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A Paleoenvironmental Analysis of Gastropods from the Middle Ordovician, Ibex Region, Utah

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by

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ABSTRACT OF THE THESIS

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Gastropods, which evolved in the earliest Paleozoic, are one of the most diverse and ecologically dominant clades in the modern ocean. The clade experienced its first global radiation event during the Ordovician, but gastropods were of minor ecological importance throughout the Paleozoic. This study aims to identify the environmental and ecological controls on gastropod occurrence during the height of the Ordovician Radiation Event through a study of the paleoenvironmental context of gastropods from the Ibex Region of the Confusion Range in western Utah, Basin and Range Province.

Gastropods, collected from Ibexian and Whiterockian Middle Ordovician strata (Wah Wah Formation, Juab Formation, Kanosh Shale and Lehman Formation), were identified and analyzed for depositional context and abundance, from which ecological dominance was interpreted. Results demonstrate that gastropods are more diverse (with eleven taxa identified) than previous studies of the Ibex Region have stated. Gastropods were most diverse in shallow environments and most abundant in harsh (low oxygen and/or high salinity) environments. Gastropod occurrences were correlated to muddy substrates, regardless of depth. The only environment in which gastropods were dominant was the hypersaline lagoon, preserved in the Lehman Formation.

Table of Contents

List of Figures

Introduction

The Ordovician Radiation was one of the most dynamic evolutionary events in the history of life on Earth. Global marine diversity expanded three-fold, at a previously unprecedented and since unparalleled rate (Figures 1 & 2) (Alroy, 2010; Droser et al., 1995). Although this diversification occurred primarily at lower taxonomic levels (class, order, family), innovation was nonetheless dramatic. This radiation marked the advent of the Paleozoic Evolutionary Fauna, which would go on to dominate marine ecosystems for the following 250 million years, until the rise of the Modern Evolutionary Fauna in the Mesozic (Figures 1 & 2) (Sepkoski, 1981). Marine benthic ecosystems, dominated by trilobites, inarticulate brachiopods and other members of the Cambrian Evolutionary Fauna, evolved radically during the Ordovician Radiation (Finnegan & Droser, 2003, 2008a; Sepkoski, 1981). Organisms refined and expanded on Cambrian body plans and began to exploit new ecospace through tiering: burrowing more deeply into the sediment and extending higher up into the water column (Finnegan & Droser, 2008a; Droser et al., 1995; Ausich & Bottjer, 1981). Benthic ecosystems also became much more densely packed compared to the sparse Cambrian sea floor (Finnegan & Droser, 2008a).

Many studies have utilized brachiopods and trilobites to study evolutionary trends through the Ordovician Radiation, as members of these clades tend to evolve quickly and are often well-preserved (see Adrain et al., 2001; Finnegan & Droser, 2008a; Fortey & Droser, 1999; Miller & Foote, 1996; Hintze, 1951). The ecological roles and evolutionary histories of these charismatic clades are well-understood, while minor clades like gastropods are often overlooked. Gastropods are the most diverse clade in the modern ocean, with estimates of 60-80k species (Bouchet & Rocroi, 2008), yet their early evolutionary history has been understudied due to the clade's poor preservation potential, lack of biostratigraphic application and high degree of homoplasy (leading to challenges in identification) (Fryda, 2008). This study examines gastropods across a range of Middle Ordovician depositional environments in order to determine the ecological roles that gastropods played in early Paleozoic benthic ecosystems. This study was conducted in the Ibex region of the Confusion Range in western Utah, a region that has been the focus of numerous paleoecological studies since the 1950's (see Hintze, 1951, 1973; Li & Droser, 1999; Adrain et al., 2001; Boyer & Droser, 2003; Finnegan & Droser, 2005). The Ibex region serves as an ideal locality to conduct a detailed paleoenvironmental analysis of a specific clade (like gastropods), as the sedimentology and general paleoecology of the region has already been examined in detail. This is the first study to focus on gastropods in this region. The Ibex region offers an opportunity to examine the paleoenvironmental associations of these early Paleozoic gastropods, and ultimately better understand the evolutionary history of this very important modern marine clade.

The Ordovician Radiation marks a key moment in the evolution of benthic marine ecosystems, as this was one of the earliest global biodiversification events. Many studies of Ordovician biodiversity conclude that the period was characterized by a high degree of regionalism, and so the patterns and trends observed in Laurentia may not be relevant in other parts of the globe (Miller, 2001). Nevertheless, detailed field studies of ecosystems on Laurentia are necessary for understanding how evolutionary trends on Laurentia were related to global trends. Because few studies of the Ordovician gastropod diversification have been conducted, this study provides insight to both gastropods Laurentia and the clade's global diversification.

Modern gastropods are a dominant clade in modern benthic ecosystems, and they have integrated into a diversity of ecosystems, from deep marine trenches to tidepools and even to the terrestrial realm (Hughes, 1986). Gastropods evolved in the Late Cambrian and the Ordovician Radiation was the first major biodiversification of the clade (Novack-Gottschall & Miller, 2003; Erwin & Signor, 1990). Throughout the Paleozoic, gastropods diversified slowly and suffered relatively less during extinction events when compared to other marine clades, leading Erwin & Signor (1990) to describe gastropods as an "extinction resistant" clade. The mechanisms of this atypical evolutionary trajectory are poorly understood. Despite the clade's longevity, gastropods did not become ecologically dominant, like they are in modern benthic ecosystems, until the Mesozoic Marine Revolution (Ewrin & Signor, 1990; Vermeij, 1977). In the Mesozoic, gastropods engaged in an "evolutionary arms race" with decapods, evolving ornate spines and thicker, more protective shells in response to increased predation (Vermeij, 1977).

The first studies of Laurentian gastropods were conducted as secondary studies of large-scale surveys and mapping expeditions by the US Geological Survey in the early twentieth century, and not only were gastropods not the focus of these studies, only well-preserved and easily collected specimens were cataloged, so a significant taphonomic bias was introducted (Hintze, 1951). Most recent work on Laurentian gastropods has necessarily focused on taxonomy and diversity, rather than paleoecology, in order to determine first-order diversity patterns. Rohr and colleagues (see Rohr, 1994; Rohr, 1996; Fryda & Rohr, 2001) have identified and described many of the Ordovician gastropods from Antelope Valley Limestone and Pogonip Group of Central Nevada. The Rohr studies focused on localities at which the gastropod specimens were silicified, making them easy to extract from the matrix and identify, but potentially biased, both taphonomically and environmentally.

Novack-Gottshall and Miller (2005), in a global survey of Ordovician gastropod and bivalve diversification and their depositional environments, determined that Middle Ordovician gastropod diversity on Laurentia was highest in near-shore environments. While Novack-Gottshall and Miller (2005) provide an excellent global context for gastropod paleoecology, the study necessarily relied on records in the Paleobiology Database rather than new field survey and collection. While this study sets a framework for examining gastropods and environments, it fails to examine the detailed and highly complex relationships between gastropods and the environments in which they lived.

In the first paleontological study of the Ibex Region, Hintze (1952) reported gastropods in the faunal assemblage but did not analyze the clade’s roles within these Middle Ordovician ecosystems. In a study of Middle Ordovician shellbeds in the Basin and Range Province, Li and Droser (1999) demonstrated that gastropod-dominated beds comprise only a small percentage (less than 10%) of most Ordovician strata, with the notable exception of the Lehman formation, in which gastropod-dominated beds comprise almost 20% of the total shellbeds. Furthermore, a study by Finnegan and Droser (2005) showed that gastropods comprise less than 1% of fossil material in the shellbeds of the Wah Wah and Juab formations. While these studies begin to quantify the relative abundance of gastropods in Middle Ordovician benthic ecosystems, none of them focus on gastropods or consider the ecological niches the clade may have filled.

The Ordovician Radiation is preserved exquisitely in the Basin and Range Province of the Western United States (Ethington *et al.*, 1995). Cambrian through Silurian strata are exposed in multiple, easily accessible localities in western Utah, across Nevada and in Eastern California (Ethington *et al.*, 1995). This study was conducted at one of the most well-studied localities: the Ibex Region in the Confusion Range of western Utah, where Ibexian and Whiterockian age strata are particularly well-exposed. Because many stratigraphic and paleoecological studies have been conducted on this package of rocks, the Ibex Region serves as an ideal laboratory in which to test patterns of innovation and adaptation during the Ordovician Radiation (see Hintze, 1951, 1953, 1973; Adrain *et al*, 2001; Boyer and Droser, 2003; Finnegan and Droser, 2005).

This field-based study uses gastropod diversity, relative abundance and sedimentological context to examine the paleoecology of gastropods at a classic Middle Ordovician locality. Furthermore, these field collections allow for the examination of the complex relationship between depositional environment, taphonomy and paleoecology in more detail than studies based in fossil databases or museum collections.

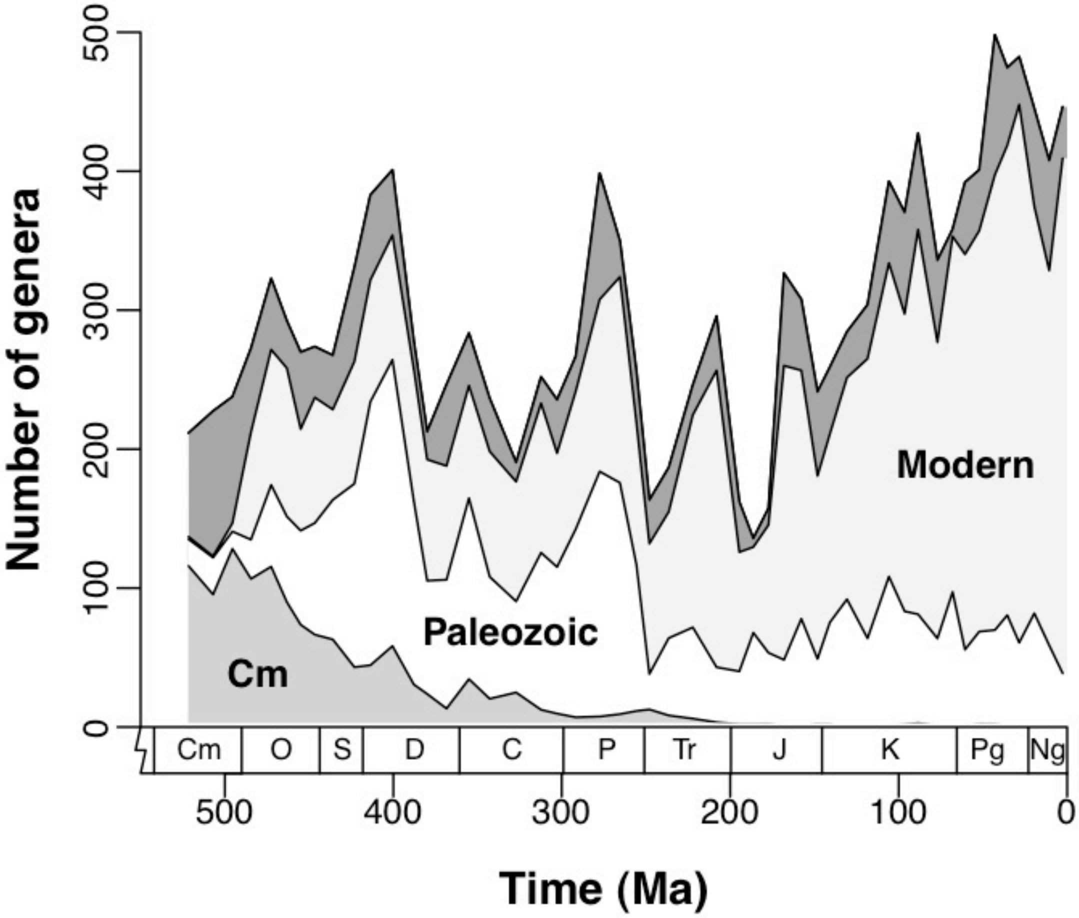


Figure 1. Sampling standardized Phanerozoic diversity curve for the three marine evolutionary faunas. Values are summed curves for constituent groups that were generated independently. Unlabeled area represents groups not assigned to a fauna. (Alroy, 2010)

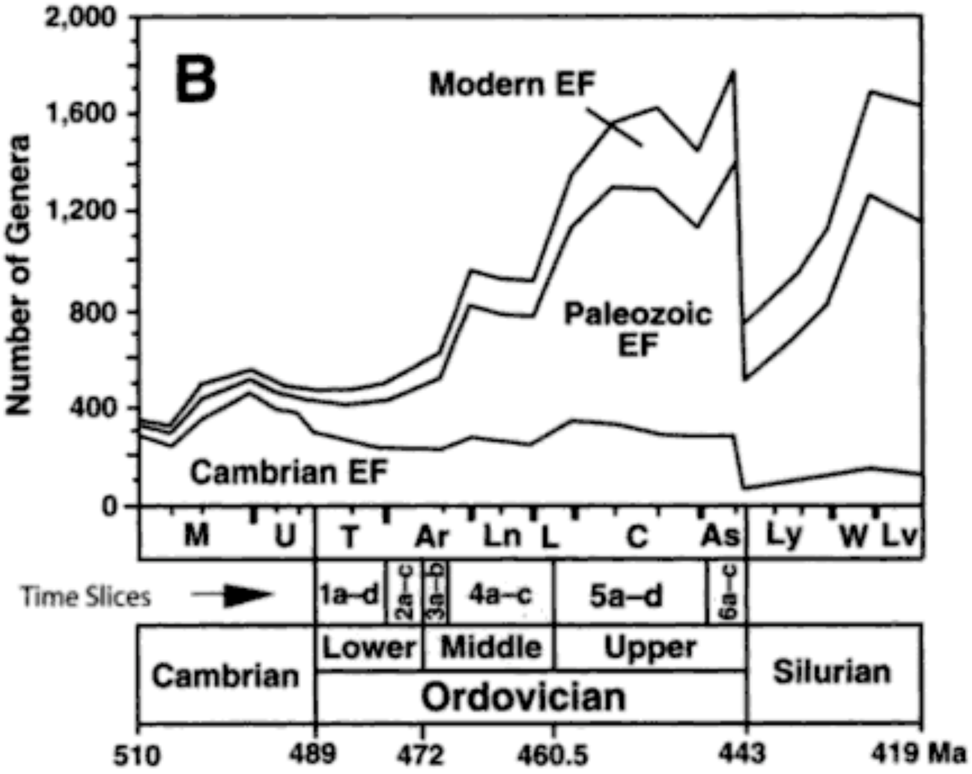


Figure 2. The Middle to Upper Cambrian, Ordovician and Silurian (except Pridoli), taxonomic diversity of marine animal genera (modified from Sepkoski 1984: figure 1). The main field of Cambrian, Paleozoic, and Modern Evolutionary Faunas is shown, as well as Sepkoski's time units, including British series for his Ordovician and Silurian subdivisions. His abbreviations are as follows: M = Middle Cambrian; U = Upper Cambrian; T = Tremadocian; Ar = Arenig; Ln = Llanvirn; L = "Llandeilo"; C = Caradoc; As = Ashgill; Ly = Llandovery; W = Wenlock; Lv = Ludlow. (Webby, 2001).

