure 9. Stratigraphic representation of the Middle Pampa de Tepuel section.

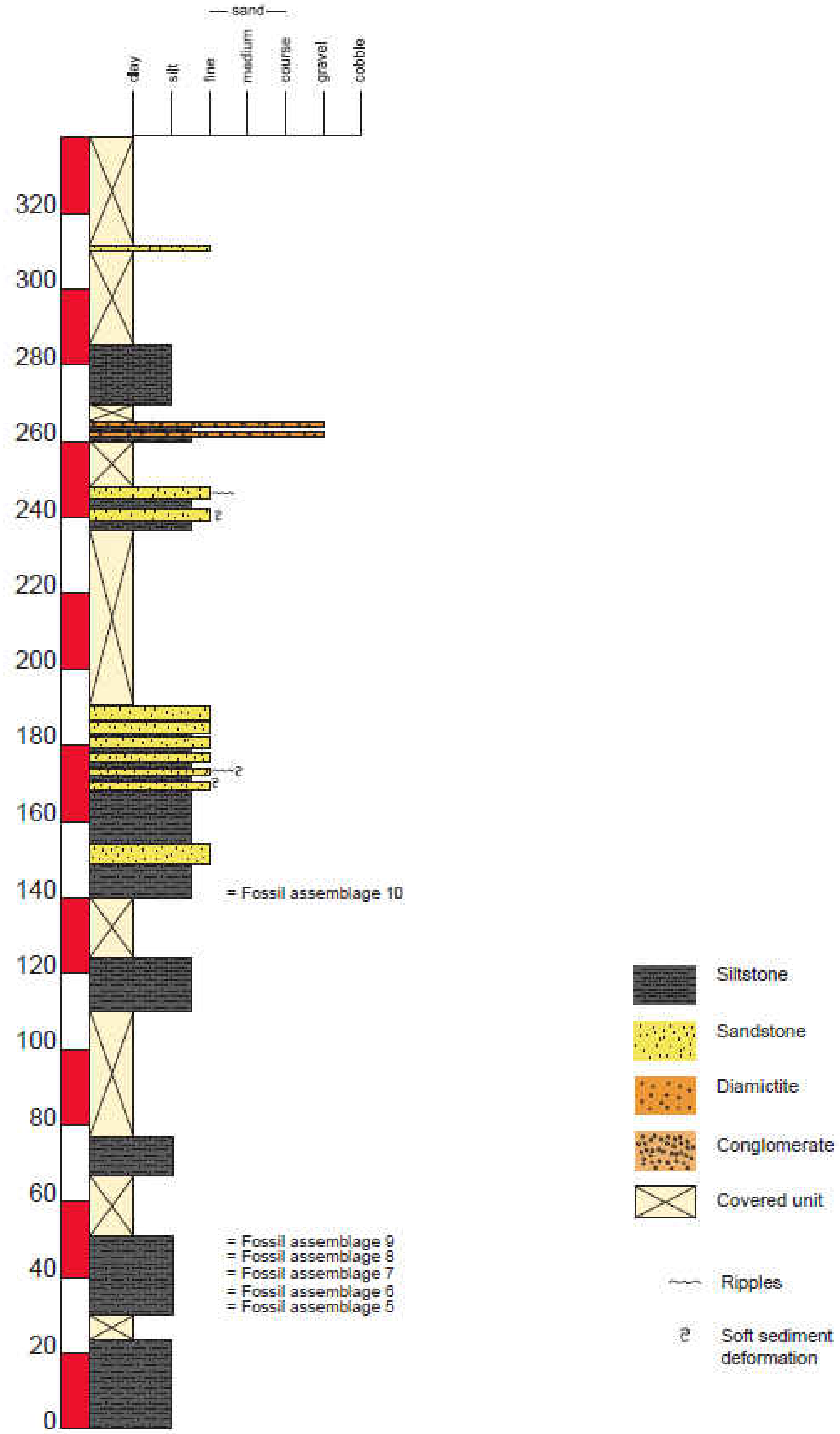
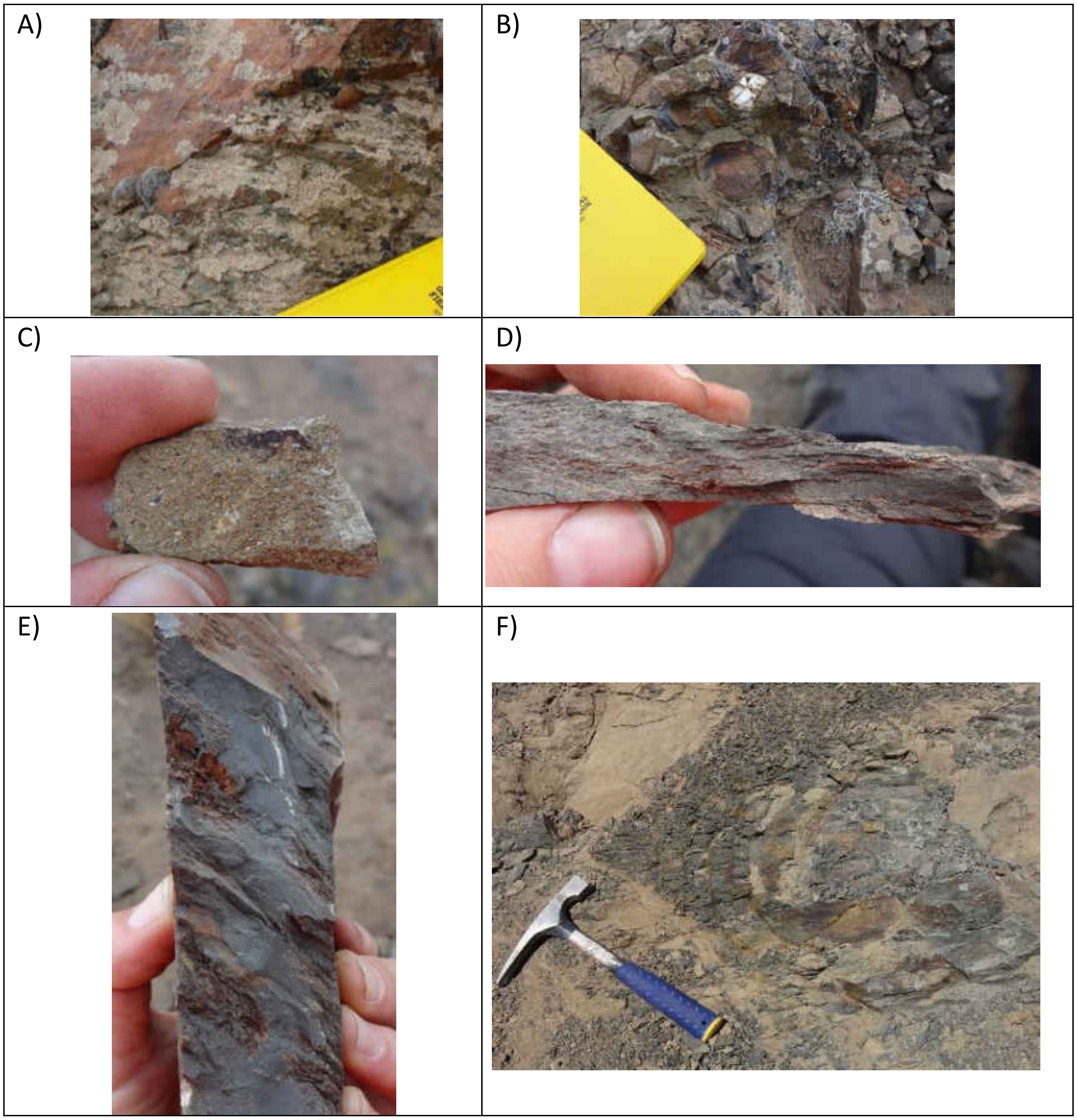


Table 1. Summary of facies found in the Lower and Middle Pampa de Tepuel Formation.

Facies Type	Lithology	Sedimentary Structures	Bedding Characteristics	Interpretations
1) Very fine- to medium-grained sandstone	Very fine grained sandstone Orange in color Lenses of medium-grained green sandstone Rounded gravel to cobble sized lone stones	Slump Structures	Massively bedded	Possible debris flow/mass transport
2) Clast-rich sandy conglomerate	Medium to course sand with rounded and sub rounded cobble size clasts Very course subangular sand size clasts Angular interclasts	None identified	Massively Bedded	Possible debris flow/mass transport
3) Fossil-rich muddy siltstone	Mud with very fine-to-fine sand and silt size grains Fossil rich	None identified	Laminations of 1 mm to 4 cm	Deep slope depostion below storm wave base

4) Fossil-poor sandy siltstone	Silt and very fine sand particles	Pockets of rounded to subrounded very course sand size grains Interclasts	Varied	Deep slope depostion below storm wave base
5) Fossil-barren sandy siltstone with lonestones	Silt and very fine sand particles Rounded cobble and gravel size lone stones	Slump and fold structures Clusters of course grained subrouned to rounded sediment.	Varied	Deep slope below storm wave base Lone stones and pockets of course grains due to distal glacial input or glaical rain-out
6) Fine-grained sandstone	Fine to very fine sand grains Yellow-orange coloration	Ripples with mud drapes Slump and fold structures	Varied	Deep slope injections due to turbidity currents
7) Clast-poor intermediate diamictite	Contains rounded clasts and fine-grained matrix of sand, silt and clay	None seen	20 cm	Small scale debris flows of glacial material

Figure 10. Images of facies and sedimentary structures found in the LPDT and MPDT. A) Contact between very fine-grained orange sandstone medium-grained green sandstone. Also a possible slump structure. B) Clast-rich sandy diamictite with rounded to subrounded lonestones and angular interclasts. C) Subangular very course sand sized grains within the very fine- to medium-grained sandstone facies. D) Laminated bedding in the fossil-rich muddy siltstone. E) Fossil layers found in the fossil-rich muddy siltstone. F) Concretions and oxidation found in the fossil-poor sandy siltstone. G) Soft sediment deformation fold nose in the fossil-barren sandy siltstone with lonestones. H) Cobble size rounded lonestone in the fossil-barren sandy siltstone with lonestones. I) Course sand and rounded pebble-sized grains in fossil-barren sandy siltstone with lonestones. J) Ripple structure in fine-grained sandstone interbedded with fossil-barrens sandy siltstone with lone stones. K) Beds of fine-grained sandstone interbedded with fossil-barren sandy siltstone with lonestones. L) Clast-poor intermediate diamictite.



