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CARBONATES IN SKELETON-POOR SEAS: NEW INSIGHTS FROM CAMBRIAN AND ORDOVICIAN STRATA OF LAURENTIA

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ABSTRACT

Calcareous skeletons evolved as part of the greater Ediacaran/Cambrian diversification of marine animals; however, skeletons did not become permanent, globally important sources of carbonate sediment until the Ordovician radiation. Representative carbonate facies in a Series 3 Cambrian to Tremadocian succession from western Newfoundland and Ordovician successions from the Ibex area, Utah, show that, on average, Cambrian and Tremadocian carbonates contain much less skeletal material than do post-Tremadocian sediments. Petrographic point counts of skeletal abundance within facies and proportional facies abundance in measured sections suggest that later Cambrian successions contain on average <5% skeletal material by volume, whereas the skeletal content of post-Tremadoc Ordovician sections is closer to ~15%. A compilation of carbonate stratigraphic sections from across Laurentia confirms that post-Tremadocian increase in skeletal content is a general pattern and not unique to the two basins studied.

The long interval (~40 million years) between the initial Cambrian appearance of carbonate skeletons and the subsequent Ordovician diversification of heavily skeletonized organisms provides important perspective on the Ordovician radiation. Geochemical data increasingly support the hypothesis that later Cambrian oceans were warm and, in subsurface water masses, commonly dysoxic to anoxic. We suggest that surface waters in such oceans would have been characterized by relatively low surface seawater saturation states for calcite and aragonite. Mid-Ordovician cooling would have raised oxygen concentrations in subsurface water masses, establishing more highly oversaturated surface waters. If correct, these links could provide a proximal trigger for the renewed radiation of heavily skeletonized invertebrates and algae.

INTRODUCTION

Carbonate skeletons emerged as part of the initial diversification of animals. Lightly mineralized $CaCO_3$ skeletons first appeared in reef environments near the end of the Ediacaran Period (Grotzinger et al., 2000; Wood et al., 2002), and skeletonized benthos expanded markedly during subsequent early Cambrian radiation (Bengtson and Conway Morris, 1992). It has been suggested that early Cambrian radiation of skeletonized organisms shifted both the mechanisms and loci of carbonate production from those typical of Proterozoic oceans (i.e., abiotic or biologically induced precipitation out of the water column or on the seafloor) to a Paleozoic regime dominated by skeletal biomineralization in shelf and platform environments (e.g., Zeebe and Westbroek, 2003). Despite the early appearance of skeletal biomineralization, however, the diversity and abundance of calcified skeletons remained low in Cambrian oceans, especially following the late early Cambrian collapse of archaeocyathids. During the subsequent Ordovician radiation, new skeletal taxa appeared, and many groups that had originated earlier diversified markedly. Prominent among these were heavily calcified taxa, including corals, bryozoans, rhynchonelliform brachiopods, lithistid sponges, echinoderms, and dasycladalean algae. The diversification of these groups long after the origins of both their general body plans and the biochemistry required for skeletal biomineralization raises important questions about both early Phanerozoic modes of carbonate deposition and the controls on Cambro-Ordovician animal (and algal) evolution.

In this study, we examine the changing contribution of mineralized skeletons to carbonate deposits from the later Series 2 and Series 3 Cambrian aftermath of archaeocyathid extinction to the Ordovician diversification of heavily skeletonized marine organisms. In previous work, Li and Droser (1997, 1999) showed that in the Ibex Area of western Utah, shell beds increase in thickness and abundance across the Ibexian-Whiterockian boundary (late Early to Middle Ordovician). These observations imply an increasing proportion of skeletal material in carbonate-rich sedimentary systems, but leave open the broader questions of skeletal abundance across facies and the geographic distribution of observed changes. To test whether this pattern documents an overall transition in carbonate sedimentation, we gathered evidence at three scales: point-counts of representative thin sections from western Newfoundland and the Ibex area of western Utah, estimates of proportional volumes of skeletal carbonate in measured sections from these two areas, and a meter-scale compilation of carbonate lithostratigraphy from multiple sections spanning the Cambrian and Ordovician of Laurentia. These data serve as a test of Li and Droser's hypothesis, as they examine multiple volumetrically significant facies including, but not limited to, shell beds. All abundance data from the sedimentary record must be interpreted with caveats of sampling and preservation firmly in mind. Nonetheless, our results support the notion that the skeletal contribution to shallow subtidal carbonate sediments did increase, possibly more than five-fold, between the Furongian and Middle Ordovician. This pattern cannot easily be accounted for by common preservation or paleoenvironmental biases; further testing will bear on the details of these biases. Ultimately, the quantification of skeletal contributions to Cambro-Ordovician carbonate accumulation sheds new light on previously identified changes in the nature of the carbon cycle between the Cambrian and subsequent periods.

GEOLOGIC SETTING

During Cambro-Ordovician time, Laurentia lay over the equator (Fig. 1) (Smith, 2001; Hodych et al., 2004), largely covered by epeiric seas. Extensive carbonate platforms developed on its northern, southern and western margins; in some areas, Cambrian carbonate strata alone attain thicknesses near 2.5 km (e.g., Ginsberg, 1982; Montanez and Droser, 1991; Osleger and Montanez, 1996). Our samples come from two regions. The Series 3-Furongian Cambrian Port au Port and Lower-Middle Ordovician St. George groups, exposed in western Newfoundland, were deposited on the southeastern margin of Laurentia. Cambrian and Ordovician carbonates of the Ibex area, Utah, accumulated at a similar latitude along its western margin.

Western Newfoundland

During Cambro-Ordovician time, autochthonous carbonate-siliciclastic strata accumulated on a shallow platform in western Newfoundland. A long hiatus separates the Lower Cambrian Labrador Group from the overlying Series 3-Furongian Cambrian Port au Port Group. Lower Ordovician strata of the St. George Group cap the succession on the Port au Port Peninsula. At the study site, Cambro-Ordovician strata are well exposed and have been extensively studied along two arms of a broad, gently-dipping anticline that makes up the south-facing shore of the Port au Port Peninsula (e.g., Pratt and James, 1982, 1986; Chow and James, 1987; Knight and James, 1987; James et al., 1989; Cowan and James, 1993a). Biostratigraphic and chemostratigraphic constraints on Cambrian strata include the Series 3 *Bolaspidella* through Furongian *Elvinia* trilobite zones (e.g., Westrop, 1992; Saltzman et al., 2004) and the geographically widespread

SPICE C-isotopic event (Saltzman et al., 2004). Lower Ordovician strata of the St. George Group preserve biostratigraphically well-constrained assemblages of conodonts (Ji and Barnes, 1994) and gastropods (Rohr et al., 2001).