Ordovician Gastropods

Gastropods comprise the largest of the molluscan classes and are a major component of the Modern Evolutionary Fauna (along with bivalves and decapods; Sepkoski, 1981). The relatively simple shell morphology of gastropods leaves little room for radical alteration: shells are univalved and coil (Wagner & Erwin, 2006; Hughes, 1986). In spite of these morphological constraints, modern gastropods have adapted to a broad range of life modes, including suspension feeding, carnivory, herbivory, deposit feeding and ecotoparasitism (Hughes, 1986). Gastropods have also evolved a diverse array of elaborate behavioral and chemical defenses and predation techniques, such as efficient drilling methods and venom, which have aided in their rise to ecological dominance (Hughes, 1986).

There are three main subclasses of gastropods: prosobranchs (shelled marine snails), opisthobranchs (shell-less marine slugs) and pulmonates (terrestrial snails and slugs) (Hughes, 1986). This study focuses on the marine prosobranchs, which comprise the oldest and largest group of gastropods (Bouchet & Rocroi, 2008; Hughes, 1986). The vast majority of Ordovician gastropods fall into the primitive Archaeogastropoda group (Fryda & Rohr, 2001). Archaeogastropoda was historically considered to form a taxonomic order, but the label has since been revised multiple times and is now considered more a descriptive group than a formal taxonomic designation (Fryda & Rohr, 2001). Archaeogastropoda are primarily herbivorous or suspension feeding, and have simple, coiled shells lacking in ornamentation (Fryda, 2008). Many of the

Archaeogastropoda have nearly-planispiral shells that more closely resemble ammonites than the ornate, high-spired shells of the modern Neogastropoda (Fryda & Rohr, 2001). While there are some examples of high-spired gastropds in the Ordovician (such as *Murchisonia*), most were nearly planispiral and flat-bottomed (Fryda and Rohr, 2001; Erwin and Signor, 1990). The best example of this morphology is the maccluritid gastropod *Monitorella auricula,* which is highly abundant in Ordovician oncolite shoals across the Basin and Range Province (Rohr, 1994).

When compared to their modern counterparts, early Paleozoic gastropods were greately restrained in morphology and lifestyle (Wagner & Erwin, 2006; Erwin & Signor, 1990). In conjunction with their suspension-feeding life mode, most Ordovician gastropods were nearly or fully sedentary (Fryda, 2008; Erwin & Signor, 1990). Evidence of predatory drilling by gastropods, a life mode often associated with post-Paleozoic gastropods, does not appear in the fossil record until the Devonian and does not become common until the Mesozoic (Benton, 1986). This suggests that Ordovician gastropods did not engage in predation by drilling. Elaborate shell ornamentation did not appear until the clade's rapid diversification during the Mesozoic Marine Revolution (Fryda & Rohr, 2001; Erwin & Signor, 1990; Vermeij, 1977).

In a study of morphological convergence in Paleozoic gastropods, Wagner & Erwin (2006) found that potential morphotypes were quickly exhausted and that these morphotypes were recycled "far beyond the expectations of simple architectural constraints." Wagner & Erwin (2006) suggest that this high level of convergence was most likely a biotic response to dominant environmental conditions in the early Paleozoic.

They attribute the decline in dominance of these early forms to changing ecological demands; early Paleozoic gastropods were primarily sessile filter feeders while Mesozoic and Cenozoic gastropods evolved more sophisticated and varied life modes (Wagner & Erwin, 2006).

The Ordovician diversification of gastropods varied globally in both magnitude and rate (Novack-Gottshall and Miller, 2003). While the global diversity trajectory shows an initial pulse of diversification in the Tremadoc followed by a second in the Caradoc, this global pattern is not reflected regionally. For example, gastropod populations in regions such as Avalonia and Baltica demonstrated almost no rise in diversity during the Tremadoc while other regions such as the Mediterranean Province diversified rapidly in the Tremadoc but very little in the Caradoc. On Laurentia, the region of focus in this study, gastropods diversified during both pulses (see Figure 4).

During the Ordovician Radiation, gastropod familial diversity tripled and the clade began to evolve new, more complex morphologies (Erwin & Signor, 1990). This innovation allowed gastropods to expand into new life modes and ecospace (Erwin and Signor, 1990). This radiation can be viewed as the first major step in gastropod evolution and the clade's earliest movement toward the ecological dominance as occurs in today's oceans. This study seeks to establish a clear understanding of the driving forces behind gastropod evolution during this radiation event.

The Ordovician Radiation was followed by a major mass extinction event at the end of the period. This event was driven primarily by rapid global cooling and glaciation, and the abruptness of the event bears strong similarities to the rapidly warming modern global climate system (Finnegan et al., 2011, 2012; Sheehan, 2001). For this reason, the paleoecological response of gastropods to that climate change event may be used to inform our understanding of how modern marine ecosystems will respond to this current warming trend. This study does not examine gastropods from the end-Ordovician, but it establishes a starting point from which to measure Ordovician gastropod response to ecological change.

Many workers (Wagner, 1995; Fryda & Rohr, 2011; Novack-Gottschall & Miller, 2003; Fryda, 2008) have attempted to define the phylogenetic relationships and diversification patterns of early Paleozoic gastropod forms, but both prove difficult to quantify due to frequent homoplasy and poor preservation of the teleoconch, which is often the most diagnostic feature for gastropod phylogenetics (Figure 5). The clade first appeared in the Late Cambrian and spread gradually across the globe through that period but did not experience a major diversification event until the Ordovician (Novack-Gottschall & Miller, 2003; Erwin & Signor, 1990).

Timing of the Ordovician diversification of gastropods differed by paleocontinent (Novack-Gottschall & Miller, 2003). Diversification initiated early in the period on the paleocontinents of Australasia (equatorial island arcs off the northeastern coast of Gondwana) and Laurentia, shown in Figure 6 (Novack-Gottschall & Miller, 2003). Gastropods of the Mediterranean Province experienced steady origination throughout the Ordovician while gastropods of Avalonia and Baltica did not diversify until the Late Ordovician (Novack-Gottschall & Miller, 2003).

Gastropod communities on Laurentia diversified most quickly yet still reflect global patterns in diversity, as they are dominated by *Archaeogastropoda* (Maccluritids, Euomphalids, Bellerophontids; Fryda & Rohr, 2001). Ordovician genera and species tend to be endemic to paleocontinents but high level taxa are found globally (Ross & Ethington, 1970; Rohr, 1994,1996).

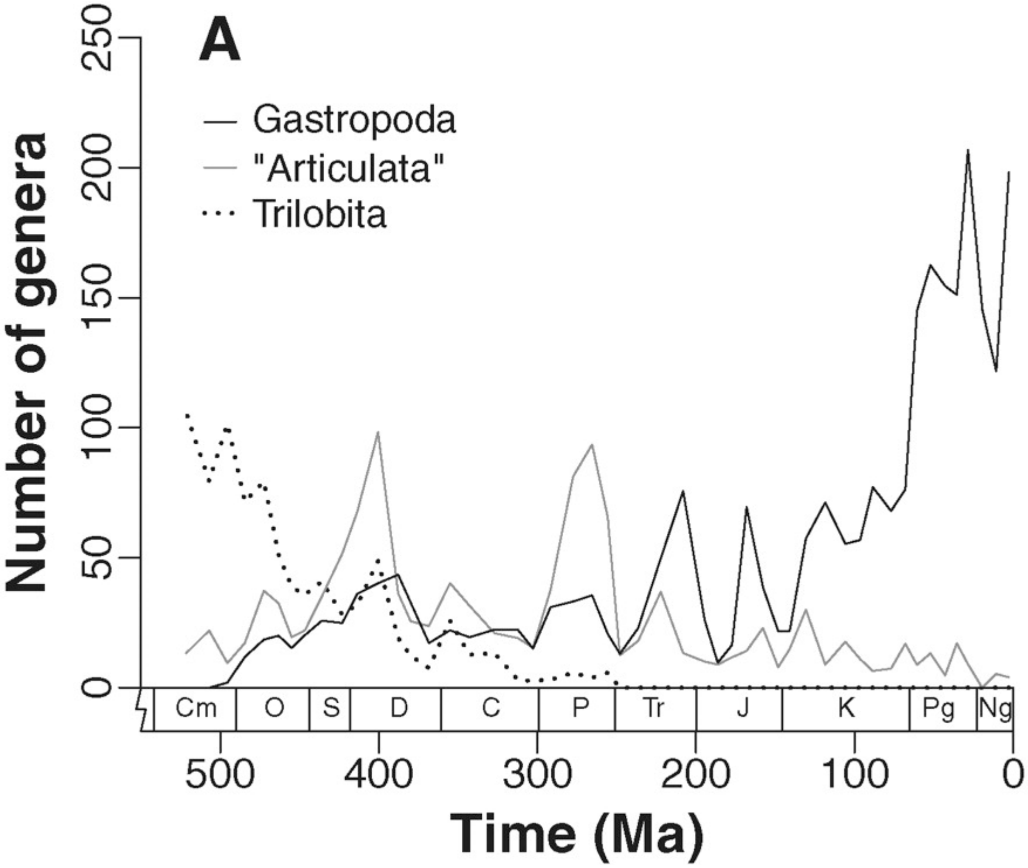


Figure 3. Diversity trajectories of three marine clades having standardized diversity levels with peaks of at least 100 genera or medians of at least 20 genera. Gastropoda (black line), articulate Brachiopoda (gray line), and Trilobita (dotted line) (Alroy, 2010).