G)

H)

I)

J)

K)

L)

4.2 Paleoecology

4.2.1 Lower Pampa de Tepuel (LPDT) Formation

A total of four fossil assemblages were excavated in the LPDT at 54.5, 56, 60, and 67 meters (Appendix A). Alpha diversity ranges from six to 10 genera distributed among seven classes in the four fossil assemblages. The total fossil count for the LPDT section was 248 fossil elements. The genera with the highest numerical abundance in all four of the levels sampled were bryozoans *Fenestella* and *Fistulamina* (Fig. 11; Fig. 12). Bivalves like *Paleolima*, *Orbiculopectin* and *Limipectin*, brachiopods *Krotovia* and *Lanipustula*, and rugose corals were present in smaller numbers (Fig. 12). An analysis of distribution of fossil individuals counted in the four fossil assemblages of the LPDT shows a relatively even distribution of fossils throughout

Figure 11. Bryozoan rich siltstone in the LPDT.

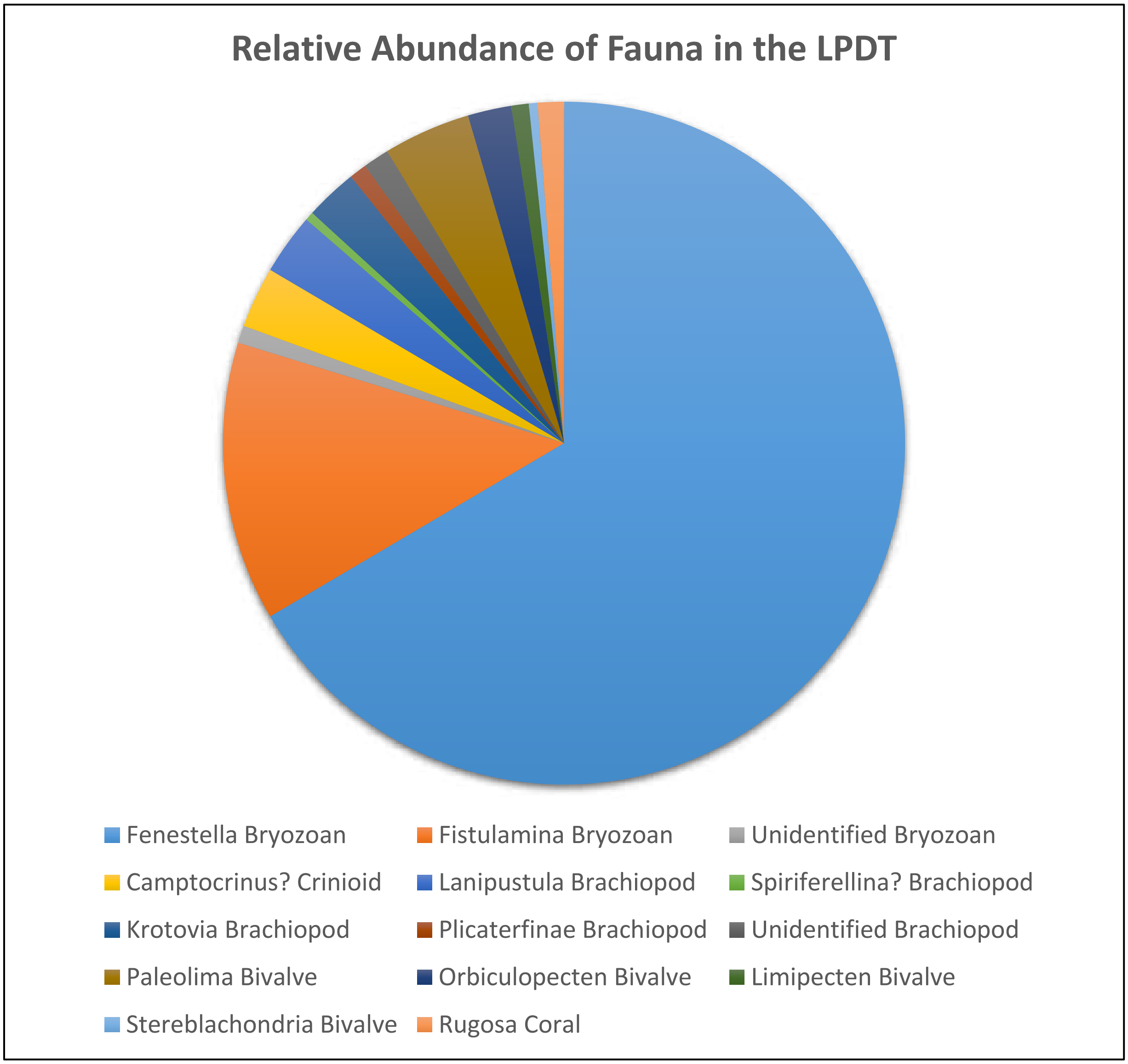


Figure 12. Relative abundance at the genus level in all fossil assemblages of the LPDT.

the LPDT. Breadth of distribution of genera showed that *Fenestella*, *Fistulamina,* and *Camptocrinus?* were found in 100 percent of the fossil assemblages, and *Lanipustula*, *Paleolima*, and rugose coral were found in 75% of the fossil assemblages in the LPDT (Table-2).

The Simpson diversity index (1-D) for dominance results ranged from 0.35 to 0.62 among the sampled fossil accumulations with values closer to 1 indicating a higher dominance of any one particular genus (Appendix A). The fossil assemblage at 56 meters shows the least dominance of any particular genus; it was the most even assemblage examined. However, all four fossil assemblages show relatively moderate eveness. The Shannon-Weiner diversity index (H') ranges from 1.04 to 1.62 and eveness (E) ranges from 0.45 to 0.7 with 1 indicating completely even paleocommunities (Appendix A). A Z-test indicates that the abundance of the bryozoan *Fenestella* in the LPDT is significanlty more abundant (p=0.0002) than other taxa in the paleocommunities of the LPDT.

4.2.2 Middle Pampa de Tepuel (MPDT) Formation

Fossil data for the MPDT was collected at 32, 35, 40, 46, 51, and 139 meters (Appendix A). Alpha diversity in the MPDT is represented by 13 genera from 9 invertebrate classes. The number of genera range from two to nine in the six tallied fossil assemblages. In the MPDT, the total fossil count for this study is 130 individuals for all six assemblages. This number makes the MPDT less taxonomically rich by about 50 percent than the LPDT. The most numerically abundant genus in this section is ostracod *Graphiadactylloides?* which accounts for over 70 percent of the counted individuals (Fig. 13). The other genera found in the MPDT include bivalves such as *Phestia* and *Paleolima*, *Lanipustula* brachiopods, hyolithes, crinoid *Camptocrinus?*, and gastropod *Glabrocingulum* (Fig. 13). Over 60 percent of the fossil elements are found at 32 meters (fossil assemblage 1) (Fig. 9). No one genus has 100% distribution in all fossil assemblages. The two most common genera in terms of breadth of distribution is crinoid

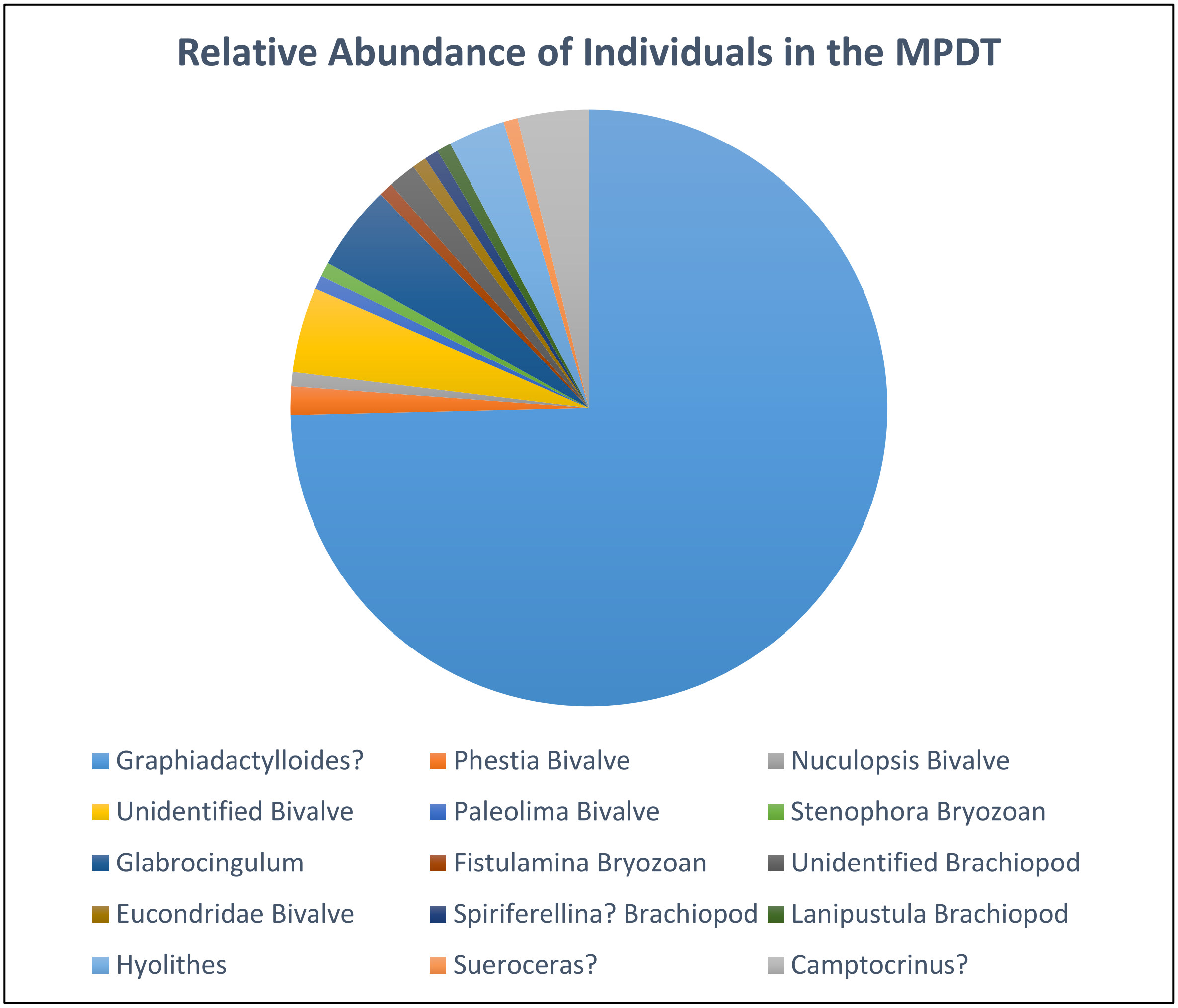


Figure 13. Relative abundance of individuals at the genus level in all fossil assemblages of the MPDT.