The Series 3 March Point Formation and Series 3-Furongian Cambrian Petit Jardin Formation make up the Port au Port Group (~190 meters; Fig. 2). Cambrian carbonates of western Newfoundland contain very few skeletal carbonates, with a few intervals of trilobite hash representing the only significant fossil accumulations exposed in the field. In contrast, oolites, microbial buildups, calcisiltites, and micrites are common, deposited in environments ranging from deep subtidal to peritidal.

The Lower Ordovician St. George Group consists (from bottom to top) of the Watts Bight, Boat Harbour, Catoche and Aguathuna formations (Knight and James, 1987). The majority of the St. George Group was deposited in shallow subtidal to peritidal settings during an interval with little siliciclastic input. Along the south facing shore of the Port au Port Peninsula, complete sections of the Watts Bight (~70 m) and Boat Harbour (~ 150 m) formations are exposed, and we examined these units in outcrop and in thin section. The Lower Ordovician Catoche Formation is exposed at the nearby Port au Choix and Point Riche Peninsula, and the Lower Ordovician Aguathuna Formation crops out near East Bay on the Port au Port Peninsula (Knight and James, 1987).

Ibex Area, western Utah

The Ibex Area of Utah, in the Basin and Range region of the western United States, was the site of nearly continuous carbonate sedimentation from Series 3 Cambrian through

Middle Ordovician time. Ordovician strata of the Pogonip Group are particularly well exposed and well-studied in the Ibex region of western Utah and adjacent areas of eastern Nevada (Hintze, 1973; Ross et al., 1997), and are biostratigraphically well-constrained by trilobites and conodonts (Miller et al., 2003). The Pogonip Group comprises the Lower Ordovician (Ibexian = Tremadocian-Arenigian) Notch Peak Formation, House Limestone, Fillmore Formation, and Wah Wah Limestone (Fig. 2), which generally record mixed carbonate-siliciclastic sedimentation on a broad, shallow, mixed carbonate-siliciclastic ramp (Ross, 1977; Ross et al., 1989) and the Middle Ordovician (Whiterockian = latest Arenigian—Llanvirnian) Juab Limestone, Kanosh Shale, and Lehman Formation, which record the development of a carbonate platform rimmed by basinward oncoid shoals. Above the Lehman Formation, the late Middle Ordovician and early Upper Ordovician are represented by thick regional quartzites. Although pure carbonate sedimentation resumes in the Upper Ordovician, Upper Ordovician-Silurian units are pervasively dolomitized (fabric destructive) and hence their fabric was not examined for this study.

The Notch Peak Formation (150m) and House Limestone (210m) are dominated by carbonate mudstones and dolostones with common stromatolites and other small microbial buildups, recording generally shallow subtidal to peritidal sedimentation. Flat pebble conglomerates and thin trilobite/lingulid/echinoderm shell beds are present but are uncommon compared to overlying units (Li and Droser, 1999). The base of the Fillmore Formation (325m) marks a clastic influx and a significant change in depositional mode – the lower 200 meters of the Fillmore Formation are dominated by flat pebble conglomerates, which contain locally abundant but highly abraded skeletal grains and are interbedded with sparsely fossiliferous shales at decimeter to meter scales. Beginning in the upper Fillmore Formation and continuing into the Wah Wah Limestone (61m), wackestones, packstones, and skeletal grainstones are increasingly abundant. Small sponge-microbial buildups are also common in several beds within the upper Fillmore Formation and Wah Wah Limestone (Johns, 1995), but microbial facies overall are a volumetrically minor component of these units.

The Middle Ordovician is represented by the Juab Limestone (55m), Kanosh Shale (~162m), and Lehman Formation (~35m). The Juab Limestone is similar to the underlying Wah Wah Limestone in overall facies architecture, recording cyclic deep to shallow subtidal sedimentation, and also contains abundant shell beds and common sponge-microbial buildups (Li and Droser, 1999; Finnegan and Droser, 2005). The transition to the lower Kanosh Shale represents significant local deepening and the onset of anoxic conditions related to the development of shelf-edge oncoid shoals in central Nevada (McDowell, 1987; Ross et al., 1989; Boyer and Droser, 2003). A shallowing trend though the upper Kanosh Shale culminates in the Lehman Formation, which is composed primarily of shallow subtidal to peritidal carbonate mudstones and packstones.

METHODS

As noted above, we analyzed Cambro-Ordovician carbonate strata at three nested scales. For a variety of units in Newfoundland and Utah, thin sections of representative peritidal to shallow subtidal carbonate facies were examined to determine how much skeletal material contributed to each carbonate lithology. Mudstones, wackestones, packstones, skeletal grainstones, oolites, and microbialites were the most common facies in outcrop, and several examples of each were analyzed in thin section. Although a variety of lithofacies exist in western Newfoundland and the Ibex area of Utah, the thin sections described here provide broad coverage of the skeletal contribution to the most common carbonate lithofacies through the study interval and allowed us to most directly compare data generated at each locality. We examined 48 thin sections from Cambrian and Lower Ordovician carbonates of western Newfoundland and 25 thin sections from Lower and Middle Ordovician carbonates from the Ibex area of Utah (see Fig. 2). Though these two stratigraphic successions do not provide an ideal sample size for robust statistical analysis, the sampled beds were chosen because they are, in our experience, representative of a range of lithofacies. Additional sampling would help to improve the statistical robustness of our estimates, and will ultimately allow us examine trends within individual lithofacies at higher resolution; however, we do not believe the further effort would alter the observed pattern at the broad scale under consideration here. Thin sections were prepared from beds characterized by good preservation of original fabric (i.e., absence of substantial fabric-destructive diagenesis). Note that although thin sections were examined from the Felix Member and Watts Bight Formation (Newfoundland), and lower Fillmore Formation (Utah), none of these slides figure in our analysis because of the poor quality of petrographic preservation. In no case were fossiliferous slides excluded from any time interval. On each slide, 200 points were counted and classified, following the grain-solid method, using a mechanical stage that stepped the slide at regular intervals (e.g., Jaanusson, 1972; Flügel, 1982; Payne et al., 2006).