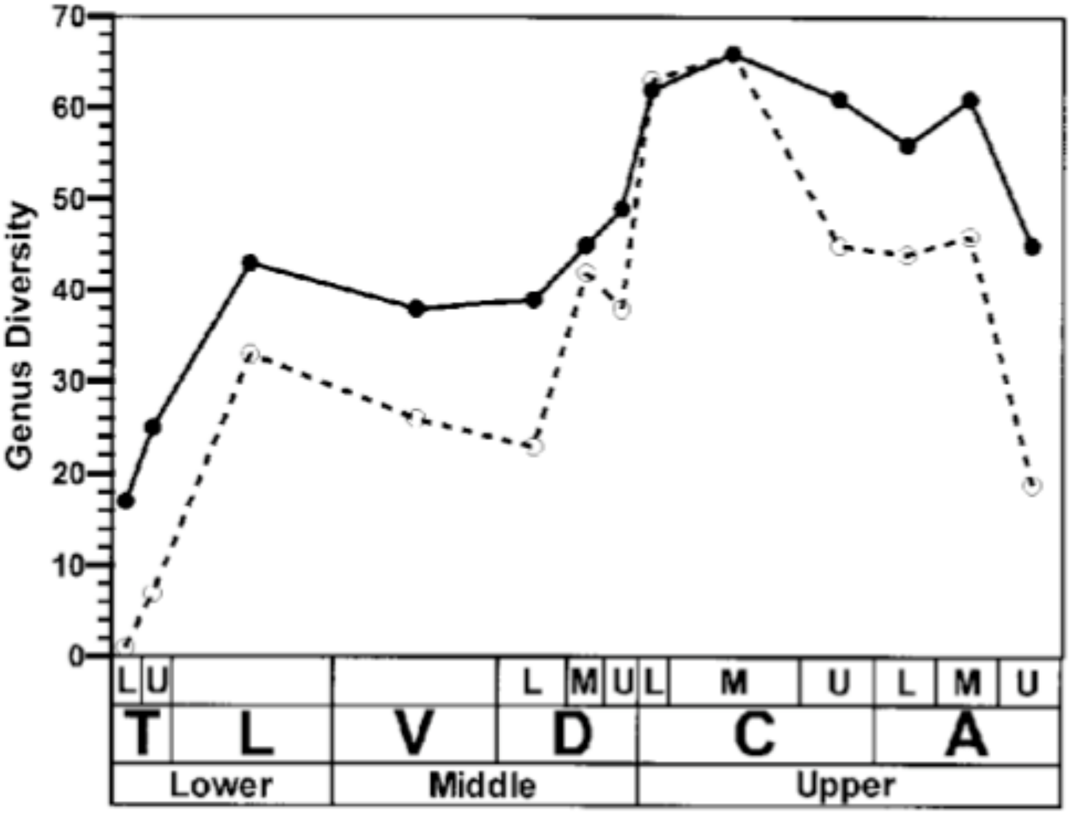
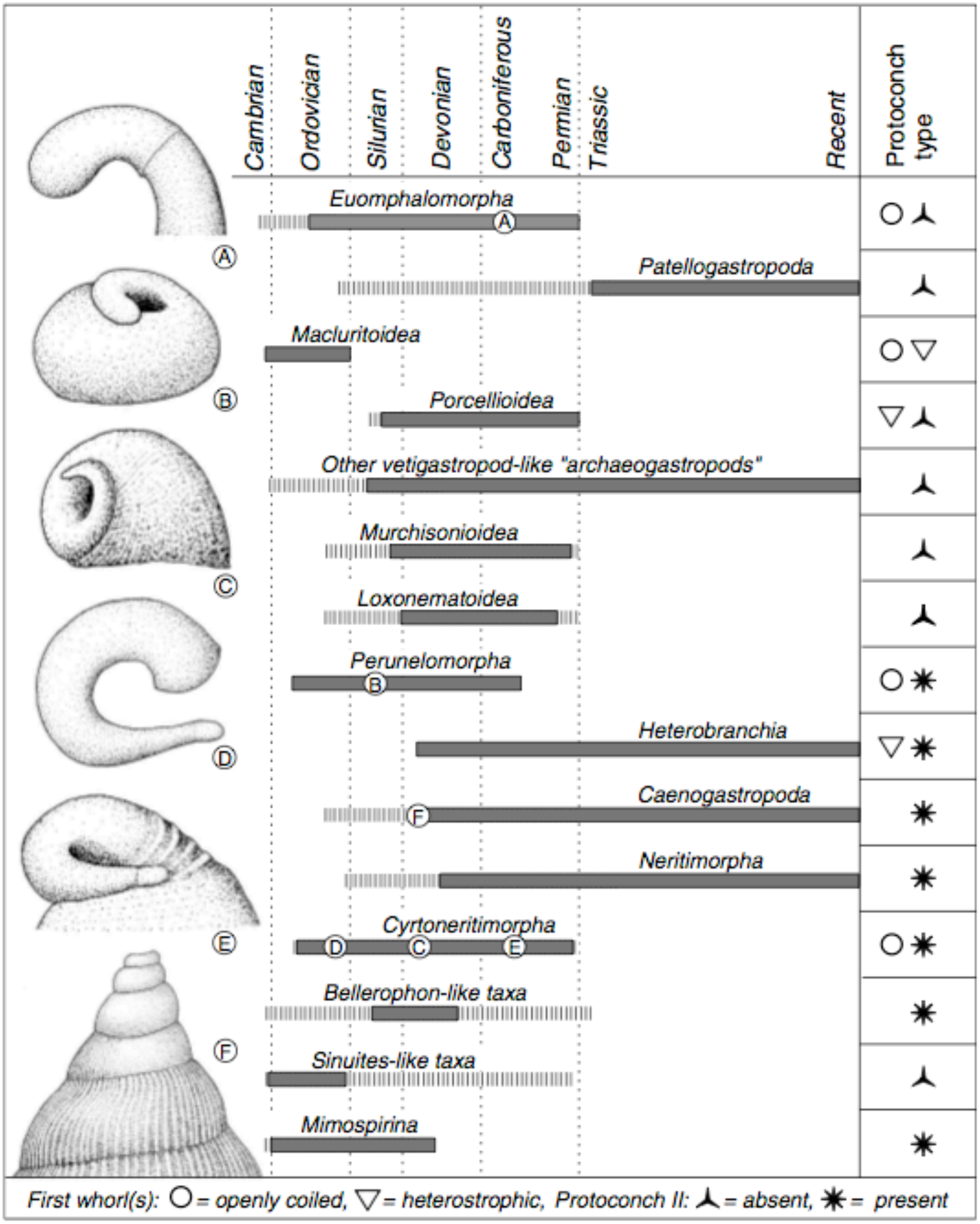


Figure 4. Global Ordovician diversity trajectories for gastropod and bivalve genera. In this figure, solid lines depict the gastropod trajectory and dotted lines depict the bivalve trajectory. The timescale, with time preceding from left to right, is based on that of Webby (1998), using abbreviations for lower, middle, and upper subseries, where appropriate: (T) Tremadocian; (L) Latorpian; (V) Volkhovian; (D) Darriwillian; (C) Caradocian; and (A) Ashgillian (Novack-Gottschall & Miller, 2003).


Cambrian
Ordovician
Silurian
Devonian
Carboniferous
Permian
Triassic
Recent
Protoconch type
Euomphalomorpha
A
○ ⅄
Patellogastropoda
⅄
Macluritoidea
○ ▽
Porcellioidea
▽ ⅄
Other vetigastropod-like "archaeogastropods"
⅄
Murchisonioidea
⅄
Loxonematoidea
⅄
Perunelomorpha
B
○ ✱
Heterobranchia
▽ ✱
Caenogastropoda
F
✱
Neritimorpha
✱
Cyrtoneritimorpha
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C
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○ ✱
Bellerophon-like taxa
✱
Sinuites-like taxa
⅄
Mimospirina
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Ⓓ
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Ⓕ
First whorl(s): ○ = openly coiled, ▽ = heterostrophic, Protoconch II: ⅄ = absent, ✱ = present

Figure 5. Diagram illustrating the stratigraphic ranges of main gastropod groups based on protoconch morphology (gray bars). Shaded bars show stratigraphic ranges inferred from teleoconch features (based on Fryda [1999a, 2005a] and Fryda & Rohr [2004, 2006]). Compare stratigraphic ranges of the Paleozoic gastropods with presumed phylogenetic relationships inferred from teleoconch and protoconch morphologies. Characteristic protoconchs are drawn on the left side. (A) Eumphalomorph protoconch of the Early Carboniferous *Sperluspira*. (B) Late Silurian perunelomorph larval shell. (C) Early Devonian cyrtoneritimorph *Vltaviela*. (D) Late Ordovician cyrtoneritimorph larval shell. (E) Larval shell of the Carboniferous *Orthonychia*. (F) Early Devonian subulitid larval shell. (from Fryda, 2008)

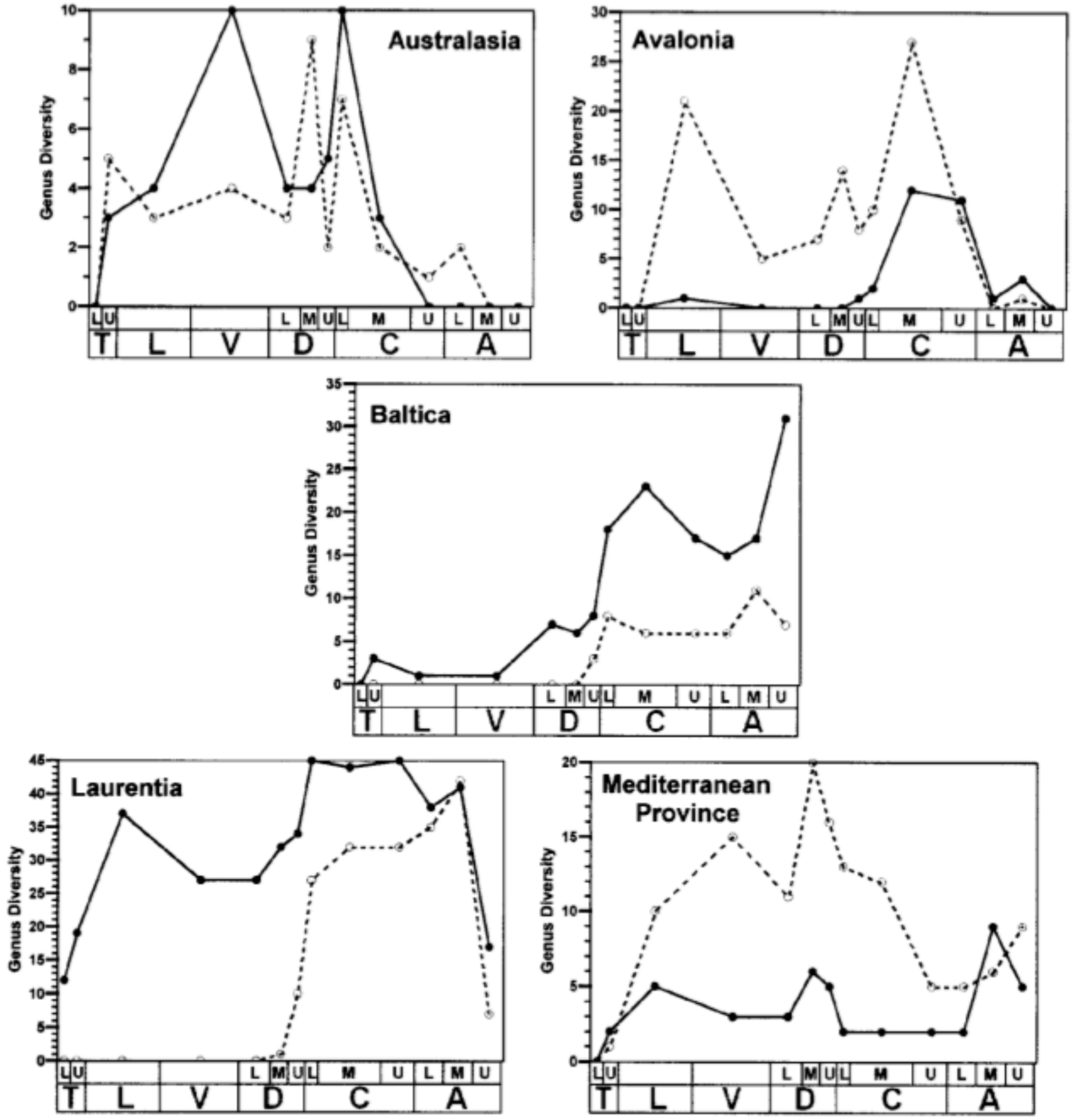

Figure 6. Global trends in Ordovican gastropod diversification, show by paleocontinent (Novack-Gottschall & Miller, 2003)

Geological Setting

The Ibex Region of the Confusion Range in Western Utah provides an excellent laboratory in which to study Ordovician benthic marine ecosystems, due to the succession of well-exposed, biostratigrahpically well-constrained and easily-accessible Ordovician strata, and the range of depositional environments represented in the region (Finnegan & Droser, 2005; Droser et al., 1995; Hinteze, 1951).

A Paleozoic succession is exposed in the generally North-South trending fault block of the Basin and Range Province, which extends from the Wasatch Range in Central Utah across Nevada to the White Mountains in Eastern California (Ethington *et al.*, 1995). This package of sediments was deposited off the passive margin of Laurentia throughout the Paleozoic and into the early Mesozoic (Hintze, 1973). Thrust faulting caused by the Sevier Orogeny during the Late the Cretaceous uplifted and exposed much of the Paleozoic strata (Hintze, 1973). The strata in this region represent a shallowing sequence that transitions from an open ocean, mid-shelf setting into a large, restricted basin and then to a highly restricted, hyper-saline lagoon environment (Hintze, 1953; Ross *et al.*, 1989). Gastropods have been reported from each of the four stratigraphic units (Hintze, 1953; Finnegan and Droser, 2005).

During the Ordovician, Laurentia was situated just south of the paleoequator (Hintze, 1973; Ross, 1977). The Ordovician succession exposed in Western Utah was preserves a large, tropical carbonate ramp that deepened to the West (Ross, 1977). Throughout the Ordovician, a complex system of basins, including the Kanosh Basin, formed across this platform (Ross, 1989). This region was often swept by large tropical storm systems, which is reflected in the storm-generated grainstones commonly preserved in Ordovician strata (Dattilo, 1993; Li and Droser, 1999; Boyer and Droser, 2005; Finnegan and Droser, 2008).

This study was conducted at three localities within the Ibex Region. These localities were originally designated and mapped in the mid-twentieth century by Lehi Hintze and have since been used in multiple paleontologic and stratigraphic studies (see Hintze, 1953; Li and Droser, 1999; Fortey and Droser, Adrain *et al.*, 2001; Boyer and Droser, 2005; Finnegan and Droser, 2008). These three localities (Section J, Section L and Camp, Fig. 8) collectively encompass four Ordovician units: Wah Wah Fm, Juab Fm, Kanosh Shale and Lehman Fm, . These Middle Ordovician units ranging from Ibexian (489-472 Ma) to Whiterockian (472-457.7 Ma) in age and capturecapturing the main pulse of the Ordovician Radiation on Laurentia (Hintze, 1953). This Ibex-Whiterock boundary interval is significant because it marks the beginning of the Ordovician Radiation event locally and globally (Ross, 1989; Droser *et al.*, 1995; Finnegan and Droser, 2005).