Camptocrinus?, found in 5 out of 6 fossil assemblages, and ostracod *Graphiadacylloides?*, found in 4 of 6 fossil assemblages (Table 2).

The Simpson diversity index (1-D) for dominance results range from 0 to 0.78 (Appendix A). Those fossil assemblages (40 m and 46 m) that have a Simpson dominance of zero had very low (two to four) numbers of genera and have one individual for each genus. The Shannon-Weiner diversity index (H')

Table 2. Class, genus, diet, tolerance to salinity change and fossil assemblage distribution for fossils found in the Pampa de Tepuel Formation for this study.

Class	**Genus**	**Diet**	**Δ Salinity Tolerance**	**Fossil Assemblage**
Crinoidea	*Camptocrinus?*	suspension feeder	stenohaline	1, 2, 3, 4, 5, 6, 7, 8, and 10
Gymnolaemata	*Fenestella*	suspension feeder	stenohaline	1, 2, 3, and 4
Stenolaemata	*Fistulamina*	suspension feeder	stenohaline	1, 2, 3, and 4
Stenolaemata	*Stenophora*	suspension feeder	stenohaline	5
Bivalvia	*Paleolima*	suspension feeder	euryhaline	1, 2, 4, and 5
Bivalvia	*Limipecten*	suspension feeder	euryhaline	1 and 2
Bivalvia	*Orbiculopecten*	suspension feeder	euryhaline	1 and 2
Bivalvia	*Streblochondria*	suspension feeder	euryhaline	1
Bivalvia	*Euchondria*	suspension feeder	euryhaline	5
Bivalvia	*Phestia*	suspension feeder	euryhaline	5
Bivalvia	*Nuculopsis*	suspension feeder	euryhaline	8
Strophomenata	*Lanipustula*	suspension feeder	stenohaline	1,2,4, and 5
Strophomenata	*Krotovia*	suspension feeder	stenohaline	1 and 2
Strophomenata	*Plicaferina*	suspension feeder	stenohaline	1
Rynchonellata	*Spiriferellina*	suspension feeder	stenohaline	3 and 5
Anthozoa	Order: Rugosa	suspension feeder	stenohaline	2,3, and 4
Hyolitha	*Hyolithes*	suspension feeder	stenohaline	6, 7, and 9
Ostracoda	*Graphiadactylloides?*	detrivore	stenohaline	5, 6, 8, and 10
Cephlapoda	*Sueroceras?*	carnivore	stenohaline	8
Gastropoda	*Glabrocingulum?*	suspension feeder	euryhaline	6 and 10

results range from 0.57 to 1.4 and evenness (E) range from 0.26 to 1.01 (Appendix A). The number of ostracod *Graphiadacylloides?* individuals in the MPDT fossil assemblages compared to other organisms is established to be significant (p=0.00017) through the use of a Z test.

4.2.3 Multivariate Analyses of the Lower and Upper Pampa de Tepuel

To be sure that the fossil counts (i.e. enough samples were taken in each of the measured sections) were accurate enough to form conclusions, a rarefaction curve was

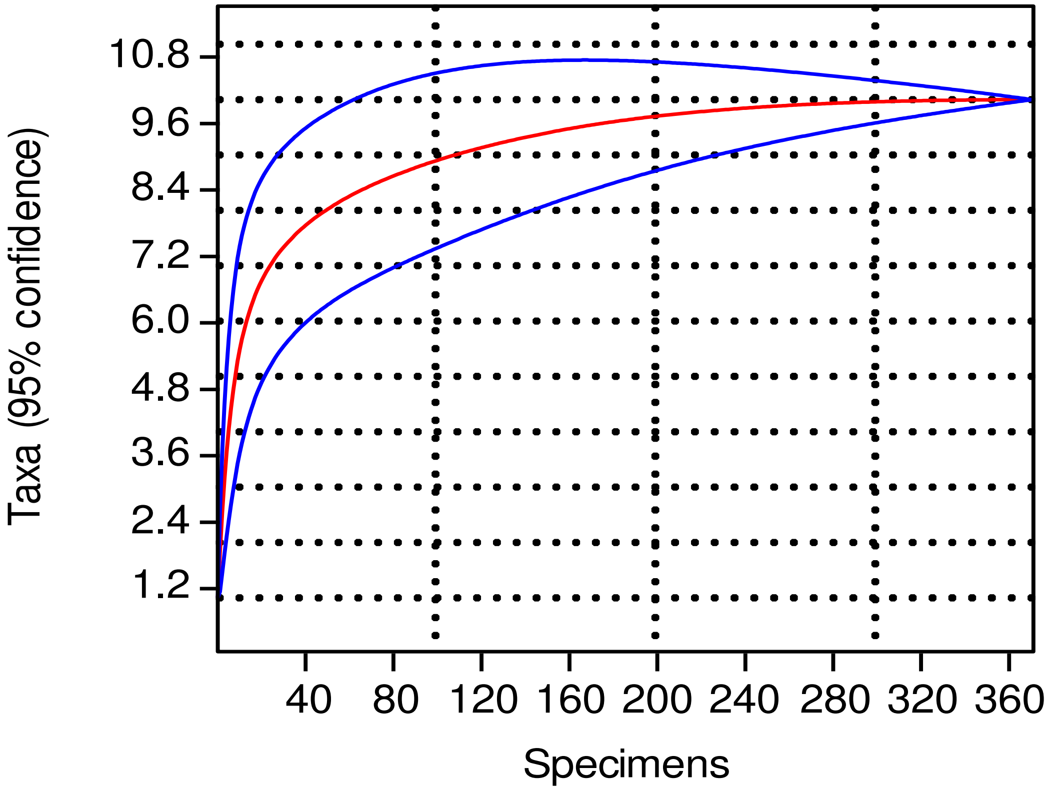


Figure 14. Rarefaction curve for the fossil counts and genera in fossil assemblages 1-10 in LPDT and MPDT.

created for the total genera and total individual counts for the LMDT and UPDT sections. The curves plateau showing that enough data were collected to ensure a complete representation of the paleocommunity.

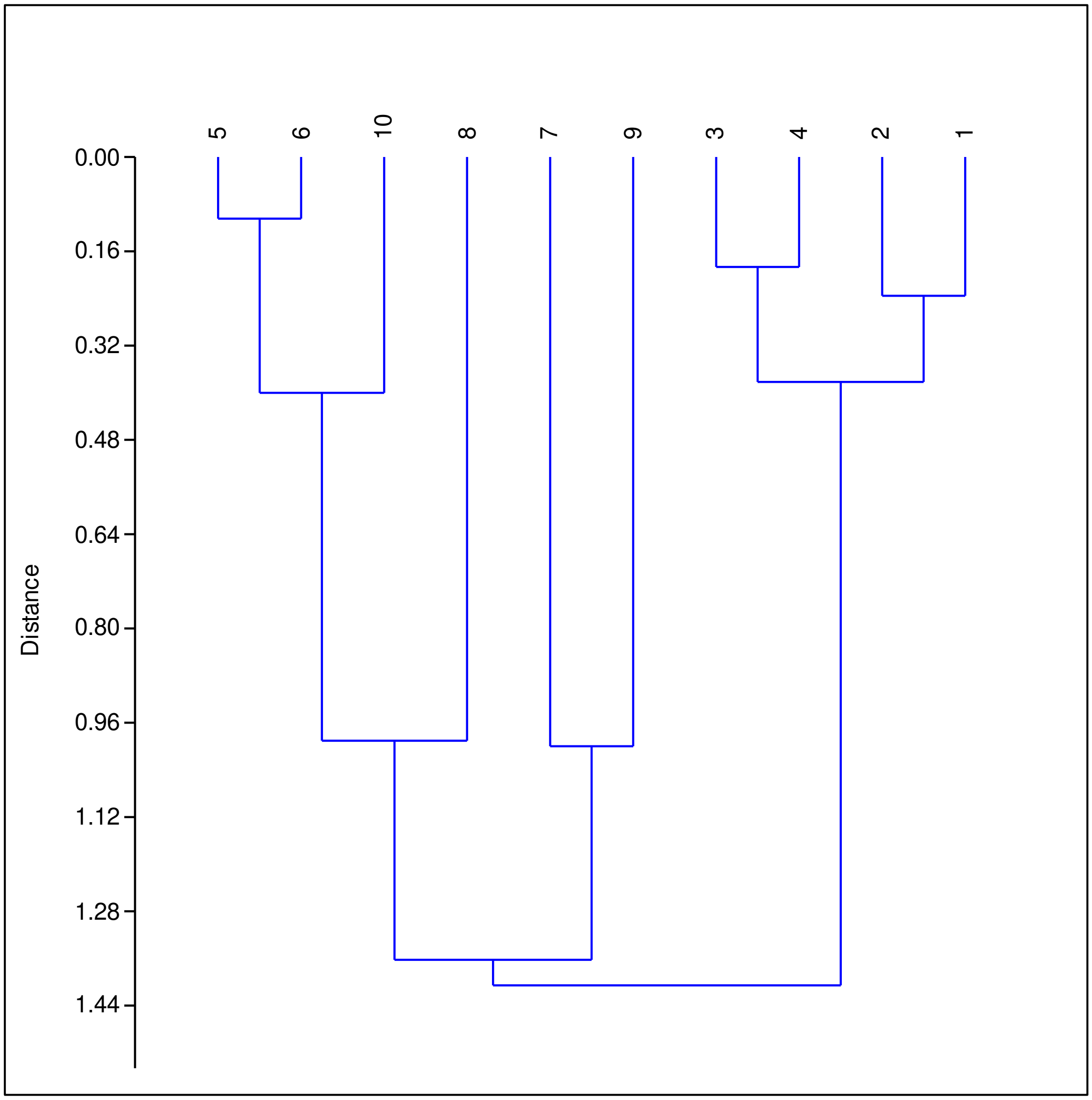


Figure 15. Cluster Analysis for the fossil assemblages in the Pampa de Tepuel Formation using the Chord cluster analysis based on similarities.