Although the point counting method provides information about the importance of skeletons within individual carbonate facies, we must also consider the relative contributions of different facies to overall carbonate depositional packages, as these changed through time, as well (Sepkoski et al., 1991; Droser and Sheehan, 1997). To estimate changes in skeletal contributions at the section scale, we measured the contribution of each facies type to overall thickness in a Series 3 Cambrian to Lower Ordovician succession in Newfoundland and three Lower-Middle Ordovician sections in western Utah and eastern Nevada (Finnegan and Droser, 2005). Thicknesses for each facies were then multiplied by the average proportion of skeletal carbonates in thin sections from the facies under consideration, and these products were summed and divided by total thickness to obtain a thickness-normalized estimate of skeletal carbonate contribution at the section scale (e.g., Payne et al., 2006). For example, in a ten meter section containing 8 m of facies A, with a mean skeletal content of 0.05, and 2 m of facies B, with mean skeletal content of 0.15, the estimate of mean skeletal content for the entire section would be:

$$[(8.0 \times 0.05) + (2.0 \times 0.15)] / 10.0 = 0.07$$

Finally, to get a broader sense of changes in skeletal carbonate production across all of Laurentia, a meter-scale stratigraphic database of carbonate sections from various sites in Laurentia was compiled. We selected literature sources based on the detail of stratigraphic columns and/or presence of detailed written descriptions. Pure carbonate sections were first-order targets, but mixed carbonate-siliciclastic successions were used as long as carbonates comprised ≥50% of the section. We selected sections to provide a broad geographic coverage of the eastern, western and southern margins of Laurentia and to encompass a diversity of shallow to deep subtidal depositional settings. We did not tabulate heavily dolomitized sections unless their fabrics were sufficiently preserved to determine original skeletal composition. The stratigraphic resolution of these data is lower than those available for Newfoundland and the Ibex area, and we cannot provide direct estimates of proportional skeletal contribution for these sections, but this compilation allows us to place the local patterns evident in our field observations within a broader paleogeographic context.

We categorized each meter of carbonate in the selected sections according to the following coarse binning scheme: micrite, oolite, microbialite, or skeletal limestone (fossil packstones and grainstones, broadly equivalent to shell beds of Li and Droser, 1997; 1999). For our purposes, a section is defined as a single formation or member at a single locality. When available, multiple sections of the same formation were tabulated to observe variation within a single stratigraphic unit. We calculated the proportion of skeletal carbonate for 34 sections of Series 3 and Furongian Cambrian carbonates and 24 Ordovician sections.

Principal Components Analysis (PCA; Joliffe, 2002) was used to ordinate the stratigraphic sections according to the cumulative relative thicknesses of the above four compositional categories. While it is traditional to use ternary diagrams for point count modal data, PCA allows us to quantitatively examine higher dimensional data (in this case, the four genetic categories of carbonate sediment). The PAST package (Hammer et al., 2001) was used for analyses. Other commonly used multivariate ordination techniques such as Detrended Correspondence Analysis and Nonmetric Multidimensional Scaling give closely similar ordinations—unsurprising given the small number of variables. For this reason, alternative ordinations are not presented.

Both our field sampling and literature compilation focused on carbonate and mixed carbonate-siliciclastic strata. Although carbonate skeletal material can also be preserved in siliciclastic rocks, it is difficult to establish a relationship between skeletal abundance and changes in the nature of carbonate production in these settings. Temporally, our sampling is limited to the Series 3 Cambrian to Late Ordovician interval. Despite the dramatic radiation of animal life during the Cambrian Explosion, shell bed analyses of Lower Cambrian sections suggest that carbonate skeletons were a relatively minor component of level-bottom carbonate production during this time (Li and Droser, 1997). Relatively little work has been done to quantify the local and/or global influence of archaeocyathid reefs on carbonate sedimentation during the early Cambrian, but this is an interesting area for continuing study, as Lower Cambrian carbonates may well be more skeleton-rich than those deposited later in the period (e.g., James et al., 1989). Whatever impact archaeocyathid and other sponge-rich reefs had as a skeletal sink for carbonate, it was relatively short-lived, as metazoan reefs virtually disappeared at the end of the early Cambrian (Zhuravlev and Wood 1996) and did not reappear in abundance until Middle Ordovician time (e.g., Rowland and Shapiro, 2002)

RESULTS

Point counts

Figure 3 shows the percentage of skeletal material identified in point counts of our Cambrian and Ordovician carbonates, and Table 1 shows the identified points. In Cambrian samples, skeletal material accounted, on average, for about ~8% of points counted. Fossil content ranges up to 23%, but the (weak) mode is 0%. In total, we analyzed 12 grainstone thin sections (excluding oolites), and these contained the highest average skeletal content (~10 %). Lower Ibexian (Tremadocian) samples are similar to those of Cambrian age, with skeletal material accounting for an average 4% of points counted, but late Ibexian and Whiterockian samples are distinctly different, with skeletal material accounting for 18% and 16% of total points, respectively. The maximum is 42% – near the observed maximum potential for shell beds of ~50% (Payne et al., 2006). Both micrite and microbial microfacies occur in abundance in many Cambrian and Ordovician slides; the notable difference between Cambrian and Ordovician thin sections is the contribution of fossil material to total points counted (see Table 1).

Similar facies in the Cambrian and post-Tremadocian Ordovician sections also show different proportional abundances of skeletal material. For instance, Cambrian grainstones contain at most 23% fossil material, whereas mid-Arenig grainstones contain as much as 42%. Similarly Cambrian flat-pebble conglomerates, formed by the local redistribution of carbonate clasts during storms (e.g., Sepkoski, 1982) contain at most 9% fossil material, whereas fossil material accounts for 23% of points counted in both Ordovician flat-pebble conglomerates examined. (Flat-pebble conglomerates were sampled in thin section but were not separated into a distinct category when calculating the volume of carbonate for Cambrian sections because these units are often lenticular and are commonly recessive in Newfoundland). Sample sizes were largely selected to capture the variation within facies and to reflect local stratigraphy, and clear outliers were excluded (e.g., heavily dolomitized samples). In no case, however, did we exclude unusually fossiliferous Cambrian rocks.

In the Ibex area, at least, the major shift in the proportional contribution of skeletal materials thus occurs in samples deposited between the Tremadocian (early Ibexian) and the mid-Arenigian (late Ibexian to early Whiterockian) (Fig. 3) – no post-Tremadocian samples contain less than 5% skeletal material, a minimum that is higher than median values for both later Cambrian and Tremadocian samples. Correlative formations to the west in central Nevada show a similar pattern of low skeletal concentration at the outcrop level in the Tremadocian and a mid-Arenigian to Llanvirnian increase, though skeletal concentrations are generally lower in these deeper-water units (SF, unpublished observations).

In addition to secular change in the abundance of fossil material, we see differences in the taxonomic composition of carbonate skeletons from pre- and post-Tremadoc samples (Table 1). Similar changes were documented at Ibex and in other areas of the western United States by Li and Droser (1997, 1999). Fossil material preserved in Newfoundland Cambrian thin sections is dominated by trilobite and echinoderm debris. Uncommon trilobite-rich beds occur primarily in deeper water facies of the March Point Formation (MF17, MF38; see Table 1). Echinoderms show a different distribution, with plates preserved most abundantly in the interstices of microbial mounds, particularly thrombolites, (CMCC1 and CM28MI3) and in associated shallow water grainstones (MWU6 and CM15). Trilobites and echinoderms generally dominate the skeletal carbonate signal in early Ibexian (Tremadocian) samples from the Ibex area, but post-Tremadocian fossil material from Ibex Area thin sections is more diverse. Trilobites and echinoderms are still significant components (UF1, WW5), but calcitic brachiopods are also common (L.NM1). Less common fossil grains include ostracods, mollusks, and sponges. Outcrop observations suggest a similar pattern of skeletal diversification in Ordovician carbonates from Newfoundland (SP, unpublished observations).