Each of these three localities preserves a portion of the Middle Ordovician succession, so all three must be considered together for a complete record. Section J preserves the oldest units, starting in the upper portion of the Wah Wah Formation and ending in the lowermost Kanosh Shale. Section L preserves almost all of the Kanosh Shale and the lower portion of the Lehman Formation. Camp preserves roughly half of the Kanosh shale and all of the Lehman formation.

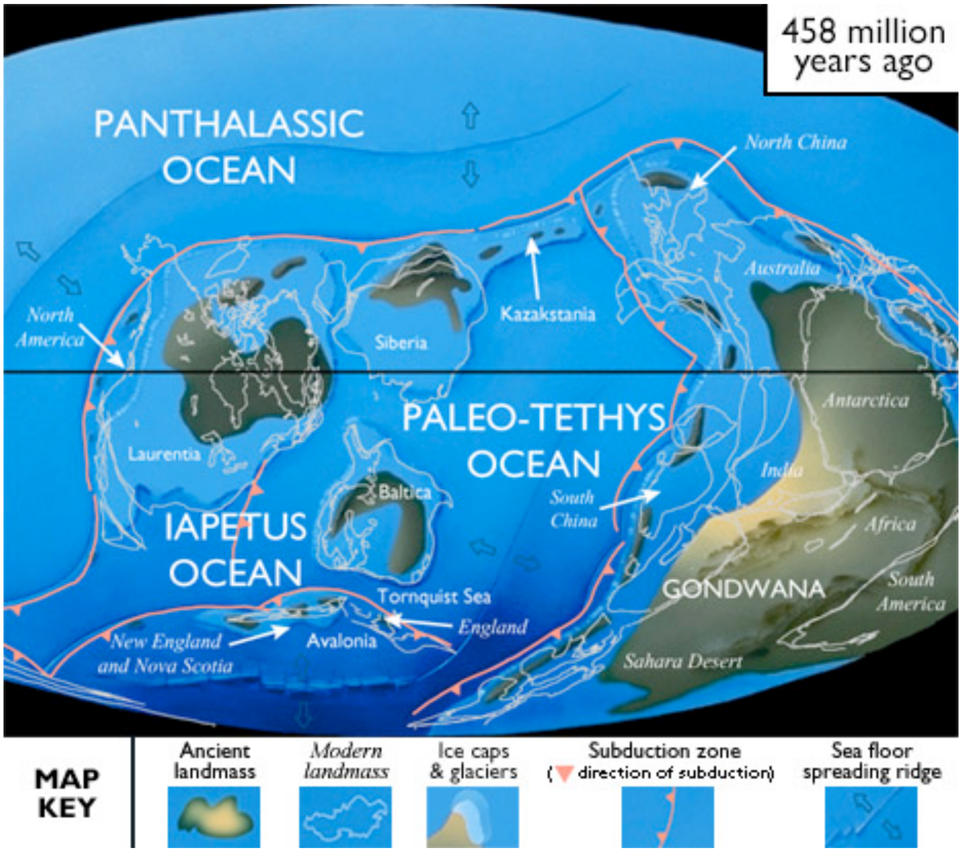

Figure 7. Ordovician paleogeography (www.paleoportal.org)

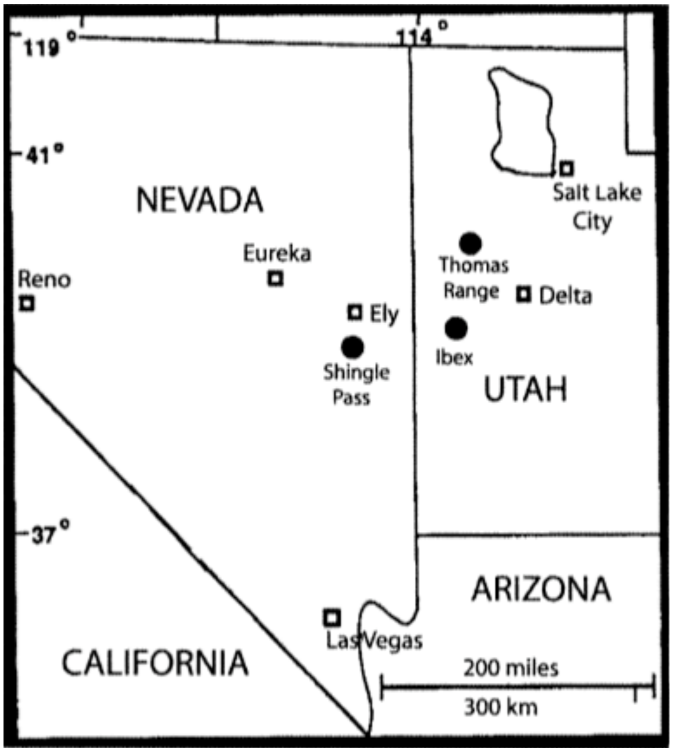

Figure 8. This study was conducted in the Ibex region of the Confusion Range, in western Utah. Locality is marked on the map as "Ibex." (Finnegan & Droser, 2005).

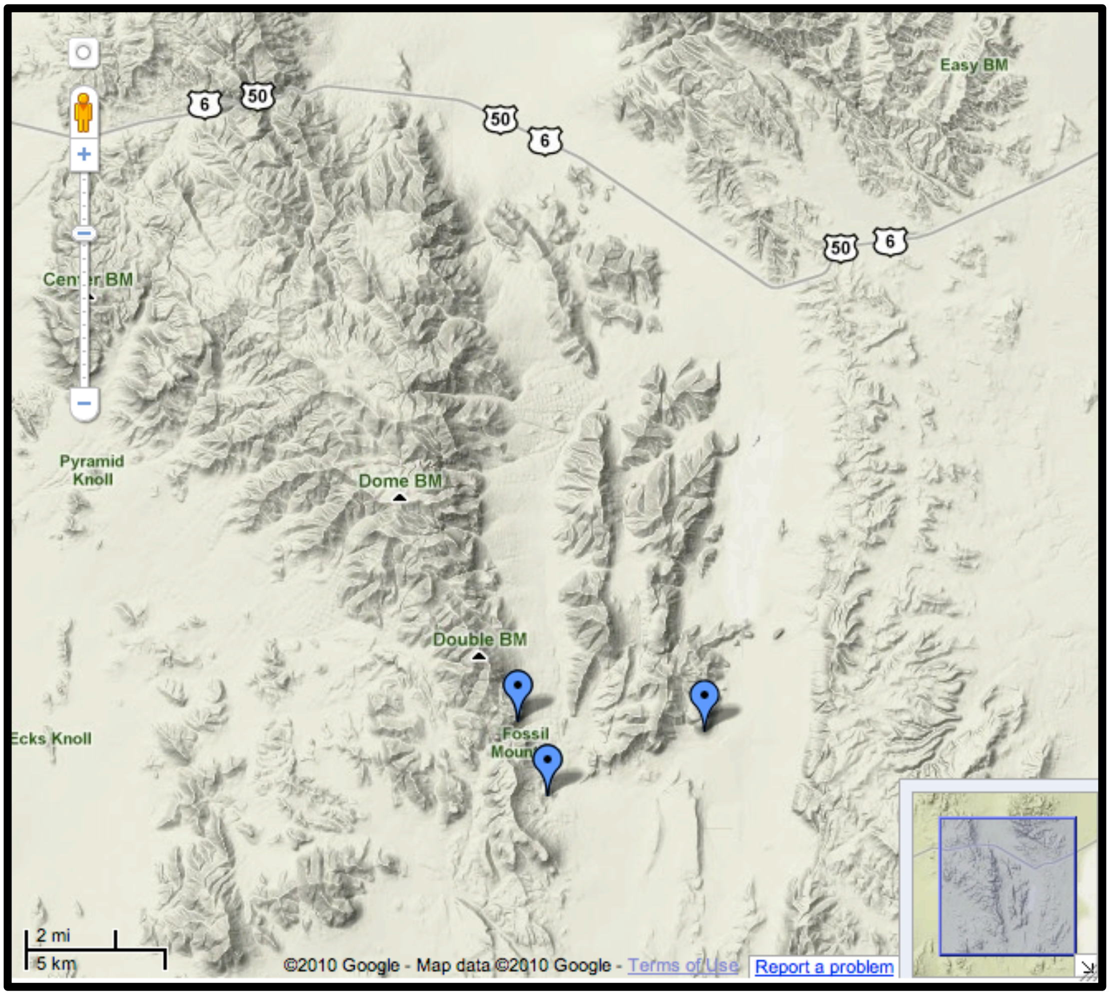

Figure 9. Detailed locality map, showing collections taken at Section J, Section L and Camp. (image from Google Maps)

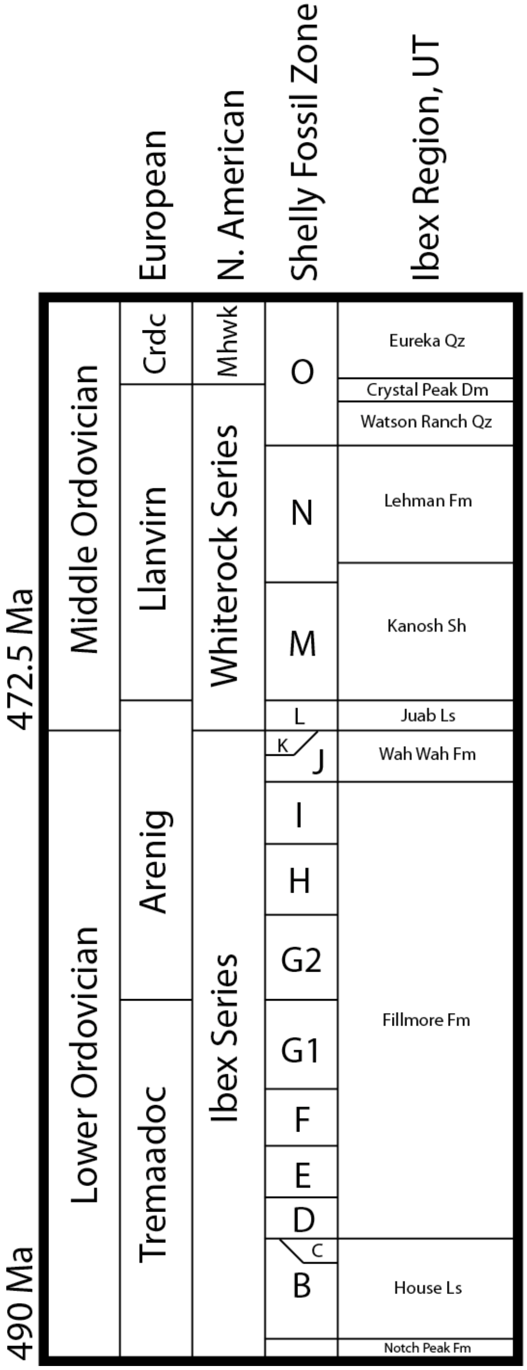

Figure 10. Stratigraphy of the Ibex Region, the study area. This study examined the Wah Wah formation, Juab formation, Kanosh shale and Lehman formation, which span the Ibexian/Whiterockian boundary. Shelly fossil zones are designated by Hintze (1952).

Methods

Detailed stratigraphic sections were logged at each of the three localities. Lithology was characterized using the Dunham scale (mudstone, wackestone, packstone, grainstone; Dunham, 1962). The range of facies and fossil taxa at each locality were characterized in the field and bulk samples (weighing roughly 7-8 kg) were taken of each unique facies. During the measuring and logging of each section, gastropod-rich beds were noted and these were later bulk sampled. Individual gastropod specimens and slabs with gastropods found in float were also collected for overall diversity measurements. This process of bulk sampling allows for the later determination of relative abundance (Finnegan and Droser, 2005).

Bulk sampling proved difficult in the Wah Wah Fm because of the nature of the thick (1-3m) grainstone ledges. These limestones were too hard to easily break and sample with a sledge, and so much of our collecting was limited to bed tops and float material. Float material was only collected if it could be reliably matched with outcrop less than 1 m away.

In the laboratory, fossil material from each bulk sample was extracted by hand using a sledge, rock hammer and chisel (the “crack out” method; Finnegan and Droser, 2005). This processing method was chosen because the gastropods are not silicified and cannot be dissolved out of the carbonates. Breaking down the bulk samples by hand allows for precise collection of fossil material. During the crack out process, gastropod specimens were counted and identified. Other fauna were counted by class, in order to determine the community structure and relative abundance of gastropods in each assemblage.

In addition to using the crack out method, some samples were also slabbed and polished. This method provides a view of shell bed structure and can aid in deciphering the taphonomy of the bed. Furthermore, examining the cross section of Archaeogastropoda can be helpful in identification, as the whorl cross section can vary in morphology, ranging from triangular to square (Rohr, 1994).