The cluster analysis resulted in three general dendrogram patterns. One pattern groups fossil assemblages 1 through 4 and fossil assemblages 5 through 10 together (Rho, Bray-Curtis, and Chord). The Dice analysis groups fossil assemblages 1-5 together and fossil assemblages 6-10 together. Euclidian cluster analysis groups fossil assemblages 1 and 5 as outliers and displays three groups of 2, 3 and 4; 6 and 10; and 7, 8 and 9. In all but one of the cluster analyses, fossil assemblages 1 and 5 are the farthest apart from each other meaning they had the largest differences. The dendrogram with the highest correlation (99.5%) is the result of the Chord cluster analysis (Fig. 15). The Chord analysis grouped the fossil assemblages of the LPDT together and the fossil assemblages of the MPDT together showing the fossil assemblages within each section of the Formation (either LPDT or MPDT) are more similar to each other than to the other. The cluster analysis with the lowest correlation is the Dice analysis with 86%.

The results of the cluster analysis is mirrored in the DCA graph, which had a separation of points that correspond to the fossil assemblages of the LPDT and the MPDT (Fig. 16).

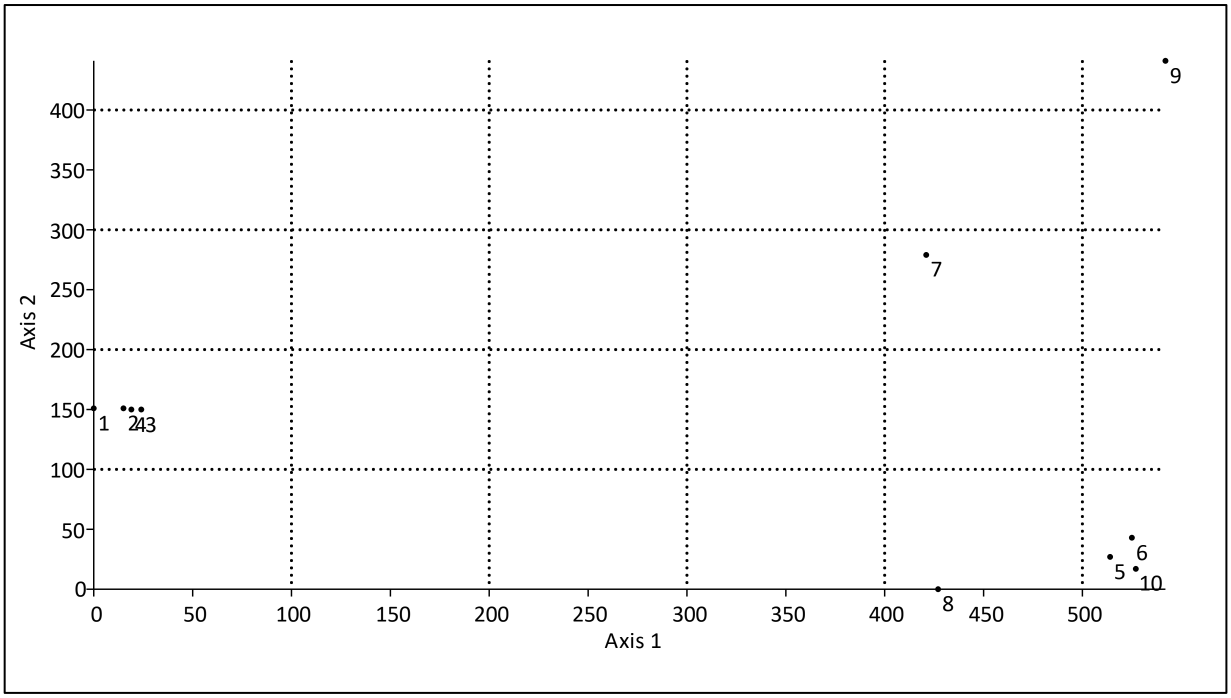


Figure 16. Detrended correspondence analysis for fossil assemblages 1 through 10 based on genus and fossil counts in each fossil assemblage.

5. Discussion

5.1 Lower Pampa de Tepuel (LPDT)

5.1.1 Sedimentology

I interpret the LPDT studied herein to have been deposited in a slope environment distal to glacial influence and during a transition into an interglacial period. The muddy nature of the fossil-rich muddy siltstone facies suggests deep slope deposition below storm wave base (Pauls et al. 2014; Braun et al. 2015). The expression of very few sedimentary structure in this facies also suggests a relatively quiet environment that would be found in a deep-slope setting. The very fine-to medium-grained sandstone facies and clast-rich sandy conglomerate facies are interpreted to be the result of a mass transport as an effect of structure failure from the shelf (e.g.; Hampton, 1972; Pickering and Hiscott, 2015). Research shows that this type of event can be triggered by destabilization of underlying sediments on the shelf as a result of decreased loading by the receding of glaciers (e.g.; Bryn, 2005; Steel et al. 2008). The very fine- to medium grained sandstone facies and clast-rich sandy conglomerate facies may have been deposited in a shallower setting than the fossil-rich muddy siltstone facies. This general fining upward or deepening sequence in this section may have been triggered by glacial retreat (Pagani and Taboada, 2010; Braun et al., 2015). However, the soft sediment deformation within these two facies is more in line with the slumping and debris flows that occur with mass transport (e.g.; Hampton, 1972; Pickering and Hiscott, 2015). Further, the fossil-rich muddy siltstone facies in the LPDT does not show evidence of glacial input as course grained sediments and lonestones were absent in this facies.

5.1.2 Paleoecology

The paleoecology of the LPDT displays moderately diverse paleocommunities with the largest counts of individual fossils belonging to the Phylum Bryozoa. The Shannon-Weiner diversity index (H') values (1.037-1.589) are in a moderate range. Average scores for the Shannon-Weiner diversity index range between 1.5 and 3.5 (Magurran, 2004). Evenness (E) is slightly above mid-range (0.45 to 0.7) for possible scores (between 0 and 1) showing that the paleocommunities in the LPDT were moderately even meaning individuals were somewhat distributed among taxonomic groups. The overall LPDT paleocommunity was solely comprised of one functional group (benthic filter feeders). This may explain why alpha diversity was moderate (Clapham et al., 2006). It is also possible that only the benthic filter feeders were preferentially preserved.

Aragonite, a form of calcium carbonate that it less stable than the calcite form, is preferentially dissolved in sea water and can skew alpha diversity in paleoecological studies (Bush and Bambach, 2004). Calcium carbonate utilizing invertebrates, such as bryozoans and brachiopods, in cold water environments experience even higher rates of dissolution post-mortem (e.g.; Smith et al., 1992; Clark, 1993; Zamelczyk, 2014). In the LPDT and MPDT, calcium carbonate is the dominant material used by invertebrates to create shell material. Due to this fact I do not believe that there was preferential preservation of just one type of functional groups since members of many types of functional groups can be composed of calcium carbonate.

The most abundant fossil in this LPDT section was "*Fenestella*", from the Order Fenestrata. Research on the distribution of bryozoan structural types in a present day Antarctic glacial fjord shows that encrusting, low profile bryozoans are most likely seen in areas that are highly disturbed by glacial sedimentation, turbidity and ice scour (Pabis et al., 2014). The fan-shaped, erect morphology of the bryozoans found in the LPDT fossil assemblages lends more support for the lack of glacial input in fossil-rich muddy siltstone facies due to the lack of breakage of the fragile bryozoan colonies.

The bryozoan fossils are found in layers (Figure 8-E) and many are whole (shown by rounded ends of the bryozoan instead of sharp, broken ends) or only slightly broken (shown by sharp or abrupt ends together with partial colonies). The deposition in layers may suggest possible transport of the bryozoans down the slope from the shelf due to storm wave activity (*sensu* Barns and Kuklinski, 2010). However, the lack of damage to the fragile colonies supports quick burial due to storm energy (Hess, 1999; Lefebvre et al., 2016). Crinoid ossicles are commonly found deposited disarticulated and at different orientations, although some were found in intact with up to 20 ossicles articulated. This preservation is an indication for some movement of these specimens after death and may suggest they were parautochthonous to this site (Hunter and Underwood, 2009).

In the LPDT rugose corals were found in three out of the four fossil assemblages that were excavated in the fossil-rich muddy siltstone facies. Their presence suggests that the depositional environment was warmer, either due to a shallower environment or even possibly because of a glacial low or interglacial period (Bonn et al., 1994; Cisterna, 2010; Balserio, 2016). Due to the interpretation that this is a slope depositional setting, this advocates for a warmer environment during an interglacial period. This is in accord with the lack of glacial sediments in the fossil-rich muddy siltstone of the LPDT.

Further evidence supportive of an interglacial climate interpretation for the LPDT is the presence of a high percentage (75%) of stenohaline genera that have narrow salinity tolerances. When glacial ice is present there are seasonal variations in salinity due to the melting and freezing of ice resulting in fluctuations in freshwater input (e.g.; Dierssen et al., 2002; Barns and Conlan, 2007). Brine formation due to the salt seep from the creation of sea ice can also cause fluctuations in the colder months when more sea ice forms (Jardon et al., 2013). The lack of salt-fluctuation- tolerant genera suggests the absence of sea ice and glacial input.

5.2 Middle Pampa de Tepuel (MPDT)

5.2.1 Sedimentology

Figure 17. Slump structure in the fine-grand sandstone of the MPDT.

I interpret the MPDT to have been deposited in a slope setting more proximal to glacial influence than the LPDT. The presence of siltstone is evidence of a slope depositional setting (Oliveira et al., 2009).

Sedimentary structures such as soft sediment deformation in the form of folds and slumps were evident in the fossil-poor sandy siltstone facies. The fossil-barren sandy siltstone with lonestones facies signifies a position higher on the slope where it can be influenced by clastic influx (turbidity flows or tectonic processes as seen in fracturing and slickensides in this facies) on the shelf and upper slope (e.g.; Bonn et al., 1994; Bryn, 2005; Steel et al. 2008). Within the MPDT section the evidence for glacial influence is strong. Lonestones and pockets of course grained sediments are found in the in the fossil-barren sandy siltstone. The lonestones are interpreted here to signify debris deposited by ice rafting and iceberg roll (dump structures; Thomas and Connell, 1985). The interbedded fossil-barren sandy siltstone with lonestones facies and fine-grained sandstone facies have sharp contacts. I am interpreting this as a channel of fine sand sediments being deposited in the slope due to turbidity currents that can be caused by distal glacial activity (e.g. Bonn et al., 1994). Soft sediment deformation such as slumping and folding can also be seen near these channels signifying that these are the result of this turbidity (Henry, 2010; Pickering et al., 2015; Figure 17). It is unknown as to the cause of the turbidity flows but glacial evidence in the MPDT section points to glacial influence as a source. Two beds of clast-poor diamictite near the top of this measured section suggest that the glacier would be in its most proximal position and depositing glacial sediments due to gravity flows and meltwater plumes. Near the top of the section a finely laminated fossil-barren sandy siltstone facies returns but without lonestones. At the top of the measured section a medium to course-grained sandstone occurs. This sandstone was not measured, but a coarsening upward succession was recorded which suggests the occurrence of a regressional succession. Such deposits are the result of progradation and in the deep ocean suggest potential changes in base level (cf. Catuneanu, 2006).