Measured sections

When generalized to the section scale, these results point to a substantial increase in the skeletal contribution to carbonates between the Furongian Cambrian and the Middle Ordovician. In the Cambrian Port au Port Group of western Newfoundland, carbonate mudstones and oolites make up the bulk of the section (Fig. 4) and in thin section, contain very little skeletal material (1% and 4%, respectively). As expected, grainstones contain the most recorded skeletal material in thin section (~10%). As a proportion of total carbonate production, skeletal carbonate makes up 2.8% of Cambrian units examined (Fig. 5), corroborating qualitative observations that most later Cambrian carbonates do not have a demonstrably skeletal origin. A wide range of environments is preserved in the Port au Port and St. George groups of western Newfoundland. Subtidal and peritidal settings are present in the Cambrian March Point and Petit Jardin formations and facies become increasingly restricted in the Lower Ordovician (See Fig. 4).

Although they preserve a range of environments broadly similar to those in the Port au Port, late Arenigian (late Ibexian and early Whiterockian) sections in western Utah show a much higher contribution of skeletal material to total carbonate production. The most abundant carbonate lithofacies in these sections is mudstone/wackestone (See Fig. 4), which contains, on average, 13% fossil material in thin section – much higher than skeletal abundances in upper Cambrian mudstones. The next most abundant facies, which makes up only 10% of total carbonates, is grainstone. Again, these Ordovician grainstones are far richer in skeletal debris than their Cambrian counterparts, containing an average of 32% carbonate fossil material in thin section. In total, the Thomas Range, Ibex, and Shingle Pass areas show that skeletons make up 15%, and 14% of total carbonate volume, respectively, when normalized for abundances of different lithofacies (see Fig. 5). Although the Ibex section displays some environmental variation, the range of variation is relatively constrained and does not appear to influence temporal changes in skeletal abundance (see Fig. 3). For example, the House Limestone, Wah Wah Limestone, and Juab Limestone all show similar parasequence development indicative of shallow subtidal deposition, but the bioclastic content of the latter two units is substantially higher than the former.

Plotting the proportion of each stratigraphic unit logged as bioclastic limestone against age (Fig. 6) demonstrates that despite differences in depositional environment and basin evolution, these two areas show broadly similar trends in bioclastic production through time. The proportional representation of bioclastic limestones is generally higher in the Ibex area, reflecting both genuine and methodological differences, but both sections exhibit comparatively low values in the Furongian, intermediate values in the Tremadocian (early Lower Ordovician), and high values by the late Arenigian (latest Lower Ordovician) time.

Literature Compilation

To test whether the trend apparent in these two regions is representative of the broader pattern, we compiled measured sections of Cambrian and Ordovician strata throughout North America. As in Fig. 6 above, proportions of skeletal carbonates were calculated by tabulating the meters of skeletal limestone, as reported in published measured sections, and dividing by the total thickness of the section.

At the continental scale, skeletal grainstones account for 8% of all meters of carbonates binned in the 34 Series 3 and Furongian Cambrian sections analyzed. Proportional abundance of fossiliferous meterage ranges among sections from 0 to 72%, with a median for individual sections of 2.8%. Lower Ordovician carbonates are similar to Cambrian carbonates in containing on average about 10% carbonate skeletal meterage, with a range of 0-54% and a median of 1.5%. Middle and Upper Ordovician carbonates show a significant increase in skeletal material in outcrop; skeletal limestones account for 60% of total measured meters of carbonates. It is striking that the minimum value for any individual Middle or Upper Ordovician unit is 12%, with a median of 53%.

A Principal Components Analysis (PCA) of carbonate composition for all sections in the dataset illustrates the general trend: Series 3-Furongian Cambrian sections and Middle to Upper Ordovician sections comprise essentially non-overlapping groupings, with Lower Ordovician sections spanning the full range (Fig. 7). Skeleton-rich limestones formed in later Cambrian seaways, but Cambrian sections are dominated lithologically by micrites, oolites, and microbialites. In contrast, post-Tremadocian Ordovician sections are dominated by skeletal limestones.

DISCUSSION

The Late Cambrian-Early Ordovician interval stands out as distinctive against the broad background of Phanerozoic marine evolution. Skeletons, largely trilobite and echinoderm remains, make only a limited contribution to limestones of this age, with abundant ooids, microbialites and micrites suggesting a carbonate factory dominated by physical and microbial processes. In particular, reef-forming metazoans were scarce for

40 million years following archaeocyathid extinction (Rowland and Shapiro, 2002), radiating again in the Middle Ordovician.

Following this interval, a sharp global increase in the generic diversity of carbonate-secreting metazoans (Sepkoski, 2002; Webby et al., 2004; Peters, S., online database) (Fig. 8) and an increase in the depth and complexity of bioturbation suggest rapid diversification and ecological transformation (Droser et al., 1996; Miller and Foote, 1996; Adrain et al., 1998; Webby et al., 2004). The observation that the diversity and abundance of well skeletonized organisms increased in the Ordovician is long-standing; however, quantification of the patterns presented here permits more focused evaluation of competing explanatory hypotheses.

Our data permit a test of the trends reported by Li and Droser (1997, 1999) for the Ibex area of Utah. The three data sets assembled here confirm a marked increase in shell bed abundance in the Ibex region; furthermore, our data (despite differing taphonomic biases) reveal that the proportional abundance of identifiable skeletons in carbonate rocks increased across facies and, indeed, throughout Laurentia. Thus, despite differing taphonomic biases, all observations point toward the same conclusion (Appendix 1; Fig. 7). For comparison, skeletons can account for 90% of total carbonate production in some modern settings (e.g., Harney, 2003) (although we recognize that estimates of modern bioclastic carbonate can not be compared directly to the diagenetically altered samples from the Paleozoic described in this study). The skeletal contribution to Cambrian carbonates was high locally, but on average, skeletal material accounted for a comparatively small proportion of total carbonate production on later Cambrian shelves and platforms. Several of the units examined contained no significant skeletal carbonate contribution, including some in western Newfoundland. Lower Ordovician carbonates also show a relatively small contribution of fossil material to total carbonate production; like the Cambrian sections analyzed, many units contained no fossil material, with an average of 8% of all meters analyzed containing abundant fossil debris.