Taphonomy

Gastropod shells are composed of aragonitic calcium carbonate ($CaCo_3$) and are notoriously difficult to preserve over geologic timescales (Hughes, 1986) because aragonite is not stable at Earth surface conditions and so tends to dissolve or recrystalize into its more stable polymorph calcite. Dissolution or recrystalization results in the loss of both fine shell microstructure and large-scale morphological features like shell ornamentation and growth lines. For these reasons, Paleozoic gastropods are difficult to identify to species-level accurately. The most detailed morphological studies of Great Basin Paleozoic gastropods have focused on silicified specimens, most often from the Antelope Valley region of Nevada (see Rohr, 1994; Rohr 1996). While the replacement of aragonite by silica still fails to preserve fine detail like shell microstructure, large-scale features are well preserved.

Gastropods in the Ibex Region are primarily preserved as steinkerns, molds and casts; no silicified gastropods were found. Furthermore, these poorly preserved specimens are commonly fractured and difficult to distinguish from the surrounding matrix (see Fig. 10). Thus, species-level identification is nearly impossible in most cases. However, the inability to tease apart detailed taxonomy of the gastropods in these facies does not preclude us from completing an evaluation of the environmental context of gastropods. We used relative abundance to infer the role gastropods in these communities and a combination of large-scale shell morphology and modern gastropod ecology to evaluate life mode. The orientation of shells within shell beds is used assess whether the fossils were *in situ* or transported. When a majority of gastropod shells in a bed are preserved "posterior up," we inferred the assemblage of gastropods to be *in situ*. We also inferred gastropod accumulations to be *in situ* when they occur in monospecific aggregations, lenses or "pockets," as modern marine gastropods assume this life mode for purposes of protection from predation and reproduction (Stoner and Ray, 1993).

Figure 11. Example of very poorly preserved *Murchisonia* gastropods from the Wah Wah Formation.

Depositional Environments

The early Paleozoic depositional environments of the Basin and Range Province, and the Ibex region in particular, have been a focus of stratigraphic, biostratigraphic and paleoecological studies studies in large part because of the extensive expo (see Ross *et al.*, 1989; etc(see Hintze, 1951; Ross, 1977; Adrain *et al.*, 2001; Finnegan and Droser, 2005). We use these previous studies as a starting place to develop a depositional model for the uppermost lower to Middle Ordovician succession at Ibex

The four units examined preserve a large-scale shallowing sequence, from mid-shelf, open ocean conditions to extremely shallow and hypersaline lagoon (Hintze, 1953; Boyer and Droser, 2003). The Kanosh shale and Lehman formation represent preservation within a large basin (Boyer and Droser, 2003). It is most effective to consider the Wah Wah and Juab formations separately from the Kanosh shale and Lehman formation, as the Wah Wah and Juab formations were likely deposited in mid-shelf, normal marine conditions while the Kanosh shale and Lehman formation were deposited under restricted, non-open marine conditions.

Wah Wah and Juab Formations

The Wah Wah and Juab formations have been interpreted to represent deposition in open shelf, normal marine conditions (Ross et al., 1989; Finnegan and Droser, 2005). In their paleoecological study of the Wah Wah and Juab formations, Finnegan and Droser (2005) provide a useful description of the two units, which are comprised of 2 to 8m thick parasequences. The parasequences of the Wah Wah formation shallow up from shales interbedded with nodular carbonate mudstones and wackestones to carbonate mudstones and wackestones with substantial siliciclastic fractions (10-30%). These parasequences are capped by intraclastic skeletal grainstones (Finnegan and Droser, 2008). Gastropods are rare in the Wah Wah formation and occur either as solitary specimens within the skeletal grainstone caps (*Murchisonia* sp.; Fig 20) or in distinct lenses within the carbonate wackestones (*Liospira americana, Murchisonia* sp.; Fig 20).

Based on common sedimentary structures in the Wah Wah formation (grainstone event beds, planed-off hardgrounds, skeletal megaripple sets), the unit likely represents deposition above storm wave base but below normal wave base (Ross et al., 1989; Finnegan and Droser, 2005). Near the top of the Wah Wah formation is a nearly monospecific shellbed formed by *Hesperonomiella minor* (referred to as the *H. minor* bed). The only other taxon present in this bed is the gastropod *Lophospira* sp., and it occurs in very low abundance. This bed marks the beginning of the Whiterock Series, which is considered to signal the start of the Ordovician Radiation (Hintze, 1953; Ross et al., 1989; Finnegan and Droser, 2005).

The Wah Wah formation is best exposed at Hintze's Section J, where 70m crop out to form 2-8m thick ledges that correspond to the parasequences described above. Transition to the Juab Formation is marked the *H. minor* bed. Though it is interpreted to represent deposition in mid-shelf, normal marine conditions, the Juab formation contains less siliciclastic sediments and is less fossiliferous than the underlying Wah Wah formation (Hintze, 1953; Ross et al., 1989). The Juab formation is poorly exposed at Section J, forming ~80m of gently sloping slabs of grey silty limestone before gradually transitioning into the Kanosh shale. The Juab formation consists of interbedded mudstones and wackestones comprised of brachiopods, trilobites, orthocone cephalopods and rare Macluritid gastropods. The lithologies and depositional environments of the Wah Wah and Juab Formations are described in Figure 12 and generalized schematics of sediment packages in the two formations are show in Figures 14 and 15.

Wah Wah & Juab Formation Lithologies		
Lithology	**Description**	**Environment**
Shale	Siliciclastic, tan in color, unfossiliferous. Shale horizons 5-15 cm in thickness, may be absent from parasequence	Wah Wah and Lehman Formations are characterized by 2-8 m, ledge-forming parasequences, comprised of a shallow sequence of shale, wackestone, packstone and grainstone, often capped by a planed-off hardground. Likely deposited mid-shelf, between storm and normal wave base (Finnegan & Droser, 2008a)
Wackestone	Trilobite skeletal material with brachiopods, echinoderms and ostracods, and rare cephalopods and gastropods, in a mixed siliciclastic-carbonate matrix. Wackestone horizons 5 cm, up to 15 cm in thickness	
Packstone	Primarily trilobite skeletal material with brachiopods, echinoderms and ostracods, and rare gastropods, bryozoans and cephalopods, in a mixed siliciclastic-carbonate matrix. Packstone horizons 30 cm to 3 m in thickness.	
Grainstone	Grain-supported mixed siliciclastic-carbonate with dense trilobite and brachiopod skeletal material, echinoderms and ostracods with rare gastropods. Grainstone horiozons 2-15 cm in thickness	
H. minor Coquina	Grainstone marking the boundary between the Wah Wah and Juab Formations, comprised of imbricated *Hesperonomiella minor* brachiopods, with very rare *Lophospira perangulata* gastropods	

Figure 12. Table of Wah Wah and Juab Formation lithologies, with depositional environments.

Kanosh Shale and Lehman Formation

The Kanosh Shale represents deposition in a large basin within the carbonate ramp (Ross et al., 1989). The fossil assemblage (dominated by brachiopods and ostracods and lacking echinoderms) preserved in the Kanosh Shale indicates that oxygen on the basin floor was likely restricted (Boyer & Droser, 2003; McDowell, 1987). The Kanosh Shale preserves repeated shallowing sequences, capped at the top of the unit by a rapid shallowing event and an influx of terrestrial siliciclastics, which forms a 2 m thick sandstone bed. The Lehman Formation overlies the Kanosh Shale and is dominated by thin (2-10 cm thick) beds of micritic carbonate mud. Previous studies suggest that the thin-bedded micrite precipitated from a warm, shallow lagoon. Moreover, these conditions would have resulted in increased evaporation and ultimately in hypersalinity (Boyer & Droser, 2003; McDowell, 1987). Hypersalinity is supported by fossil assemblage preserved in the Lehman Formation. The unit is less fossiliferous than the Kanosh Shale but is dominated by monospecific beds of *Clathrospira glindmeyeri* (gastropod) and *Modiolopsis* sp. (bilvalve). Both gastropods and bivalves are members of the Modern Evolutionary Fauna and very rarely dominate Early Paleozoic shell beds (Li & Droser, 1999).

Hintze (1951) divided the Kanosh and Lehman succession into five stratigraphic members (1. Lower olive shale and calcarenite member, 2. Silty limestone member, 3. Upper olive shale and calcarenite member, 4. Sandstone and shale member, and 5. Calcisiltite member). McDowell (1987) revisited this interval and informally divided the succession into four members (1. Lower shale and packstone member, 2. Wackestone-micrite member, 3. Upper shale member, and 4. Upper packstone member).

In their study of the shell beds of the Kanosh shale and Lehman formation, Boyer and Droser (2003) divided the Kanosh and Lehman into five lithofacies rather than stratigraphic members: 1. Distal, 2. Proximal, 3. Tidal flat, 4. Sandstone, and 5. Restricted) as well as multiple subfacies based on detailed sedimentology. Our work takes a similar approach but does not use all of the Boyer and Droser (2003) lithofacies, but instead describes five new lithofacies that are better suited for examining paleoecology, rather than shell bed dynamics.

Kanosh Shale & Lehman Formation Lithologies		
Lithology	**Description**	**Environment**
Shale	Olive in color, very little fossil material (trilobite sclerites, inarticulate brachiopods, ostracods), most often interbedded with packstones & grainstones, though dominant in the lowermost Kanosh Shale	Deepest part of the Kanosh Basin, restricted oxygen, low energy (Boyer & Droser, 2003)
Brachiopod & Ostracod Shellbeds	Densely packed orthid brachiopods and ostracods (*Hintziella lehi, H. crassipuctata, H. parvipuctata, Ballardina geniculata, Punctoschidtella minor* and *Leperditela valida*; Berdan, 1988), uniform in size and lacking abrasion or fragmentation, few gastropods, trilobites, cephalopods and bryozoans. Carbonate matrix contains up to 30% siliciclastics.	Nearly-autocthonous accumulations, aggregated by storm activity (Finnegan & Droser, 2008a), likely restricted in oxygen
Carbonate (Micrite) Mudstone	Dark grey to black micrite, 1-10 cm thick beds, fossil concentrations comprise less than 10% but are monospecific when they occur. Beds are taxonomically dominated by gastropods (*Clathrospira* sp.) or bivalves (*Modiolopsis* sp.) and are preserved as steinkerns (Boyer & Droser, 2003)	Hypersaline, shallow lagoon (Boyer & Droser, 2003)
Burrowed Limestone	Mixed micrite & very fine grained sand, light grey in color, forming 2-15 cm thick beds, bioturbated and fossiliferous	Shallow, closer to normal-marine than other Kanosh Shale and Lehman Formation lithologies (Boyer & Droser, 2003)

Figure 13. Table of Kanosh Shale and Lehman Formation lithologies, with description and environmental interpretation.

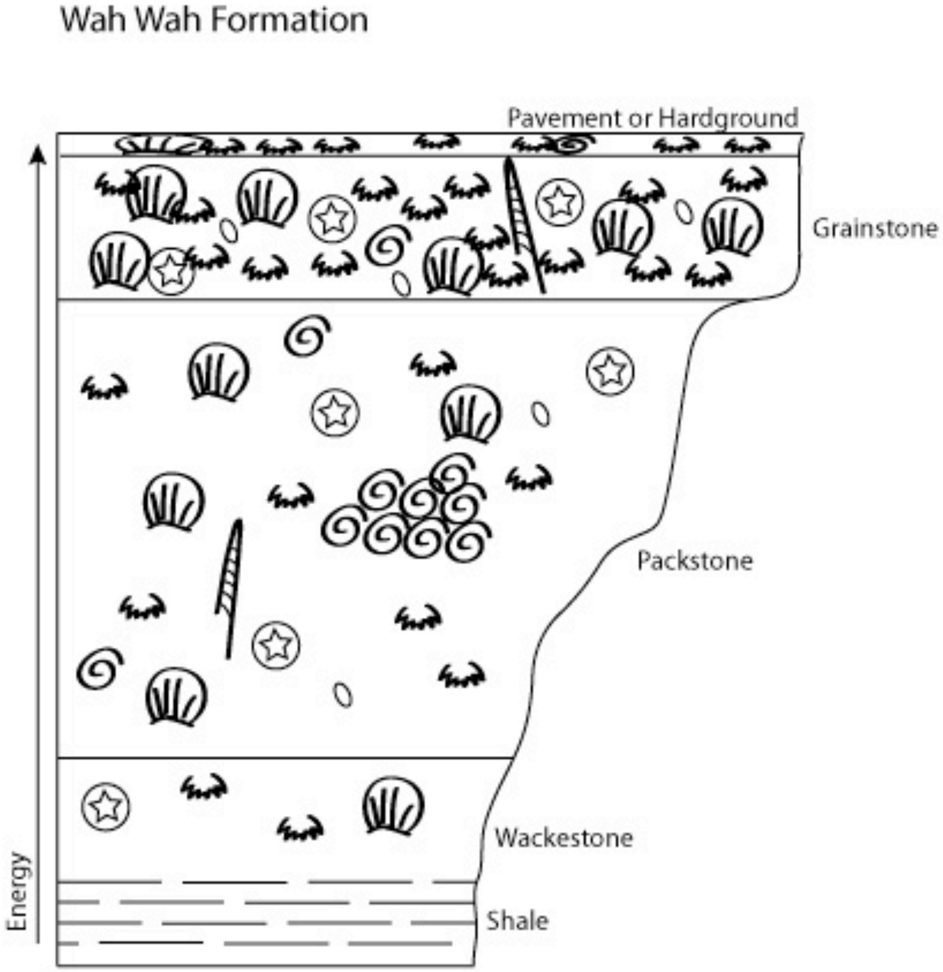

Figure 14. Generalized lithology of sediment packages in the ledge-forming Wah Wah formation, showing pattern of gastropod preservation. Gastropods were found in aggregations or "lenses" within the packstone lithofacies. Solitary specimens were found in the grainstone and pavement lithofacies.