5.2.2 Paleoecology

Fossil assemblages are rare in this portion of the MPDT. Shannon-Weiner diversity values (H’) (ranging from 0.6931 to 1.386) are low. Dominance (1-D), however, results in higher values for the first two fossil assemblages (0.7 and 0.8 in fossil assemblages 5 and 6 respectively) and lower values in fossil assemblages 7, 8, 9 and 10 (values between 0 and 0.5). Three of the excavated fossil assemblages (40 m, 46 m, and 51 m that correspond with assemblages 7, 8 and 9) have exceedingly low fossil counts. The low numbers of individuals skew the results for evenness to have high scores of 1 or close to 1 meaning they have high evenness. These same skewed results are also reflected in the low Simpson diversity index (1-

D) values (values of 0) in fossil assemblages 7 and 8, which do not reflect the actual health of the paleocommunities in these locations (figure 20).

I interpret that increased amounts of glacial input had a significant effect on diminished benthic taxonomic diversity found in the MPDT. The transition between the fossil-poor sandy siltstone facies and the fossil-barren sandy siltstone facies with lonestones, around 140 m (fig. 9), exemplifies complete loss of body fossils. Overall, taxonomic richness was low; the MPDT contains half the number individuals collected compared to that of the LPDT. The most abundant genus in this section was ostracod *Graphiadactylloides?.* Ostracods are benthic, such as *Graphiadactylloides*, or planktonic, and most are detritus feeders although some can also be filter feeders (e.g.; Díaz Saravia and Jones, 1999; Nigro et al., 2016). The significance of the large number of ostracods found in this section to the near exclusion of other benthic invertebrates may indicate that they are an opportunistic taxon, meaning they will thrive when other fauna in the community go absent (Pauls, 2014; Braun, 2015). The bivalve *Phestia,* another opportunistic taxa (Sterren and Cisterna, 2010), was also found in the MPDT but not the LPDT. The presence of these opportunistic taxa may signify the onset of environmental changes in this section of the Pampa de Tepuel Formation due to glacial input or changing base level conditions.

Though lack of fossils in the fossil-barren sandy siltstone can be attributed to the increase of sedimentations seen in this faces, the low fossil counts in the fossil-poor sandy siltstone are not as easily explained. This invertebrate absence could be because there are simply were not living in this setting due to environmental changes or it could be a taphonomic bias. The fossil-barren sandy siltstone has no evidence of debris flows or turbidity, such as in the fossil-barren sandy siltstone, that indicate removal the fauna from the slope (Thatje et al., 2005; Pasotti et al., 2015). There are also no lonestones or evidence of an increase in sediments that could have buried and suffocated the fauna (Holte and Gulliksen, 1998). Wlodarska-Kowalczuk et al. (2005), in a study of Arctic fjords, found that organisms near high sedimentation were much smaller and are often motile deposit feeders. This may be an explanation for high ostracod counts in this section. Sediment rates may have already been increasing but they were very fine grained resulting in a sandy instead of muddy siltstone. Water temperature changes due to the onset of glaciations could have caused those invertebrates that were more susceptible to temperature changes to migrate or perish, leaving behind a more tolerant fossil assemblage. Water circulations patterns could also be altered during an onset of glaciations that could alter both oxygen that is available to benthic communities as well as food supply (e.g.; Kawagata et al., 2006; Cottier et al., 2010; Shi and Waterhouse, 2010). Environmental changes would cause preferential selection of fauna that were metabolically more capable of handling this type of stress such as brachiopods. Brachiopods, with a higher metabolism than bivalves, are able to handle changes to their environment more readily (Payne et al. 2014). In the MPDT the number of bivalve genera outnumber the number of brachiopod genera five to three. The opposite is true in the LPDT.

The other scenario would be a taphonomic bias that would result in the hindered preservation carbonate fossils. Research on the taphonomy of carbonate shells in cold water regions shows that cold water can increase the solubility of carbonate hindering fossil preservation (e.g.; Clark, 1993; Zamelczyk, 2014). If this was the case it would also be challenging to create shell material of dissolution was high. This would then point back to environmental changes as the cause for the lack of fauna in the MPDT.

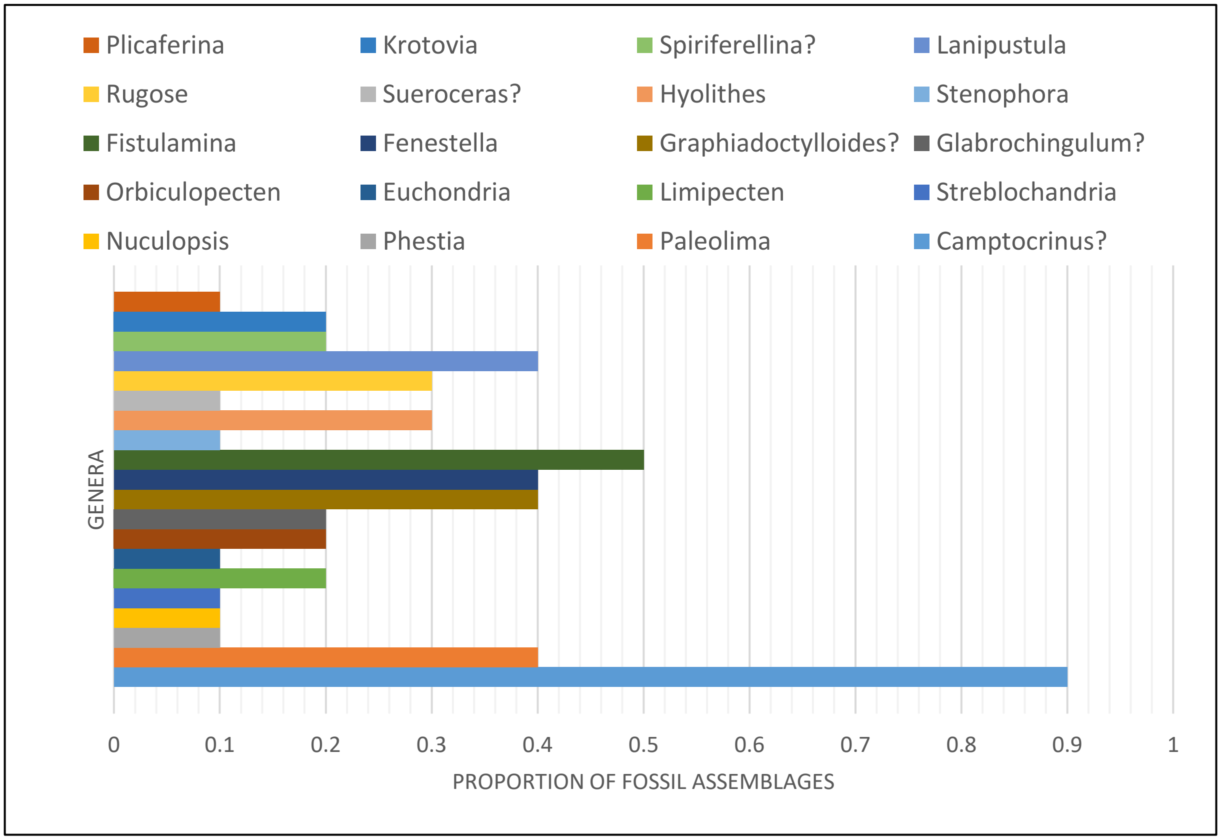


Figure 18. Breadth of distribution at the genus level of all 10 fossil assemblages. Bar length corresponds to the proportion of fossil assemblages in which each is found.

5.3 Abundance and Diversity Comparisons between the Studied Sections

Though the LPDT and MPDT faunas have significant differences, some similarities exist. Crinoid *Camptocrinus?* was found in both of the sections (LPDT and MPDT) and in 9 out of 10 of the fossil assemblages (Fig. 18). *Lanipustula*, *Fistulamina*, and *Palaeolima* were also found in both the LPDT and MPDT sections (Fig. 18; Fig. 19).

Overall individual fossil count was higher in the LPDT (248 individuals) than in the MPDT (136 individuals) regardless of the two extra fossil assemblages in the MPDT. However, the compositions of the two sections, especially the most dominant genus, were different. In the LPDT bryozoan *Fistulamina* was found in the greatest numbers in comparison with the MPDT which had the largest group of individuals as ostracod *Graphiadactylloides?* (Fig. 19). *Fistulamina* was not found in the MPDT and *Graphiadacylloides?* was not found in the LPDT.