The distribution of skeletal content in Middle and Upper Ordovician carbonates is strikingly different. Although fossil-rich limestones make up a relatively small proportion of a few individual Middle and Upper Ordovician carbonate sections (Platteville Group, 122 m, 12% fossiliferous limestones; Fanton, 2004), the general trend shows a dramatic increase in the total amount of skeletal contribution to carbonates. In rare instances, skeletal materials made up the vast majority of limestones analyzed (Hull Formation 1, 45 m; 90% fossiliferous limestones; Kiernan, 1999; Galena 2, 130 m, 100% fossiliferous limestones; Fanton, 2004). We note that the successions we examined commonly contain trace fossils, and interbedded shales in Newfoundland preserve abundant invertebrate cuticle (SP, unpublished observations). For this reason, we doubt that the patterns reported here derive principally from low oxygen or some other inhibitor of metazoans on late Cambrian shelves and platforms (Peters, 2007) – animals appear to have been abundant; only carbonate skeletons are scarce. In this context it is also notable that the average degree of bioturbation in Basin and Range carbonates is essentially unchanged between the Series 3 Cambrian and the Middle Ordovician (Droser and Bottjer 1989) despite a substantial increase in skeletal content over the same interval (Li and Droser 1996, 1999; this study). Put another way, we do not argue that organisms such as mollusks and cnidarians were rare in Late Cambrian oceans, but rather that these taxa contributed little to the marine carbonate cycle.

Our compilation is limited to shallow-to-deep subtidal pure carbonate and mixed carbonate-siliciclastic depositional systems, and regional environmental variation is thus only coarsely controlled. It is likely that the signal we see is influenced both by a secular trend in skeletal biomass and by changes in environmental representation through time (in carbonate settings, these will not be independent of skeletal evolution). We emphasize, however, that the Cambro-Ordovician time is one of the relatively few Phanerozoic intervals that show rapid and significant increases in diversity even after accounting for variation in outcrop area (Peters, 2005); further work on the macrostratigraphic character of the Cambrian-Ordovician transition (e.g., Peters, 2006) will be necessary to untangle temporal and environmental effects completely.

While the Ordovician radiation of skeletal taxa has long been recognized (e.g., Sepkoski, 1978; Webby et al., 2004) the drivers of this event remain poorly understood (Botting and Muir, 2008). A variety of explanations ranging from purely biological (Peterson, 2005) to purely physical (Patzkowsky and Holland, 1993; Miller and Mao, 1995) have been proposed, and no consensus has emerged to date. One key insight is that the Ordovician radiation extends across clades; heavily calcified skeletons came to characterize rhynchonelliform brachiopods, echinoderms, mollusks, bryozoans, sponges, and corals alike, not to mention the diversification of skeleton-forming algae (Fig. 7). Many of these organisms were sessile filter-feeders; but motile grazers, carnivores, and primary producers were represented, as well. Thus, clade- or function-specific explanations cannot account for the observed pattern of diversification. The second key observation is that a long interval of time (more than 40 million years) separates the initial Cambrian appearance of many skeletal taxa from their subsequent Ordovician diversification (e.g., Rowland and Shapiro, 2002). What might explain this apparent delay? We suggest evolving seawater carbonate chemistry over this interval may provide a key to understanding the apparent delayed timing of the Ordovician radiation.

In all cases, skeletal biomineralization requires energetic input by individual organisms, and this energetic input (or cost) is a strong function of the availability of the chemical constituents required to assemble a skeleton (Ca^{2+} and CO_3^{2-}, in this case, along with associated organic molecules). Given the abundance and diversity of skeleton forming organisms, the benefits gained by biomineralization must be worth the energy expended—energy that might otherwise be used for reproduction (e.g., Knoll, 2003). This cost-benefit tradeoff must have existed since the earliest biomineralizers evolved near the Proterozic-Cambrian boundary, providing a useful framework for examining times of low skeletal abundance: were the costs of skeletonization too high, or the benefits too low? In this case, which tensor tugged most strongly at the core of the Ordovician skeletal revolution: a ramping up of predation pressure (increasing the benefit), or a change in ocean chemistry (decreasing the cost)?

For many marine invertebrates, the cost associated with producing a skeleton of $CaCO_3$ is a function of the thermodynamic state of saturation in the surrounding fluid, $\Omega = [Ca^{2+}]\cdot[CO_3^{2-}]\cdot k_{sp}^{-1}$, where k_{sp} is the empirically-derived solubility constant for a particular $CaCO_3$ polymorph (e.g. calcite or aragonite). Values of $\Omega > 1$ describe geochemical systems where $CaCO_3$ tends to precipitate, whereas solutions of $\Omega < 1$ are corrosive to $CaCO_3$. The rate at which $CaCO_3$ precipitates or dissolves depends directly on the magnitude of deviation from $\Omega = 1$ (Morse et al., 2007). For organisms that must precipitate a skeleton at a given rate, living in seawater of sufficient Ω is imperative. A large number of studies have examined the effects of Ω on calcification rate for a diverse collection of extant marine organisms (e.g. hermatypic and ahermatypic corals, foraminifera, echinoderms, coralline algae, and both mesocosm and natural coral reef communities); in general, as Ω drops, so too does calcification rate, and for many taxa, dramatically so (Kleypas et al., 1999; Pörtner, 2001; Feeley et al., 2004; Pörtner et al., 2004; Langdon and Atkinson, 2005, and refs therein).

Limited data on fluid inclusions in evaporite minerals provide conflicting time series trends for [Ca^{2+}] increase in earliest Cambrian oceans (Brenner et al., 2002; Petrychenko et al., 2005). Model results do not reveal any strong variation in calcium ion abundance through the later Cambrian-Middle Ordovician interval of interest (e.g., Demicco et al., 2005). Regardless of changing seawater chemistry, when [Ca^{2+}] far exceeds [CO_3^{2-}], Ca^{2+} may saturate calcium-binding sites on organic templates long before carbonate-binding sites fill, resulting in strong [CO_3^{2-}] control of precipitation kinetics (Obst et al., 2009). For these reasons, and because Ca^{2+} is far more abundant than CO_3^{2-} in seawater (likely true for the past 540 millions years, e.g., Horita et al. 2002, and perhaps much longer), the distribution of **Ω** values in later Cambrian and Ordovician seawater must have been controlled largely by changes in carbonate ion abundances due to the addition and/or removal of CO_2.

Seawater today is characterized by strong gradients in **Ω** due, in large part, to the biological pump and the oxygenic production/aerobic respiration of organic carbon (Higgins et al., 2009). The biological pump removes CO_2 (a weak acid) from surface seawater and adds it at depth (e.g. Broecker and Peng 1982, Hotinski et al. 2004). Correspondingly, **Ω** is strongly supersaturated in surface seawater (**Ω** = 4-6 for calcite; Li et al. 1969) and tends to be undersaturated at depth in the water column and sedimentary pore fluids. Building on the observation, however, that all anaerobic carbon metabolic pathways either produce or consume alkalinity in addition to CO_2, recent work (Fischer et al., 2007, Higgins et al., 2009) has revealed that in past times when anaerobic cycling of organic carbon was more important (i.e., times of ocean anoxia) the gradients of **Ω** in seawater would have been reduced. While the average seawater Ω integrated globally likely changed little under anaerobic conditions (and therefore overall rates of carbonate production remained the same), this weakening of Ω gradients would have meant the loss of the extremes in saturation, including the strongly oversaturated surface seawater critical for the rapid production of invertebrate skeletons. As long as gradients in Ω remained reduced, the energetic costs associated with producing a skeleton of $CaCO_3$ might have been prohibitively high, especially for organisms with a limited physiological ability to pump ions selectively across membranes.