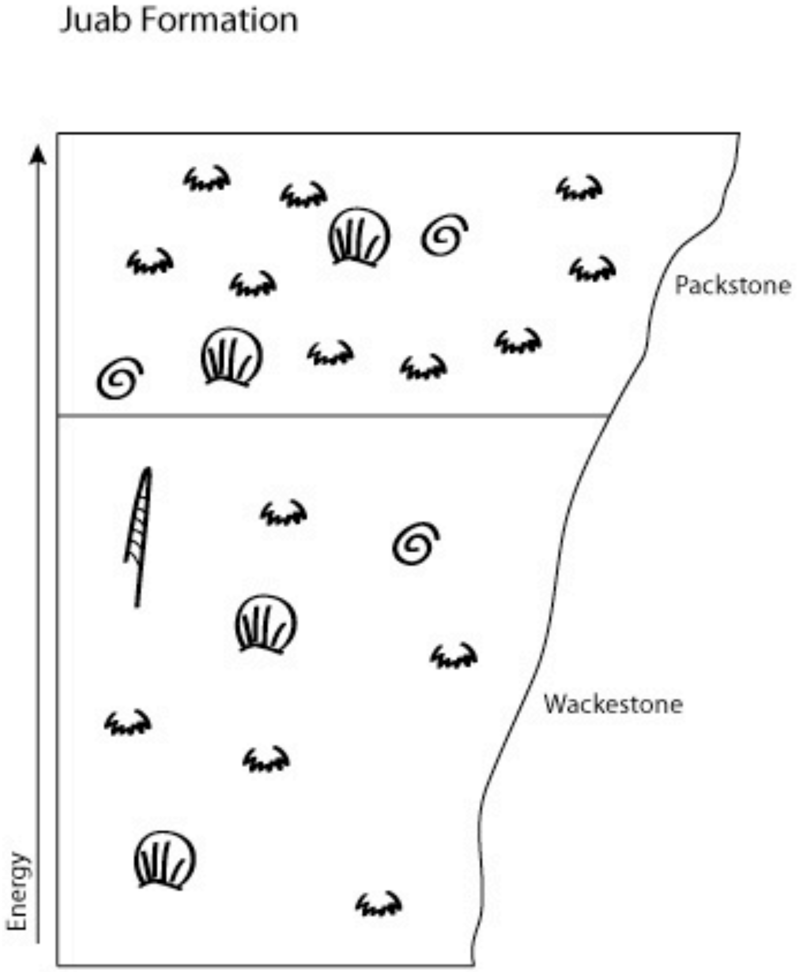

Figure 15. Generalized lithology of sediment packages in the Juab formation, showing pattern of gastropod preservation. Gastropods were found as rare solitary specimens within the wackestone lithofacies, and more commonly as solitary specimes in the packstone lithfacies.

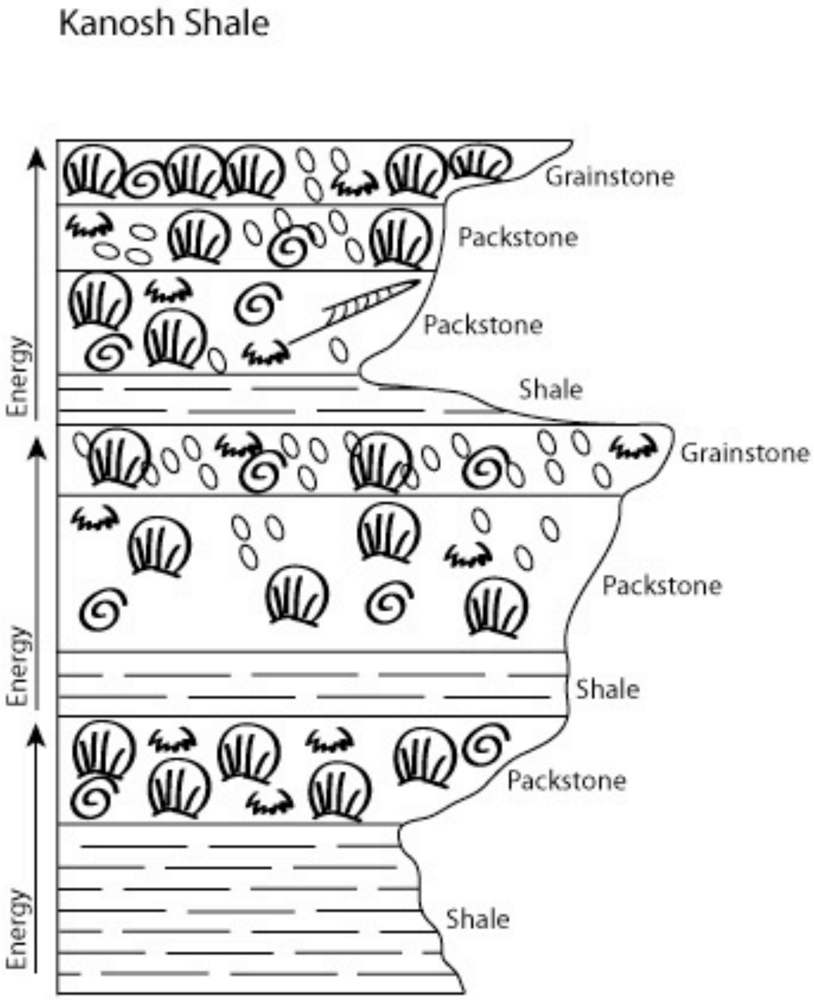

Figure 16. Generalized lithology of the Kanosh Shale, showing pattern of gastropod preservation. Gastropods were found as solitary specimens or in small clusters within packstones and grainstones.

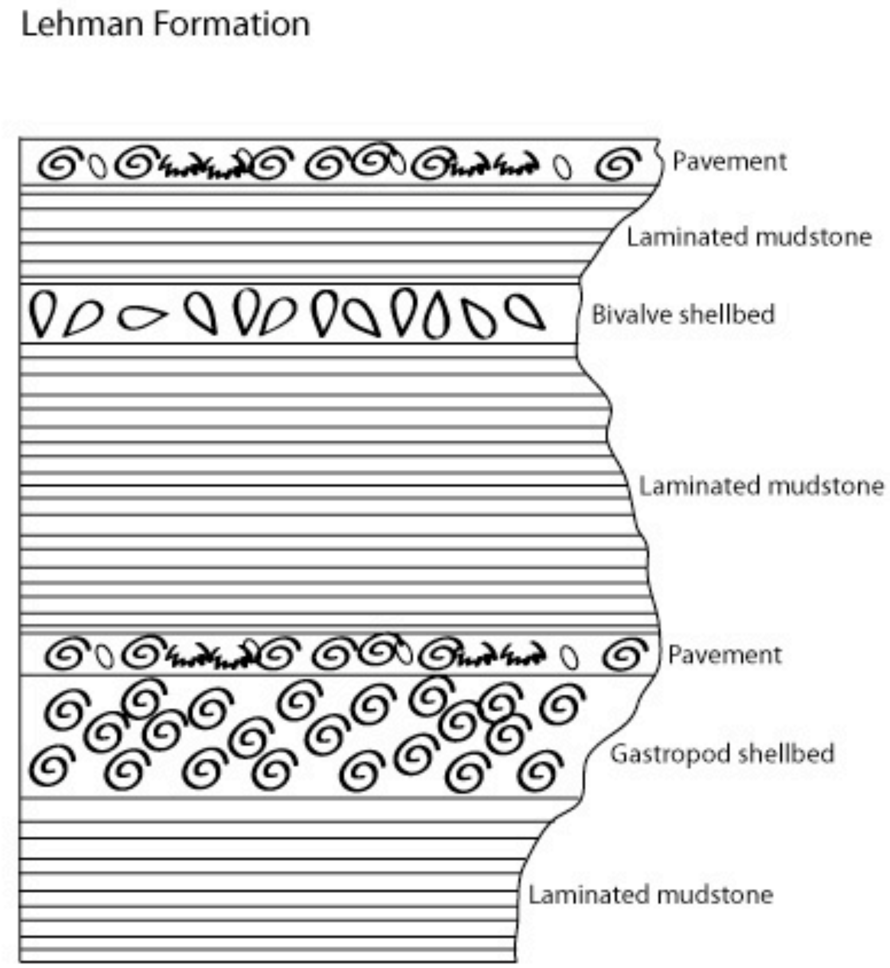

Figure 17. Generalized lithology of the Lehman Formation, showing patterns in gastropod preservation**.** Gastropods formed dense, monospecific shellbeds withing micritic mud horizons.

Gastropod Taxa

Eleven gastropod taxa from the 31 bulk samples were identified: *Barnesella measuresae, Clathrospira glindmeyeri, Lecanospira compacta, Liospira americana, Lophospira* sp., *Monitorella auricula, Malayaspira hintzei, Murchisonia* sp., *Palliseria robusta, Rossospira* sp. and *Tropidodiscus* sp (Figure 21). The relative abundance of these gastropod taxa is shown in Figure 22. All taxa, except *Murchisonia* sp., were restricted to a single unit. The relative abundance of present clades (Bivalvia, Brachiopoda, Cephalopoda, Echinodermata, Gastropoda and Trilobita) is shown in Figure 23. Due to analysis methods (destruction of rocks by "crack out"), relative abundance of clades was only analyzed for 13 of the 31 bulk samples.

The relative abundance of clades indicates where gastropods were most ecologically dominant. While only 13 bulk samples were analyzed, a trend still emerges. Gastropods were a very minor part of the assemblage in the Wah Wah Formation, where trilobites and brachiopods were dominant. While gastropods account for 100% of the fossil material identified in the Juab formation bulk samples, these gastropod specimens were the *only* fossil material recovered from the bulk samples. The wackestones of the Juab formation are much less fossiliferous than Wah Wah formation and Kanosh shale. Bulk samples 13 and 24, from the Kanosh Shale, show that gastropods are minor components, comprising 9% and 3% of the total fossil material from each bulk sample. Gastropods are dominant in the Lehman Formation, where they comprise a minimum of 18% (sample 25) and a maximum of

100% (sample 26) of the total fossil material for each bulk sample. It is important to note that while bulk samples comprised of 100% gastropod material was collected from both the Juab and Lehman Formations, bulk samples from the Juab Formation had only one or two specimens while those from the Lehman Formation had hundreds.

There is a strong substrate affinity across all depositional environments. Gastropods are most often preserved on muddy substrates, regardless of depth. In the Wah Wah Formation and the Kanosh Shale, gastropods are often preserved on mud stringers (less than 1 cm in thickness) above and below grainstones. Gastropods preserved in mud stringers and thicker mud beds are interpreted to be *in situ*, as they are oriented in life position and show no signs of transport. The presence of mud supports this interpretation, as very fine grained sediments indicate low energy environments, especially compared to the packstone and grainstone event beds.

Descriptions of the gastropod taxa collected in this study are shown in Figures 18 and 19, which pictures shown in Figure 20.

Family	Taxa	Description	Size	Environment
Superfamily EUOMPHALOIDEA de Koninck 1881				
Family Omphiletidae	*Barnesella measuresae* Rohr, 1994	Loosely coiled, discoidal with flat base and concave top… whorls triangular in cross section, slightly higher than wide, with acutely angular crest.	Up to 4 cm in diameter	Brachiopod and ostracod grainstones and packstones of the Kanosh Shale
	Malayaspira hintzei Rohr, 1994	Discoidal, loosely coiled, widely umbilicate, hyperstrophic. Greatly resembles *B. measuresae* but has a square, rather than triangular cross section	Up to 4.5 cm in diameter	Brachiopod and ostracod grainstones and packstones of the Kanosh Shale
	Lecanospira compacta Salter, 1859	Discoidal with slightly concave base and top		Brachiopod and ostracod grainstones and packstones of the Kanosh Shale
	Rossospira harrisae Rohr, 1994	Discoidal with flat base, openly coiled	Up to 4 cm in diameter	Brachiopod and ostracod grainstones and packstones of the Kanosh Shale
Superfamily MACLURITOIDEA Fischer, 1995				
Family Macluritidae	*Monitorella auricula* Rohr, 1994	Sub-hemispherical shell with flat base, Thick (up to 0.5 cm), heavy shell	Up to 8 cm in diameter	Thickly bedded limestone's of the Juab Fm
	Palliseria robusta Wilson, 1924	Sub-spherical shell with rounded base and deep, relatively narrow apical depression		Thickly bedded limestone's of the Juab Fm
Superfamily PLEUROMARIOIDEA Swainson, 1840				
	Liospira americana Billings, 1860	Large, lenticular, width twice the height, each whorl embraces previous whorl just below angular periphery, producing a slight gradate profile and impressed suture	Up to 4.5 cm in diameter	Dense lens in the Wah Wah Fm packstone

Figure 18. Table of Euomphalid, Macluritid and Pleuromarid gastropods collected in this study.