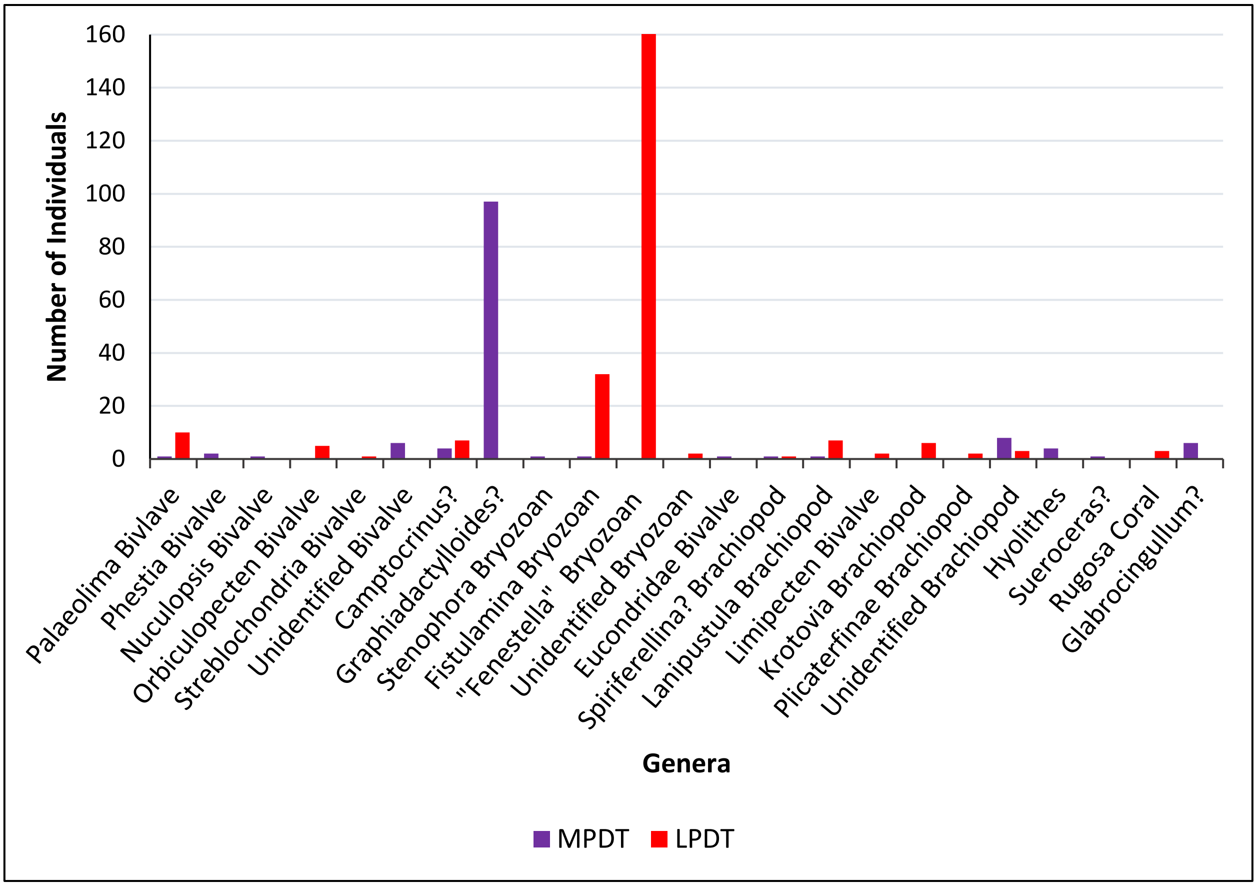
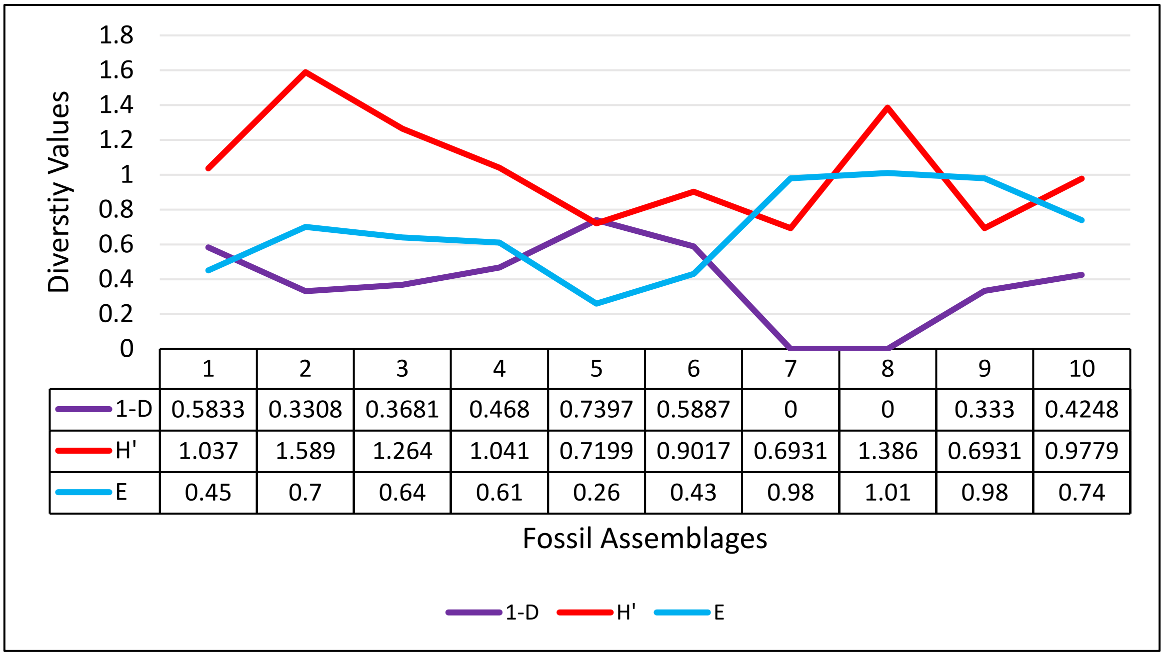


Figure 19. Numerical abundance of genera in the Lower and Middle measured sections of the Pampa de Tepuel Formation.

Diversity comparisons between the LPDT and MPDT show that the overall Shannon-Weiner diversity values (H’) in the LPDT (1.037-1.589) are higher than those of the MPDT (0.6931-1.386) (Fig. 20). The Simpson diversity index (1-D) values were more varied across the measured sections of Pampa de Tepuel Formation as well as within the LPDT and MPDT sections. This is due to the high counts of bryozoans and ostracods in the LPDT and MPDT respectively.



	1	2	3	4	5	6	7	8	9	10
1-D	0.5833	0.3308	0.3681	0.468	0.7397	0.5887	0	0	0.333	0.4248
H'	1.037	1.589	1.264	1.041	0.7199	0.9017	0.6931	1.386	0.6931	0.9779
E	0.45	0.7	0.64	0.61	0.26	0.43	0.98	1.01	0.98	0.74

Figure 20. Results of the Simpson diversity index and Shannon-Weiner diversity index and evenness values for fossil assemblage 1-10 in the Pampa de Tepuel Formation.

The multivariate analysis of the LPDT and MPDT fossil assemblages show that they have more similarities within each section than between the sections. In the cluster analysis, fossil assemblages of the LPDT (1-4) were grouped together and fossil assemblages of the MPDT (5-10) (Fig. 15) showing the similarities within each section. The DCA analysis also shows similar groupings (Fig. 16). These two analyses provide evidence of the differences between the fauna in the LPDT and that of the MPDT.

The totality of the fauna found in the LPDT were benthic suspension feeders. The MPDT displayed more variety in modes of life: the majority of the individuals (76%) were detrital scavengers/grazers due to the high number of ostracods. The second largest group were suspension feeders (24%). The nautiloid was the only carnivore found in the MPDT.

5.4 Brachiopod and Bivalve Comparisons and Significance

Brachiopods, along with crinoids, ostracods, and cephalopods, were the dominant organisms in terms of taxonomy and numerical abundance in the Paleozoic Fauna (Sepkoski, 1981; Sepkoski and Miller, 1985). The Paleozoic Fauna dominated the world’s oceans until the end of the Paleozoic and the end-Permian mass extinction (Sepkoski, 1981). This transition gave rise to the Modern fauna that included bivalves, and other taxa such as gastropods, fish, and echinoids (Sepkoski, 1981; Sepkoski and Miller, 1985). The transition from brachiopod dominance to bivalve dominance was thought to be initiated by the end-Permian mass extinction but in some instances research shows that this transitions may have already began in the late Paleozoic (Clapham et al., 2006; Clapham and Bottjer, 2007; Sterren and Cisterna, 2010; Balseiro, 2016). The data collected in this study seems to agree. Brachiopod and bivalve genus and individual counts were close to even in both the LPDT and MPDT sections. In the MPDT, as discussed above, bivalve numbers surpassed those of brachiopods making bivalves slightly more diverse than brachiopods. Previous research done by Braun et al. (2015) also confirms an increase in bivalve numbers and diversity in the Pampa de Tepuel Formation.

5.5 Previous High Latitude Research

5.5.1 Australia

Some research has been done in high latitude areas such as research done by Clapham and James (2008). Their study done in eastern Australia shows the decrease and eventual disappearance of cold tolerant genera of bivalve during the Early to Middle Permian. They also found that changes began in the deeper environments. This finding shows a disparity from the near shore fauna that was most affected in the Central Appalachian Basin which was paleoequatorial during the LPIA (Powell, 2008). In this case, the disparity may be related to the differences in the affect the LPIA glaciations had on those communities proximal versus distal to the ice.

5.5.2 Argentina (Pampa de Tepuel Formation)

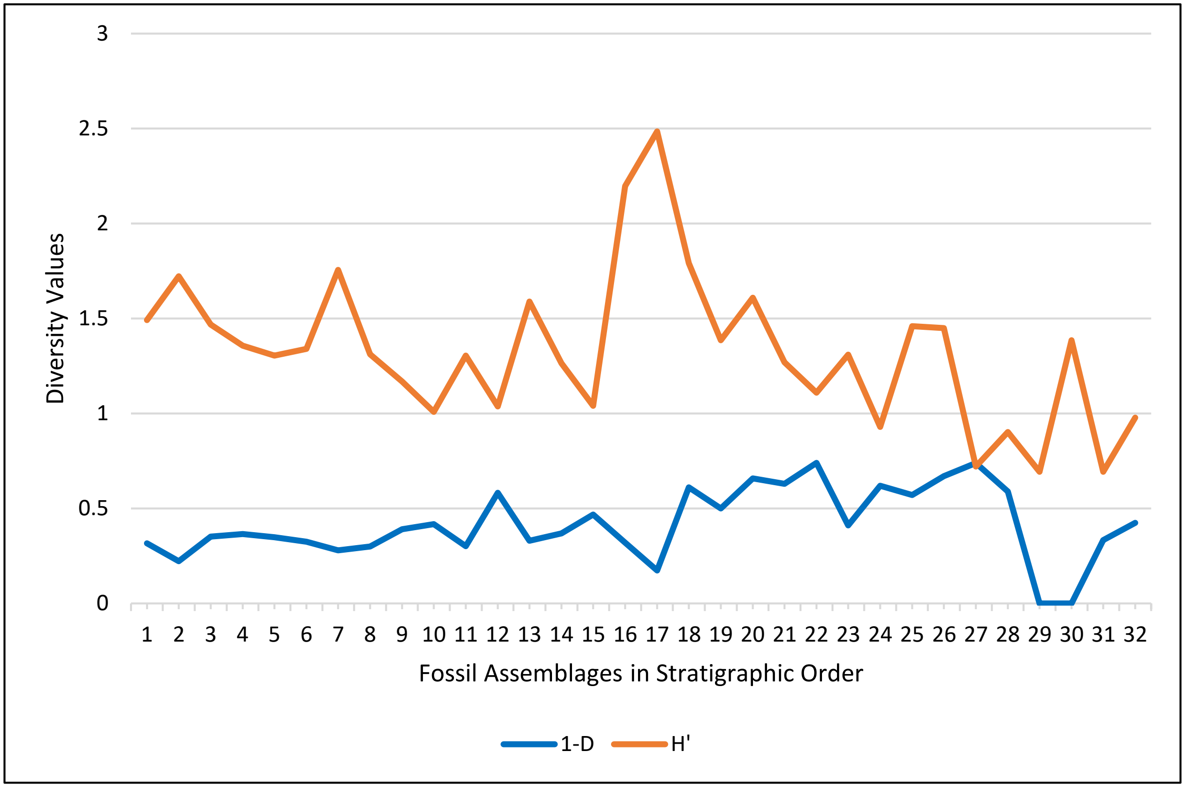


Figure 21. Comparison of Simpson diversity indices and Shannon-Weiner indices from Dineen (2010), Pauls et al. (2014), Braun et al. (2015) and Gigstad et al. (2018) in stratigraphic order. Fossil assemblages 1-11 (Braun et al., 2015), fossil assemblages 12-15 (Gigstad et al., 2018), fossil assemblages 15-20 (Dineen, 2010), fossil assemblages 21-26 (Pauls et al., 2014) and fossil assemblages 27-32 (Gigstad et al., 2018).