On the basis of widespread black shales and low C:S, widespread dysoxia and local anoxia have long been inferred for subsurface waters masses of Series 3 and Furongian Cambrian oceans (e.g., Berry and Wilde, 1978; Raiswell and Berner, 1986; Zhuravlev and Wood 1996; Hallam, 1998; Gaines et al., 2005; Hough et al., 2006; Hurtgen et al., 2009). Recent geochemical research supports earlier hypotheses and indicates that at times subsurface anoxia may have been global (Gill et al. 2007). In addition, oxygen isotope ratios in conodont phosphate support the hypothesis that later Cambrian and Early Ordovician oceans were warm, with global cooling coincident with the main pulse of the Ordovician radiation (Trotter et al., 2008). The prevalence of warm temperatures during later Cambrian and Early Ordovician time may have contributed to low levels of dissolved oxygen in subsurface seawater via the effect of temperature on the Henry's Law constant (Rowland and Shapiro, 2002); the consequent development of subsurface anoxia, then, would have reduced oversaturation with respect to $CaCO_3$ minerals in surface waters. If so, increased ventilation of Ordovician oceans, driven by global cooling (e.g. Trotter et al. 2008), would have increased the oversaturation of surface seawater with respect to calcite and aragonite, thereby reducing the physiological cost of skeleton construction.

In this view, then, the timing of the Ordovician radiation might be understood in the context of increasing availability of carbonate ion (higher Ω) in surface seawater due to the effects of long-term cooling of climate and waning ocean basin anoxia. It is important to note that taxa with carbonate skeletons are not the only organisms that diversified during Ordovician time. For example, siliceous sponges, often associated with microbial mounds, diversified in the Early Ordovician (Brunton and Dixon, 1994; Carrera and Rigby, 2004), and trace fossils, indicators of soft-bodied diversity, show an increase in diversity during the Ordovician radiation (Mangano and Droser, 2004). The overall depth and extent of bioturbation also increased, albeit not until the Late Ordovician (e.g.. Droser and Bottjer, 1989). Thus, it is clear that the Ordovician radiation cannot be divorced from the complex interactions of an evolving ecology. Nonetheless, emerging geochemical data suggest that environmental change might well have facilitated the evolution of heavily calcified skeletons across diverse clades of marine organisms. The notable increase in carbonate skeletal abundance is an important, even defining, aspect of this event.

Our focus on skeletal chemistry does not by itself rule out hypotheses such as bolide facilitation of Ordovician radiation (Schmitz et al., 2008), although it highlights a specific pattern that such hypotheses must be able to explain. Nor does it rule out bottom-up proposals that link animal radiation to changing patterns of primary production. Indeed, deep ocean ventilation might well have facilitated changes in primary production of the kind that Servais et al. (2008, 2009) called upon to explain Ordovician animal evolution. Finally, decreasing metabolic cost of skeletonization does not rule out increasing benefit associated with enhanced predator pressure; the two hypotheses are not mutually exclusive. A focus on skeleton precipitation does, however, suggest that an additional class of hypothesis must be taken seriously—one based on the changing carbonate chemistry of Cambro-Ordovician oceans. Understanding the several intervals of Phanerozoic time when skeletal abundance appears to have been low may ultimately reveal the complexity and bidirectionality of links between the carbonate cycle and evolution in the oceans.

CONCLUSIONS

Calcifying organisms regulate and respond to environmental perturbations in the carbonate system as a whole. Previous studies examined the effect that the early Cambrian emergence of carbonate skeletons exerted on shifting the locus and the mechanisms of marine carbonate production (Zeebe and Westbroek, 2003; Ridgwell and Zeebe, 2005); however, the results presented here suggest that this shift did not occur until later in the Ordovician Period. Late Cambrian and earliest Ordovician carbonate deposition remained under the dominant influence of abiotic or microbially mediated precipitation processes. Despite the appearance of calcareous organisms near the Proterozoic-Cambrian boundary, the development of a quantitatively important skeletal sink for carbonate was not established until Middle Ordovician time.

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LIST OF FIGURES AND CAPTIONS

Figure 1: Map of Laurentia with western Newfoundland and Ibex Area, Utah indicated by arrows. Note that modern day North America is represented by a dashed line and the paleocontinent is shaded gray.

Figure 2: Stratigraphic columns of sections examined in western Newfoundland and Ibex Area Utah. All samples analyzed in thin section are listed next to their position on the stratigraphic columns, and point count identifications are shown in Table 1.

Figure 3: Diagram showing % bioclastic material based on point counts of thin sections, with 200 points counted per slide. Series 3—Furongian (Cambrian) and some Tremadoc data were generated from thin sections of samples from western Newfoundland. Tremadoc, Late Arenig and Llanvirn data were generated from thin sections of carbonates of Lower and Middle Ordovician strata from the Ibex Area, Utah.

Figure 4: A) Bar graphs showing proportion of lithofacies observed in outcrop from western Newfoundland (Series 3 and Furongian, Cambrian) and Ibex Area of Utah (Lower and Middle Ordovician). B) An environmental transect showing approximate locations of depositional units from A.

Figure 5: Abundance of skeletal material as a fraction of volume of lithofacies, generated by multiplying average values of skeletal carbonate viewed in thin section to the total

meters of lithofacies observed in outcrop for the Cambrian of Newfoundland and Ordovician of the Ibex Area, Utah.

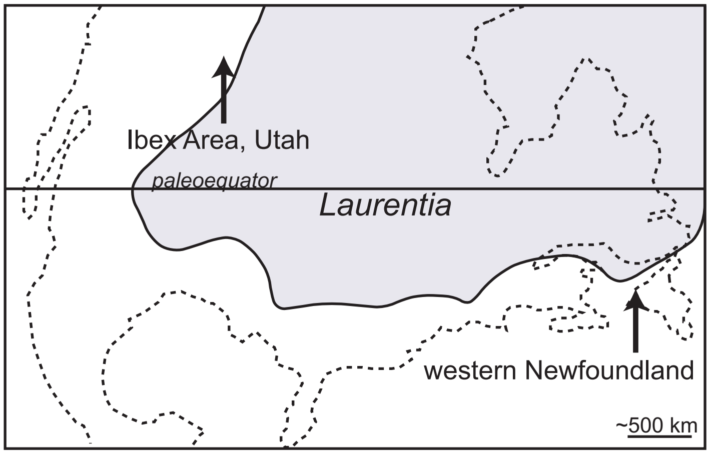
Figure 6: Proportions of stratigraphic units (formations or members) logged as skeletal limestone (fossil wackestones, packstones, or grainstones) plotted against age in measured sections from A. Newfoundland (S. Pruss, field notes) and B. Utah (compiled from S. Finnegan field notes and from Hintze, 1973). S3: Series 3.