Family	Taxa	Description	Size	Environment
Other ARCHAEOGASTROPODA				
Family Eutomariidae Wenz, 1938	*Clathrospira glindmeyeri* Rohr, 1994	Turbiniform, relatively thin-shelled, conical spire, whorl embraces previous whorl at lower-outer periphery producing a weak suture		Densely packed, monospecific shellbeds within carbonate mud beds of the Lehman Fm
Family Lophospiridae Wenz, 1938	*Lophospira perangulata* Hall, 1847	Three whorl angulations, well-developed carina bearing the selenizone on upper shoulder, weaker angulation at the lower-outer edge and a circumbilical angulation.	2.5 cm in height	*Hesperonomiella minor* brachiopod coquina of the Wah Wah Formation
Family Oristomatidae Wenz , 1938	*Murchisonia* sp.	High-spired (20-25 degrees), rounded whorls, weak selenizone at mid-whorl, sutures impressed	Up to 3 cm in height	Within shellbeds of the Wah Wah Fm, Juab Fm, Kanosh Shale and Lehman Fm
Family Bellerophontoidea M'Coy, 1851	*Tropidodiscus* sp.	Planispiral whorls, compressed, lenticular shells with wide umbilici, acutely angular. Keel aperture slightly flared		Lower Kanosh Shale

Figure 19. Table of other Archaeogastropod collected in this study.

Figure 20. Gastropod taxa. 1)*Barnesella measuresae*, 2) *Malayaspira hintzei*, 3) *Clathrospira glindmeyeri*, 4)*Tropidodiscus* sp., 5) *Lecanospira compacta*, 6) High spired *Murchisonia* sp., 7) *Monitorella auricula*, 8) *Liospira americana*

Sample #	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**
1	0	0	0	5	0	0	0	0	0	0	0
2	0	0	0	7	0	0	0	2	0	0	0
3	0	0	0	6	0	0	0	0	0	0	0
4	0	0	0	6	0	0	0	1	0	0	0
5	0	0	0	13	0	0	0	0	0	0	0
6	0	0	0	0	3	0	0	0	0	0	0
7	0	0	0	0	0	1	0	0	0	0	0
8	0	0	0	0	0	1	0	0	1	0	0
9	0	0	0	0	0	1	0	0	0	0	0
10	0	0	0	0	0	0	1	0	0	0	0
11	1	0	0	0	0	0	3	0	0	0	0
12	4	0	1	0	0	0	0	0	0	0	0
13	5	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	3
15	1	0	2	0	0	0	2	1	0	0	0
16	2	0	0	0	6	0	2	0	0	0	0
17	0	0	3	0	0	0	1	0	0	1	0
18	12	0	0	0	0	0	0	0	0	0	0
19	3	0	0	0	0	0	0	0	0	1	0
20	4	0	0	0	0	0	1	0	0	0	0
21	1	0	0	0	0	0	2	4	0	0	0
22	0	0	0	0	0	0	5	0	0	0	0
23	2	0	1	0	0	0	0	0	0	0	0
24	1	0	0	0	0	0	0	12	0	0	0
25	2	1	0	0	0	0	0	21	0	0	0
26	0	23	0	0	0	0	0	0	0	0	0
27	0	15	0	0	0	0	0	0	0	0	0
28	0	23	0	0	0	0	0	0	0	0	0
29	0	18	0	0	0	0	0	0	0	0	0
30	0	48	0	0	0	0	0	0	0	0	0
31	0	1	0	0	0	0	0	9	0	0	0

Figure 21. Gastropod occurrences for each bulk sample. Species are lettered: (A) *Barnesella measuresae***,** (B) *Clathrospira glindmeyeri*, (C) *Lecanospira compacta*, (D) *Liospira americana*, (E) *Lophospira* sp., (F) *Monitorella auricula*, (G) *Malayaspira hintzei*, (H) *Murchisonia* sp., (I) *Palliseria robusta*, (J) *Rossospira* sp., (K) *Tropidodiscus* sp.

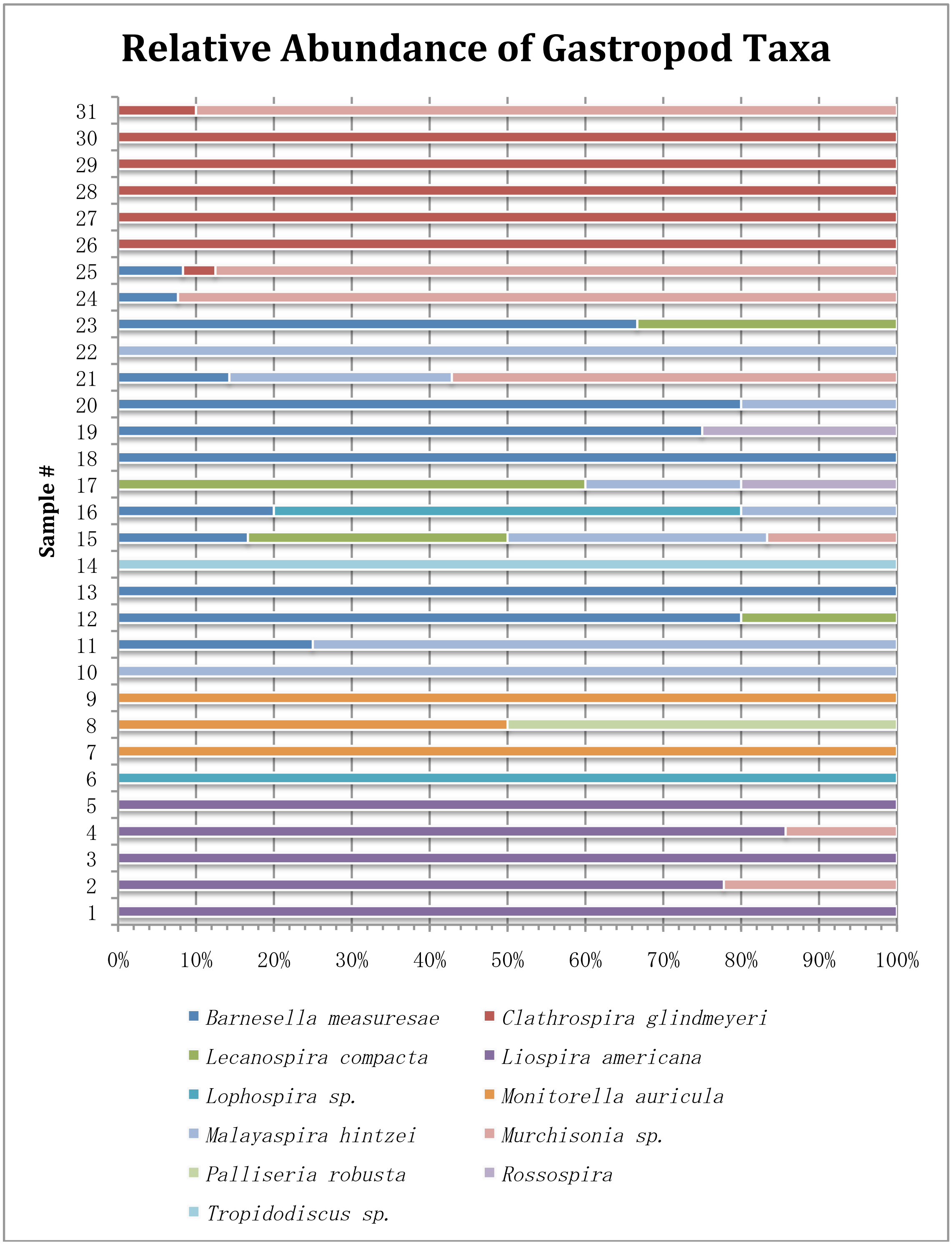

Figure 22. Gastropod occurrences per bulk sample. Sampes were collected from units as follows: (1-6) Wah Wah Fm., (7-9) Juab Fm., (10-25) Kanosh Shale, (26-31) Lehman Fm.

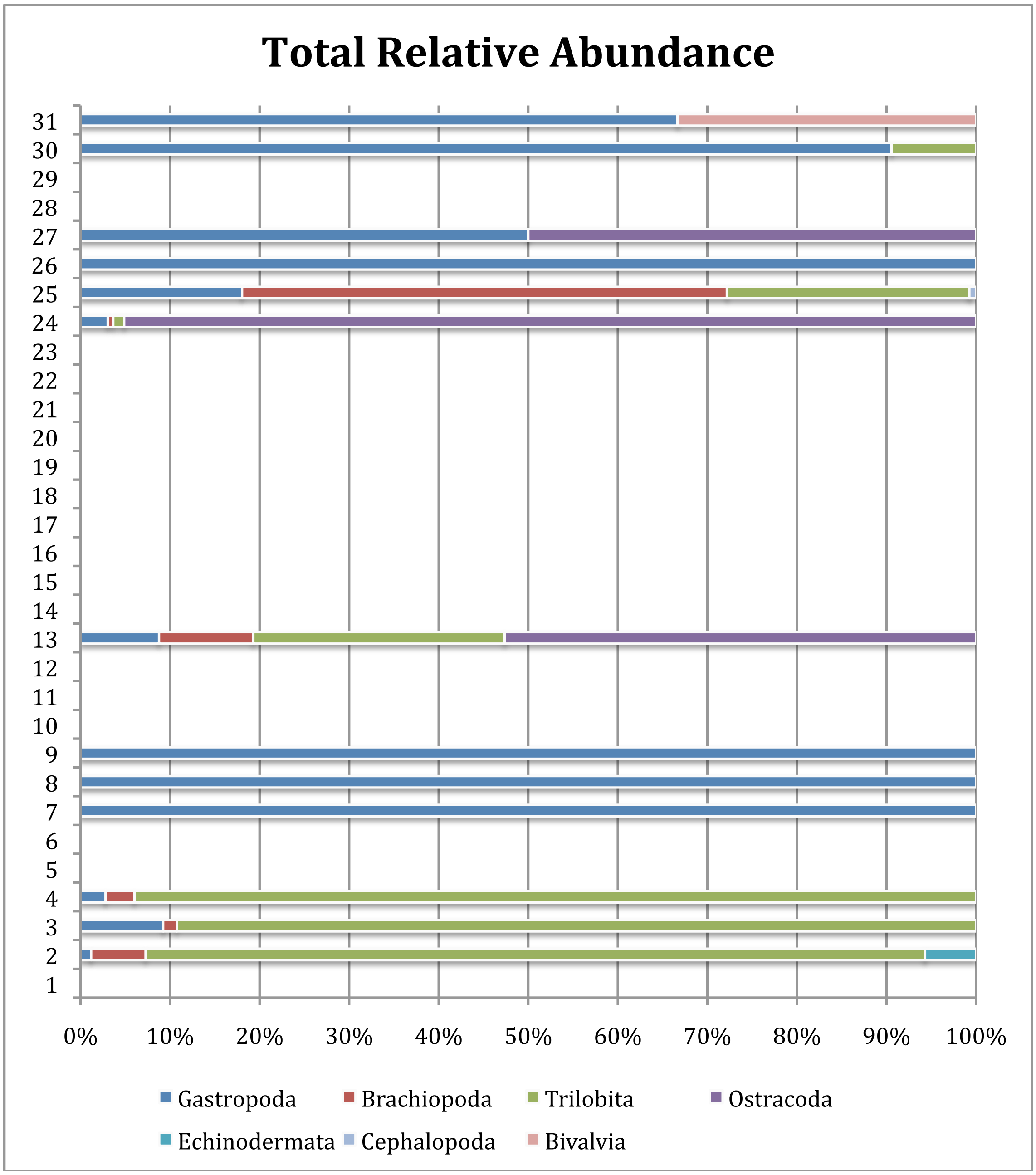

Figure 23. Total relative abundance, by clade, of select bulk samples.