In Argentina, paleoecological results varied between studies. Pauls et al. (2014) found high diversity within paleocommunities although some communities were more diverse or more established than others (Fig. 21). A previous study by Dineen (2010) showed similar results to that of Pauls et al. (2014). Braun et al. (2015) found more impoverished communities near the base of the Pampa de Tepuel Formations than Pauls et al. (2014) and Dineen (2010) near the lower middle portion of the Pampa de Tepuel formation (Fig. 21). Braun et al. (2015), like Pauls et al. (2014) and Dineen (2010), also found that environmental factors such as sediment flux due to glacial input seemed to play a major part in the diversity seen in different sections of the Pampa de Tepuel Formation. Dineen et al. (2013) also found that invertebrate communities closer to glacial input experienced greater stress than those distal to glaciers. This study found some communities had higher diversity than others which was generally reflected in the amount of glacial input found.

In a comparison of both Simpson diversity and Shannon-Weiner diversity indices, similar results were found (Fig. 22). The fossil assemblages in this study found slightly higher diversity than Braun et al. (2015), but overall similar results were found which is beneficial for showing data can be replicated in the same locality.

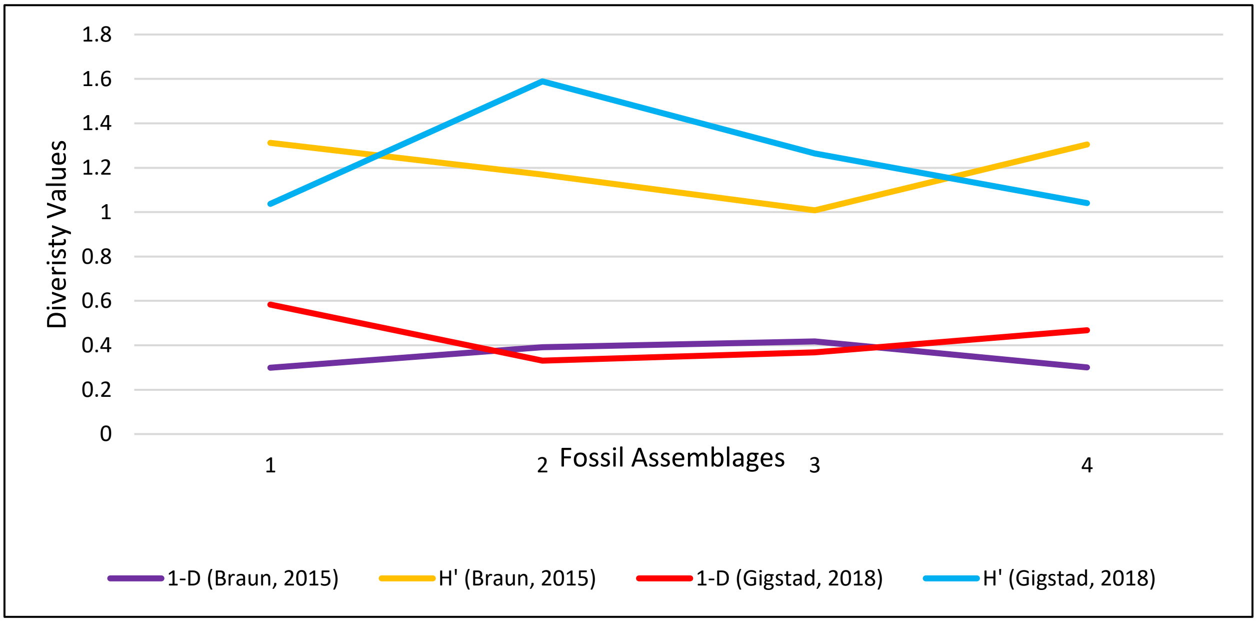


Figure 22. Comparison of over lapping fossil assemblages in terms of Simpson diversity indices and Shannon-Weiner diversity indices from Braun et al. (2015) (fossil assemblages 8-11) and Gigstad et al. (2018) fossil assemblages (1-4).

One of the main goals of this study is to continue to fill in the gaps of the paleoecological analysis of the Pampa de Tepuel Formation. The fossil assemblage sites for this study are between (and sometimes overlapping) and above the sections that have been previously analyzed in the Pampa de Tepuel Formation. When the diversity indices taken from the studies of Dineen (2010), Pauls et al. (2014), Braun et al. (2015), and Gigstad et al. (2018) are put in stratigraphic order, an overall trend of decreasing diversity (H') though the Carboniferous is seen to at least the upper middle of the Pampa de Tepuel Formation (Fig. 23). This can be interpreted as indication that the fluctuations form the waxing and waning of glaciers throughout the LPIA did have an overall negative affect on the invertebrate communities in the Pampa de Tepuel Formation over time.

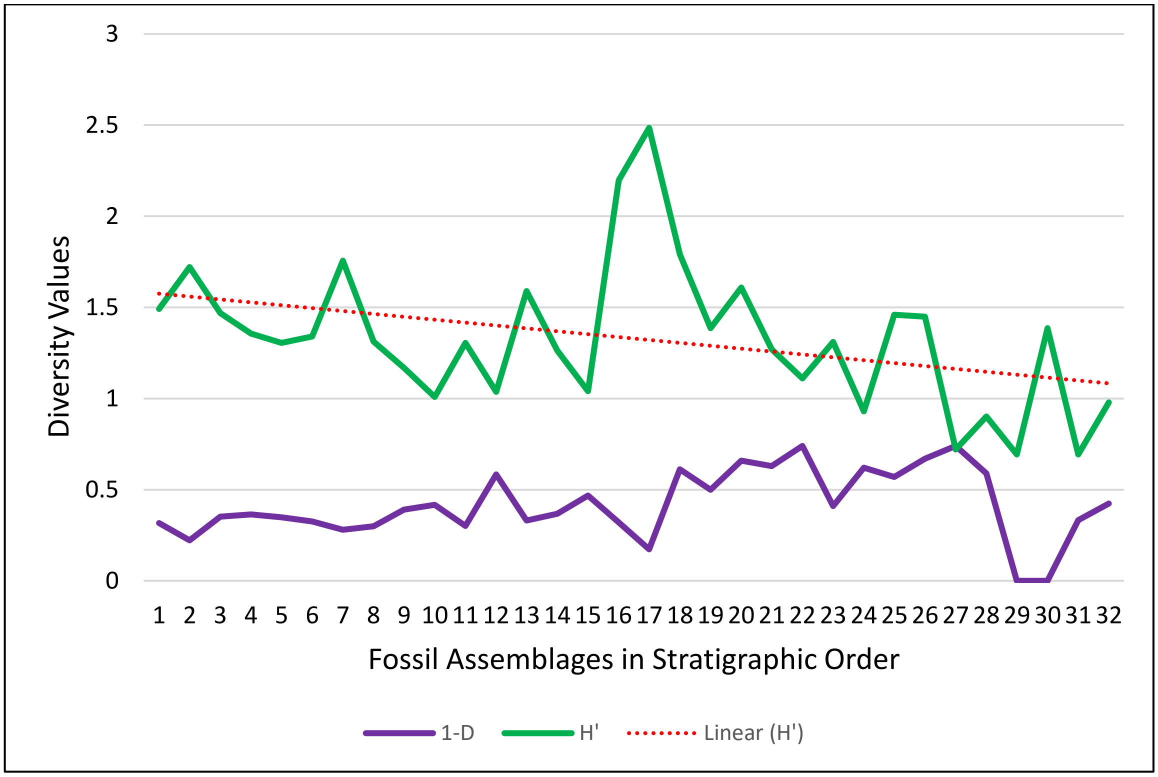


Figure 23. Diversity values from Simpson diversity and Shannon-Weiner diversity indices for fossil assemblages in stratigraphic order from Dineen (2010), Pauls et al. (2014), Braun et al. (2015) and Gigstad et al. (2018).

5.5.3 Low Latitude and High Latitude Comparisons

Studies from low latitude areas during the LPIA reflected a variety of outcomes from sustained diversity but increased turnover (Heim, 2009), to less differentiation in fauna between inshore and offshore environments (Bonelli and Patzkowsky, 2008), to second order mass extinctions (Powell, 2008). High latitude studies such as Clapham and James (2008), Dineen (2010; 2013), Pauls et al. (2014), Braun et al. (2015) as well as this one show that benthic invertebrate communities are negatively affected when situated proximal to the waxing and waning of glaciers. Heim (2009) discussed the importance of looking at these results on a regional basis in that different regions will be affected in different ways by climate change. It is also important to remember that different fauna will respond in various ways to these changes and thus will have varying degrees of success. This is definitely reflected in the varying results in both low and high latitude environments form different regions during the LPIA. This also highlights the complexity of environmental factors that are associated with climate change such as fresh water inputs, increased sedimentation, changes in salinity, sea level fluctuations, and changes in ocean circulation patterns (e.g.; Barns and Conlan, 2007; Shi and Waterhouse, 2010).