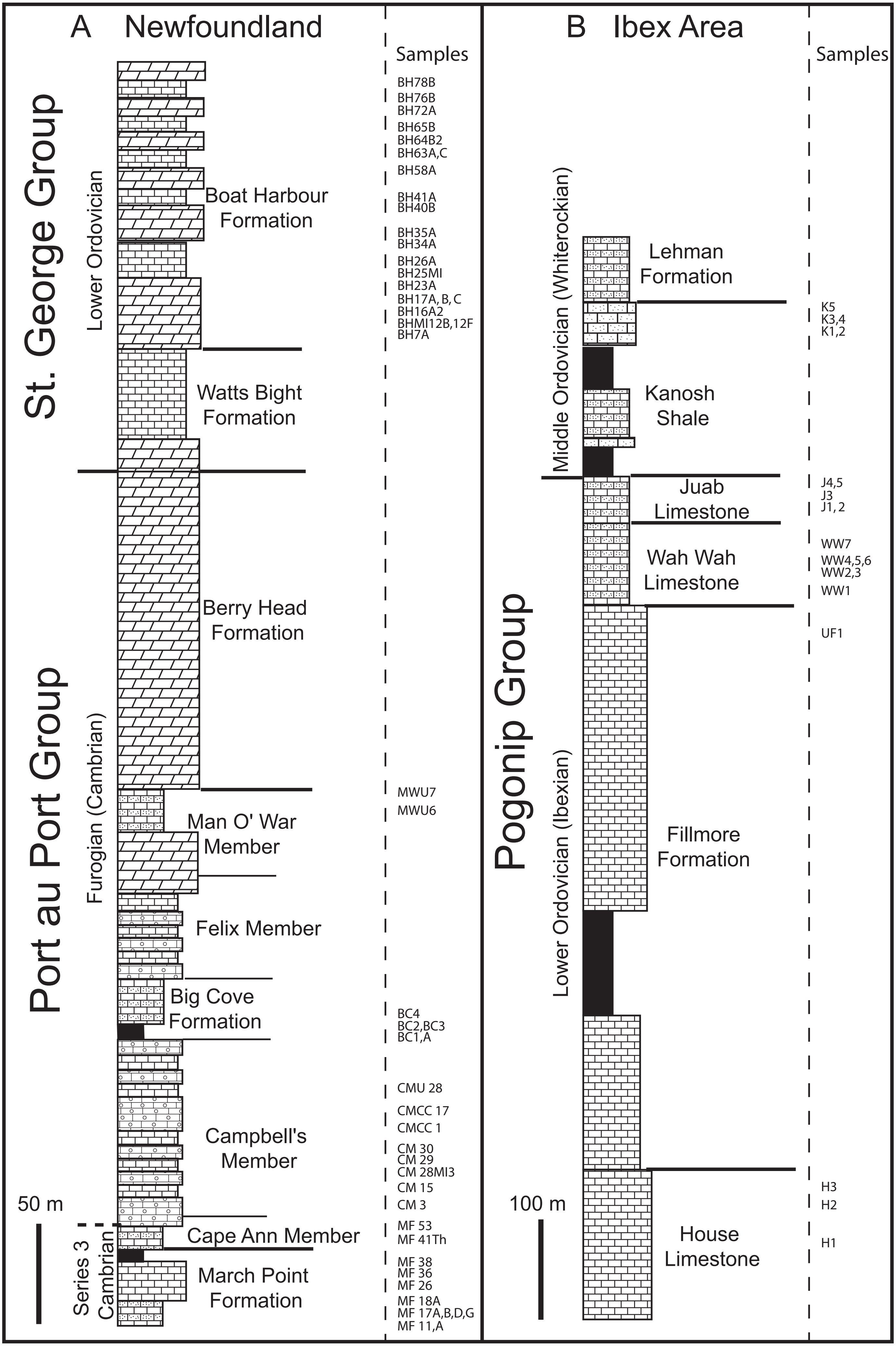
Figure 7: Principal Components Analysis of all unique formation/member/locality combinations. Four independent (but normalized) variables: %Microbial carbonates, %Oolites, % Skeletal carbonates, % Micritic carbonates. Series 3—Furongian (Cambrian) = circles, L Ordovician = triangles, M-U Ordovician = squares. Note on the diagram the labels which show where a pure micrite, skeletal limestone, oolite and microbial carbonate would occur (see Appendix 1 for sources used).