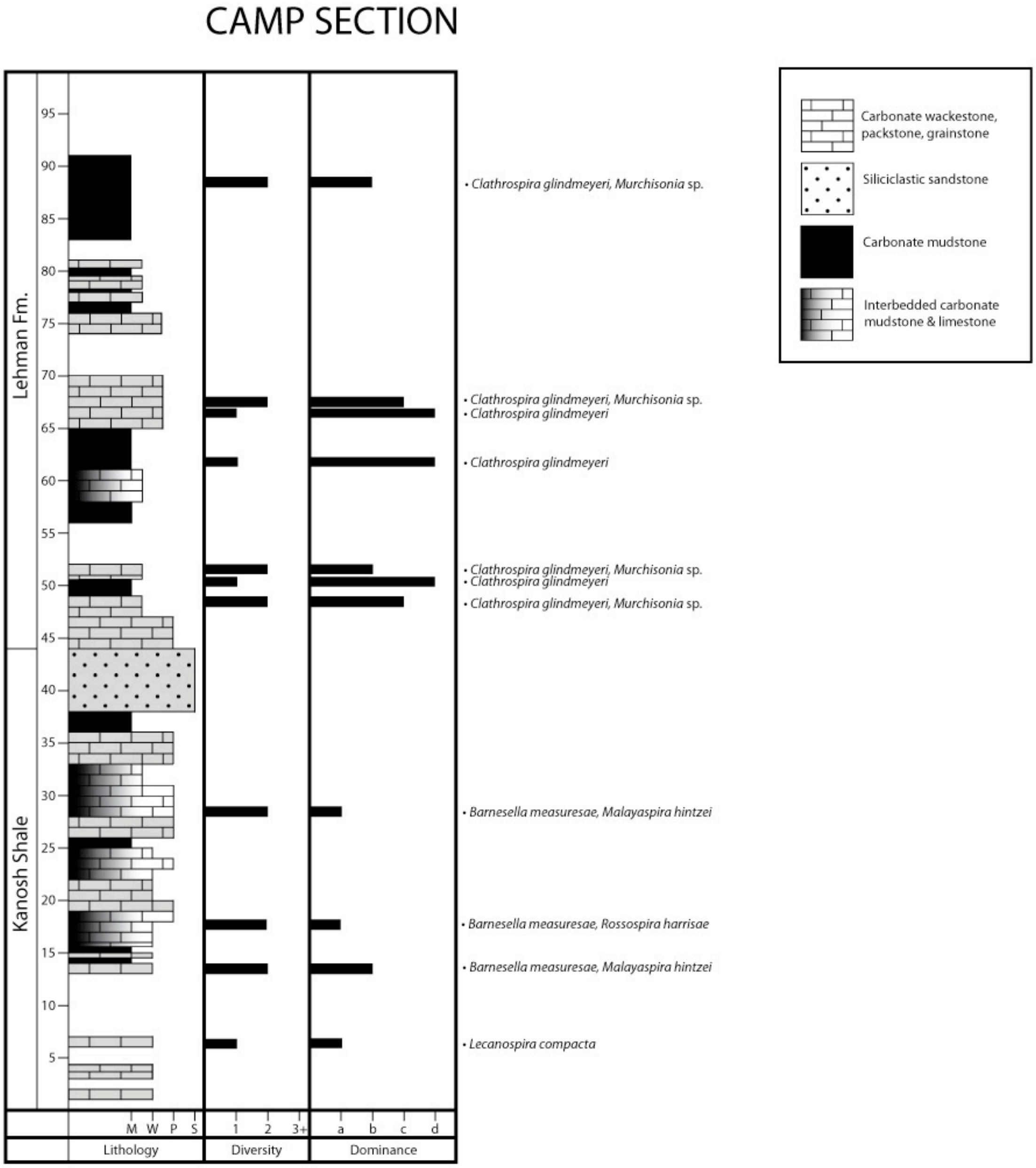

Figure 24. Stratigraphic section of the Camp locality, showing bulk samples.

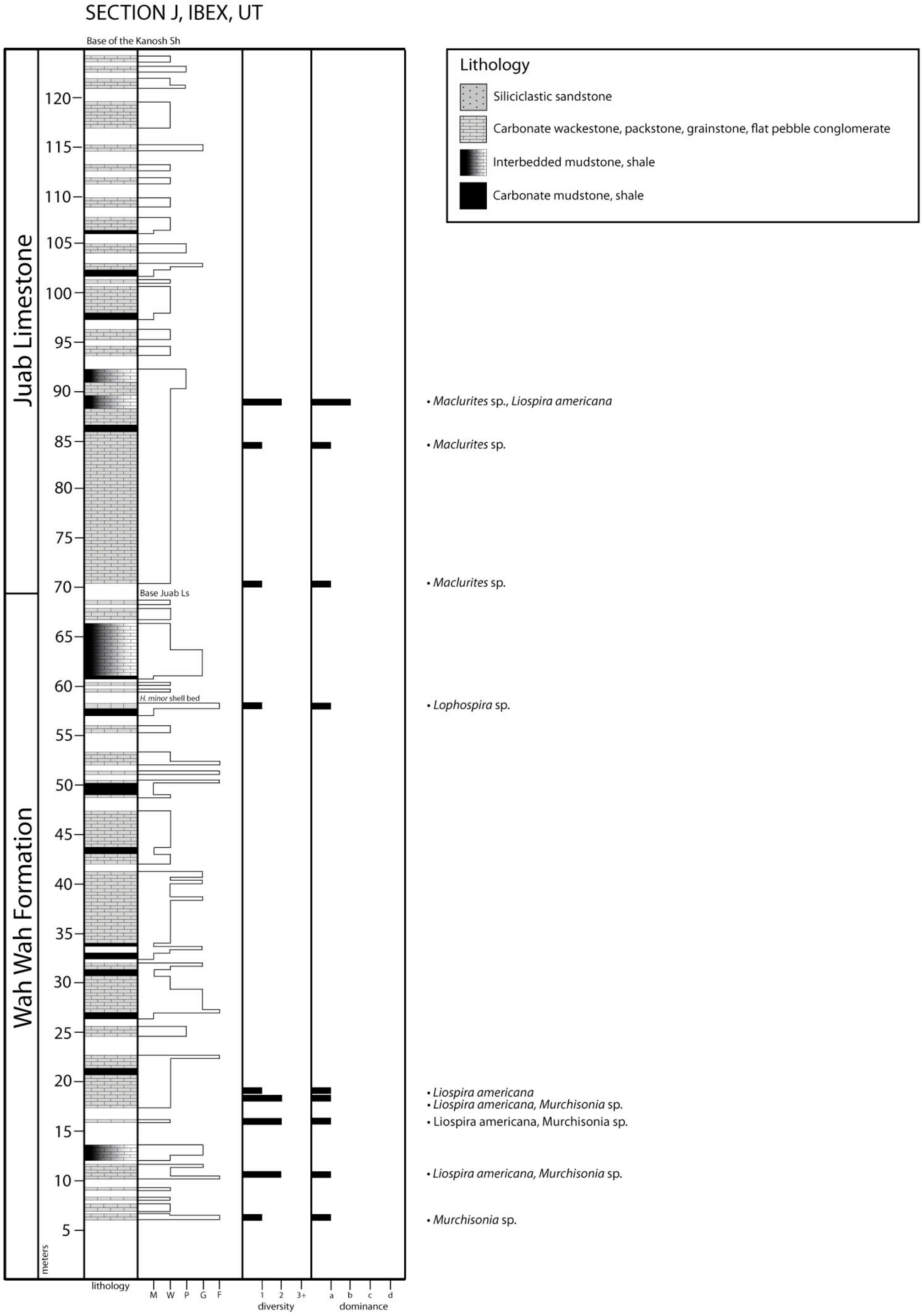

Figure 25. Stratigraphic section of the Section J locality, showing bulk samples.

Discussion

The distribution of the eleven gastropod taxa (Figure 22) indicates that these gastropod taxa were adapted to specific depositional environments. Almost every species occurs in only one lithology and within only one geologic unit. Gastropod diversity is highest in the Kanosh shale, with seven different gastropod taxa identified. The other three units (Wah Wah, Juab and Lehman formations) have only one or two gastropod taxa present.

Though gastropods are minor throughout the Middle Ordovician strata of the Ibex Region, there is a paleoecological pattern to their occurrence. In normal marine depositional environments, such as those preserved in the Wah Wah and Juab formations, gastropods are rare and are not very diverse. As environments become more restricted, as preserved in the Kanosh shale and the Lehman formation, gastropods become more diverse and abundant.

One can also consider the predictability of this clade by measuring how commonly gastropods are preserved in a given environment. In the Wah Wah formation, gastropod occurrence is very unpredictable. For example, gastropods are only found on one of every five or six grainstone beds examined. And furthermore, when they are preserved, they tend to occur in small, dense pockets, “lenses” or aggregations rather than in equal distributions throughout the bed.

Gastropods are more common in the Kanosh shale, but their occurrences are still unpredictable and they do not occur reliably in any specific depositional environment, despite accounting for a more significant portion of the fauna in Kanosh Basin ecosystems. While they may not occur in every ostracod or brachiopod grainstone, they occur in more than half. This, coupled with higher diversity and abundance in the Kanosh Shale, indicates that gastropods were likely better adapted to the restricted conditions of the Kanosh basin than to the open shelf, normal marine conditions preserved in the Wah Wah and Juab formations.

Gastropod occurrences are very predictable in the Lehman formation. They almost always occur in dense monospecific accumulations in the thick mud beds of this formation. The only other species to occur in this environment is the bivalve *Modiolopsis*, another member of the Modern Evolutionary Fauna. These mollusk-dominated mud beds are interpreted to represent deposition in a hypersaline lagoon, which was likely inhospitable to normal Ordovician marine fauna. Mollusks like gastropods and bivalves thrived by adapting to harsh ecological conditions that typical Paleozoic fauna could not survive in.

In addition to monospecific shell beds, gastropods also occur in thin shell pavements in the Lehman formation. These thin-bedded accumulations are comprised primarily of ostracods and gastropods, with less common bivalves and brachiopods. Unlike the monospecific beds of *Clathrospira glindmeyeri*, these pavements may preserve multiple gastropod taxa. *C. glindmeyeri* and *Murchisonia* sp. are the most common gastropod taxa, though a dense pocket of an unidentified microgastropod was also observed.

Gastropod diversity and abundance is roughly correlated with increasingly inhospitable environments. The restricted Kanosh Basin and hypersaline Lehman lagoon preserved both the most diverse assemblages (in the Kanosh shale) and the only monospecific gastropods shell beds (in the Lehman formation), while gastropods are rare in the open-ocean, normal marine environments preserved in the Wah Wah and Juab formations.

Gastropods are also more diverse and abundant in shallow environments. While the depositional environments examined in this study range from mid-shelf to intertidal, and thus none can be classified as truly deep water, gastropods become increasingly more diverse and abundant in the shallow environments.

Of the 11 taxa identified, all but one, *Lecanospira compacta*, have been previous recognized from the Antelope Valley Limestone in the Great Basin Region (Rohr, 1994, 1996; Yochelson, 1984). Of these eleven taxa, *Murchisonia* sp. was the only species to occur in all four units. This genus, unlike most of the taxa identified in this study, persisted throughout the Paleozoic and Mesozoic. *Murchisonia* demonstrates a very common modern marine gastropod morphology (high, tightly-coiled spire).

This adaptability may provide an explanation for the unusual evolutionary trajectory of the clade. Gastropods have been called an “extinction-proof” clade and demonstrate a slow but steady increase in diversity throughout the Paleozoic before finally diversifying rapidly and dramatically in the Mesozoic (Erwin & Signor, 1990).

Conclusions

Gastropods have never been the focus of paleoecological studies in the Ibex Region. This is due to a multitude of reasons, including lack of biostratigraphic application, poor preservation and low relative abundance compared to other clades like brachiopods and trilobites. This study has drawn five major conclusions about the paleoecology of gastropods in the Ibex Region, which are detailed below.

1. **Gastropods were found to be more diverse, with eleven taxa identified, than previous studies of the Ibex Region have stated.**

The eleven gastropod taxa identified in this study outnumber the gastropod fauna identified by Hintze (1951, 1953, 2003). All but one species (*Lecanospira compacta*) has been recognized from the Antelope Valley in the Great Basin Region (Rohr, 1994; 1996). The high diversity recorded by this study is likely due in part to diligent collecting, as gastropods have never been the focus of a paleoecological study in the Ibex Region.

2. **Gastropods were most diverse in shallow environments.**

This study supports the finds of Novack-Gottschall and Miller (2003), who used archived collections in the Paleobiology Database to conclude that Ordovician gastropods were most diverse in shallow environments. By returning to the field and closely examining the paleoecological context of Ordovician gastropods, we were able to confirm that gastropods were rare in the deepest facies (shales) and diverse in shallow environments (grainstones & packstones, carbonate mudstones).

3. **Gastropods were present in every depositional environment preserved in this interval.**

Though they were most diverse in shallow environments, gastropods were collected from every deposition environment in the four strata examined for this study, which range from mid-shelf, deep water to nearshore lagoon. This suggests that gastropods had already diversified into a wide range of marine environments by the Middle Ordovician. Gastropods did not become dominant members of marine ecosystems until the Mesozoic, so this early diversification begs the question, why did gastropods maintain only minor ecological roles throughout the Paleozoic?

4. **Gastropods were most abundant in harsh (low oxygen and/or high salinity) environments.**

Gastropods were most diverse in the Kanosh shale, which represents depositions in deep restricted basin within the carbonate platform (Ross, 1971; Boyer and Droser, 2003). Conditions within the Kanosh Basin are interpreted to be have been oxygen-restricted, evidenced primarily by the taxonomic assemblage preserved in the Kanosh shale. Gastropods, which not dominant in this assemblage, are more diverse and comprise a greater portion of the overall taxonomic assemblage than in the underlying Wah Wah and Juab formations. This may be due to the harsh environment, to which gastropods may have adapted more easily than typical Ordovician fauna like echinoderms and trilobites.

5. Gastropod occurrences were correlated to muddy substrates, regardless of depth or depositional environment.

Gastropods that were collected *in situ* showed a preference for muddy substrates, ranging from gastropod aggregations in the carbonate muds accumulated in a lagoon preserved in the Lehman formation to single specimens preserved within thin mud stringers in the Wah Wah formation and Kanosh shale.

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