5.6 Present Day Effects of Glacial influence

Modern glacial environments can shed light on the different obstacles that benthic invertebrates may have faced in or near ancient glacial environments. Modern research in the

Antarctic has shown that glacial and sea ice play a major role in the disturbance of benthic communities. As glaciers reach into the ocean basins, the grounded ice can plough through the shelf and slope removing benthic invertebrates in their path (Brey et al., 1996; Barnes and Kuklinski, 2010). During glacial maximums this can mean complete restructuring of communities or even extinction of some endemic faunas. Ice scour occurs when sea ice or icebergs come in contact with the sea floor creating a trench in the sediment. Sea ice and icebergs can dig into sediment that is as deep as 600 meters (e.g.; Gutt, 200; Pasotti et al., 2015). These scour marks can also be 350 meters wide and 15 km long (Barnes and Conlan, 2007). Gutt proposed, in a study from 2001, that every part of the Antarctic shelf could be scoured once every 340 years. The destruction left by the keels of icebergs and sea ice can be severe for benthic communities, especially in areas of high disturbance. In many cases, the scour marks themselves are described as different environments or communities than the undisturbed sea floor. In a study by Conlan et al. (1998) they found that the diversity inside the scour marks was significantly lower than outside. The benthic community structure in areas where there is increased intensity of scouring is often halted at early successional stages (Pugh and Davenport, 1997; Smale et al., 2007). Conlon et al. (1998) also found that there was an increase in deposit feeders and scavengers in the areas of scour. This idea is congruent with other studies showing that the first fauna to reoccupy scour tend to be motile (Peck et al, 1999).

Sedimentation related to glacial activity can also be a disruptive to benthic invertebrates. As glaciers meet the marine realm, they deposit sediment though glacial melt water and rafted ice debris (e.g.; Dowdeswell, J. A. and J. D. Scourse, 1990). Large sediments such as boulders can drop into the ocean and crush benthic organisms. High amounts of sediment influx can suffocate filter-feeding organisms or bury them. Research in Norwegian fjords show that increased sedimentation has an adverse effect on benthic communities. Where glacial melt is maximum in the fjords, a decrease in species richness is observe and is most likely due to the burial of infant stages of benthic biota (Holte and Gulliksen, 1998). An increase in meltwater coming off the glacial front, especially during times of dynamic environmental change and warming, can cause an influx of fresh water increasing turbidity (Pasotti et al., 2015). In near shore areas, this turbidity can cause a decrease in light penetration, which can disturb primary production affecting the rest of the food chain (Dierssen et al., 2002). Deep water turbidity currents can also play a role in the disturbance of benthic organisms on the shelf and slope especially in areas where soft sediment is dominant. Turbidity currents are propelled by gravity from the shelf and slope down to the basin, depositing courser grained sediments in a normally fine-grained environment. Turbidity currents can be initiated by glaciers, storms, currents, and sediment instability causing debris flows, landslides, and slumps (e.g.; Hampton, 1972; Harris, 2014). These processes can cause burial or removal of benthic biota due over long periods with continuous pressure and intensity (Harris, 2014).

The Modern shows us that there are many different tribulations that benthic invertebrates face living near glacial input. Within the MPDT section of this study there is evidence for ice rafted debris in the form of lonestones and pockets of course-grained sand in the fossil-barren sandy siltstone with lonestones facies. There is also evidence for glacial meltwater resulting in the clast poor intermediate diamictite facies as well as for turbidity currents supported by the fine-grained sandstone channels and soft sediment deformation in the fossil-barren sandy siltstone with lonestones facies. Any of these can result in decreased species richness and diversity and in some cases, extinction. Perhaps these recent studies on high latitude invertebrates can be used as an analog to help better understand ancient high latitude invertebrate systems both proximal and distal to glacial influence.

6.Conclusion

The Pampa de Tepuel Formation in southwestern Argentina provides an almost complete sequence of the stratigraphic recorded of Carboniferous age strata that can be compared to previous studies of low paleolatitude regions of the United States. Low latitude studies have shown varied results from turnover but no loss in diversity to mass extinctions. (Stanley and Powell, 2003; Powell, 2005 and 2007; Heim, 2009). These varied results show the importance of looking at the climate changes associated with the LPIA at a regional level instead of the all high paleolatitude regions as a whole (Heim, 2009). The results of this study are also varied, but on a smaller scale. Within the sections of the Pampa de Tepuel Formation that were in this study, variations in diversity occurred with changes in environments.

The sedimentation in the LPDT displays a lack of glacial evidence. Diamictite is not found in this 88 m of the lower Pampa de Tepuel Formation and lonestones are not found in the fossil-rich muddy siltstone facies. Within the LPDT paleocommunities taxonomic richness is high as well as the abundance of bryozoan *Fenestella*. Moderate Shannon-Weiner diversity values are also found the LPDT paleocommunities. The presence of rugose coral and a high percentage of stenohaline fauna deduce a warmer interglacial climate.

The sedimentation in the MPDT exhibits evidence of a more proximal glacial setting. Within the 312 meters of the MPDT section, diamictite, fossil-barren sandy siltstone with lonestones facies, turbidity deposits, and soft sediment deformation in the form of slumps and folds all support this evidence. The lack of taxonomic richness and low Shannon-Weiner diversity index values in the MPDT locality are interpreted as being the result of this increased sedimentation. High abundance of the ostracod *Graphiadacylloides?*, known as being an opportunistic taxa (Pauls, 2014; Braun, 2015), and higher percentages of euryhaline fauna support the hypothesis that these paleocommunities, more proximal to glaciers, were more stressed.

The hypothesis that near-field invertebrate paleocommunities differed greatly from far-field paleocommunities is supported by this study. Paleocommunities in low latitude areas saw some decreases in diversity by region or no decrease at all. In contrast, in the high latitude paleocommunities, diversity varied with changes in the environment expressed by influxes in course-grained glacial sedimentation. This paints a picture of a dynamic environment of the waxing and waning of glaciers throughout the LPIA that must have created many challenges for marine fauna.

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APPENDIX A

Fossil Assemblage 1 (LPDT 54.5 m)	**Count**	**Groups**		**LPDT Groups**	
Camptorinus? Crinoid	1	Crinoid	1	Crinoid	7
"*Fenestella*" Bryozoan	67	Bryozoan	70	Bryozoan	195
Fistulamina Bryozoan	3	Bivalve	11	Bivalve	18
Palaeolima Bivalve	5	Brachiopod	6	Brachiopod	19
Limipecten Bivalve	1	Coral	0	Coral	9
Orbiculopecten Bivalve	4				
Streblochondria Bivalve	1				
Lanipustula Brachiopod	2				
Krotovia Brachiopod	2				
Plicatiferina Brachiopod	2				

Fossil Assemblage 2 (LPDT 56 m)	**Count**	**Groups**	
Camptocrinus? Crinoid	2	Crinoid	2
"*Fenestella*" Bryozoan	32	Bryozoan	35
Fistulamina Bryozoan	3	Bivalve	5
Palaeolima Bivalve	3	Brachiopod	9
Orbiculopecten Bivalve	1	Coral	6
Limipecten Bivalve	1		
Lanipustula Brachiopod	3		
Krotovia Brachiopod	4		
Unidentified Brachiopod	2		
Rugosa	6		

Fossil Assemblage 3 (LPDT 60 m)	**Count**	**Groups**	
Camptocrinus? Crinioid	2	Crinoid	2
“*Fenestella*” Bryozoan	25	Bryozoan	40
Fistulamina Bryozoan	13	Bivalve	0
Unidentified Bryozoan	2	Brachiopod	2
Spiriferellina Brachiopod	1	Coral	2
Unidentified Brachiopod	1		
Rugosa	2		

Fossil Assemblage 4 (LPDT 67 m)	**Count**	**Groups**	
Camptocrinus? Crinoid	2	Crinoid	2
“*Fenestella*” Bryozoan	37	Bryozoan	50
Fistulamina Bryozoan	13	Bivalve	2
Palaeolima Bivalve	2	Brachiopod	2
Lanipustula Brachiopod	2	Coral	1
Rugosa	1		

Fossil Assemblage 5 (MPDT 32 m)	**Count**	**Groups**		**MPDT Groups**	
Camptocrinus? Crinoid	1	Crinoid	1	Criniod	5
Graphiadactylloides?	68	Bryozoan	2	Bryozoan	2
Stenopora Bryozoan	1	Bivalve	6	Bivalve	11
Fistulamina Bryozoan	1	Brachiopod	4	Brachiopod	4
Palaeolima Bivalve	1	Ostracod	68	Ostracod	97
Euchondria Bivalve	1	Gastropod	0	Gastropod	6
Phestia Bivalve	2	Hyolith	0	Hyolith	4
Lanipustula Brachiopod	1			Cephlapod	1
Spiriferellina Brachiopod	1				
Unidentified Bivalve	2				
Unidentified Brachiopod	2				

Fossil Assemblage 6 (MPDT 35 m)	**Count**		**Groups**	
Camptocrinus? Crinoid	1		Crinoid	1
Graphiadactylloides?	17		Bryozoan	0
Glabrocingulum? Gastropod	1		Bivalve	2
Hyolithes	1		Brachiopod	0
Unidentified Bivalve	2		Ostracod	17
			Gastropod	1
			Hyolith	1

Fossil Assemblage 7 (MPDT 40 m)	**Count**	**Groups**	
Camptocrinus? Crinoid	1	Bryozoan	0
Hyolithes	1	Bivalve	0
		Brachiopod	0
		Ostracod	0
		Gastropod	0
		Hyolith	1
		Crinoid	1

Fossil Assemblage 8 (MPDT 46 m)	**Count**	**Groups**	
Camptocrinus? Crinoid	1	Criniod	1
Graphiadactylloides?	1	Bryozoan	0
Nuculopsis Bivalve	1	Bivalve	1
Sueroceras? Nautiloid	1	Brachiopod	0
		Ostracod	1
		Gastropod	0
		Hyolith	0
		Cephlapod	1

Fossil Assemblage 9 (MPDT 51 m)	**Count**	**Groups**	
Unidentified Bivalve	2	Criniod	0
Hyolithes	2	Bryozoan	0
		Bivalve	2
		Brachiopod	0
		Ostracod	0
		Gastropod	0
		Hyolith	2
		Cephlapod	0

Fossil Assemblage 10 (MPDT 139 m)	**Count**	**Groups**	
Camptocrinus? Crinoid	1	Criniod	1
Graphiadactylloides?	11	Bryozoan	0
Glabrocingulum? Gastropod	5	Bivalve	0
		Brachiopod	0
		Ostracod	11
		Gastropod	5
		Hyolith	0
		Cephlapod	0

Fossil Assemblage	**1-D**	**H’**	**E**
1 - LPDT – 54.5 m	0.58	1.04	0.45
2 - LPDT – 56 m	0.33	1.62	0.7
3 - LPDT – 60 m	0.37	1.24	0.64
4 - LPDT – 67 m	0.47	1.09	0.61
5 - MPDT – 32 m	0.78	0.57	0.26
6 - MPDT – 35 m	0.72	0.59	0.43
7 - MPDT – 40 m	0	0.69	0.98
8 - MPDT – 46 m	0	1.40	1.01
9 - MPDT – 51 m	0.33	0.68	0.98
10 - MPDT – 139 m	0.48	0.81	0.74