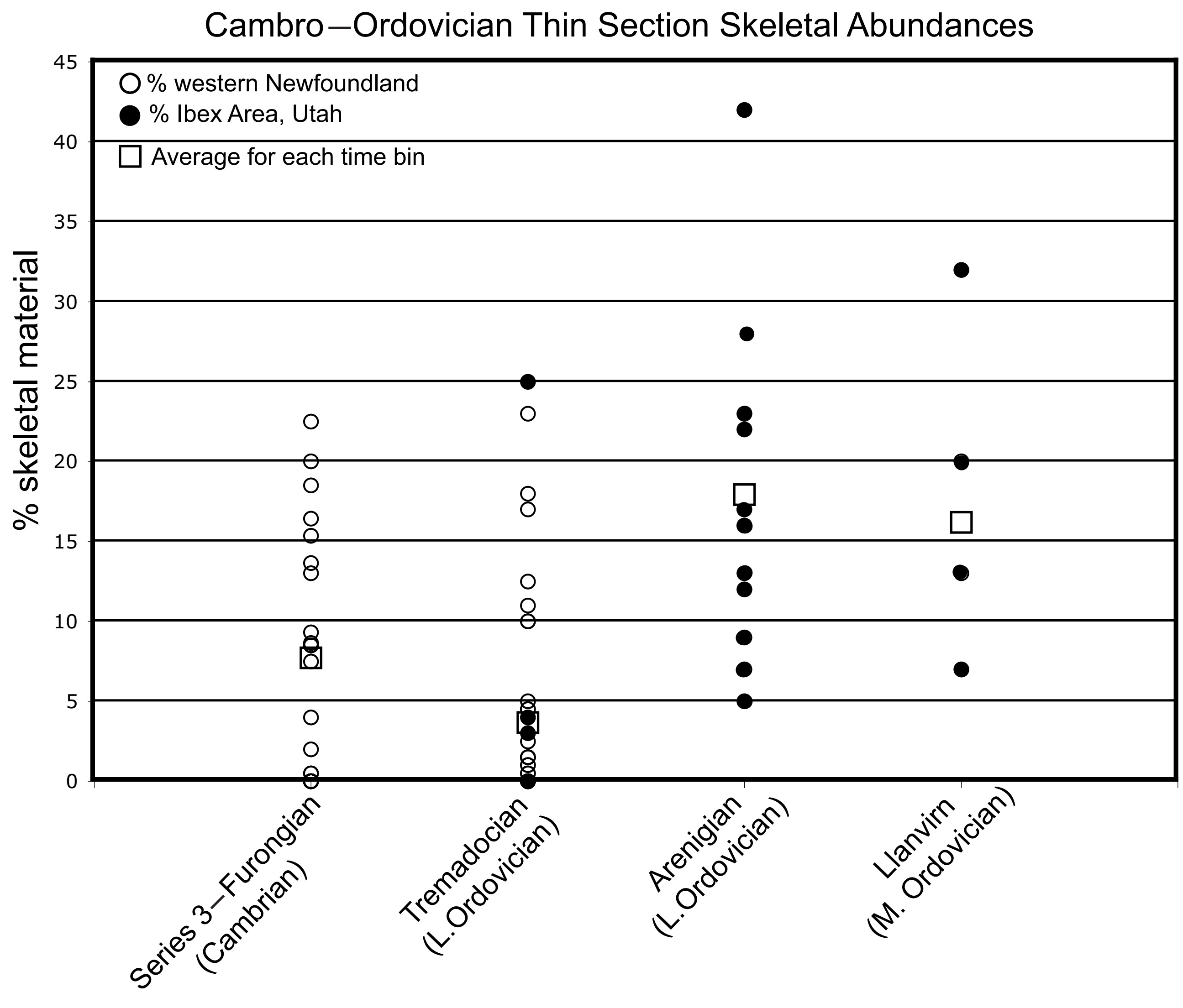
Figure 8: Generic diversity of calcifying animal groups from the Cambrian into the Ordovician (from Shanan Peters online database, using Sepkoski's data, 2002).

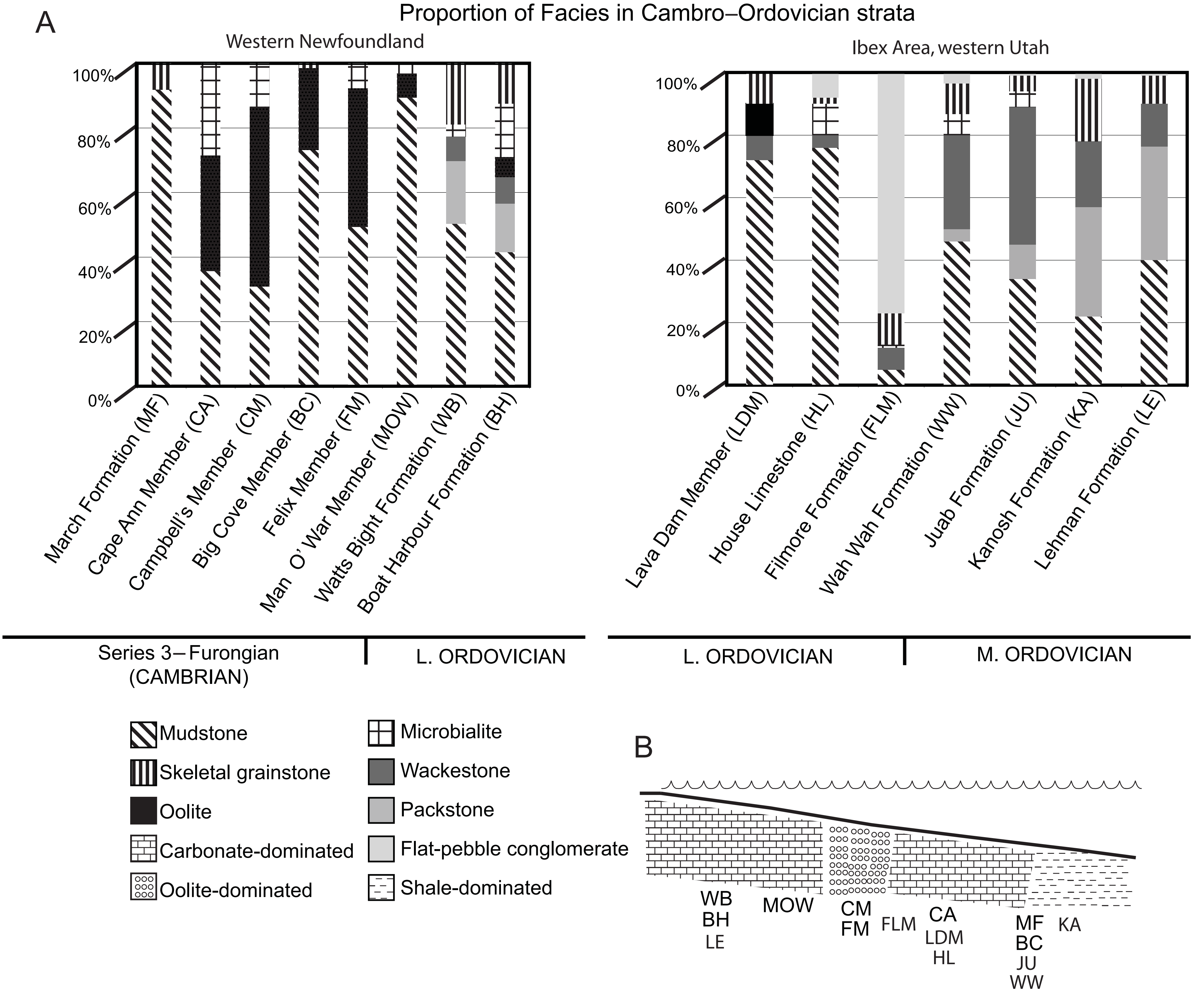
Table 1: Abundance of identified carbonate components counted in thin section. Sam is sample, Dunham is the Dunham classification assigned to each sample, Micr is micrite, Microb is microbial microfacies, and FP is flat pebble.

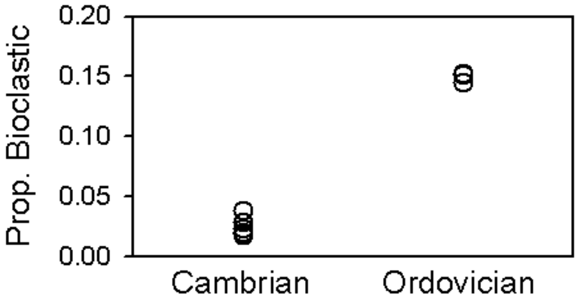
Appendix 1: Data used in literature compilation including locations, references, and proportion of skeletal carbonates.

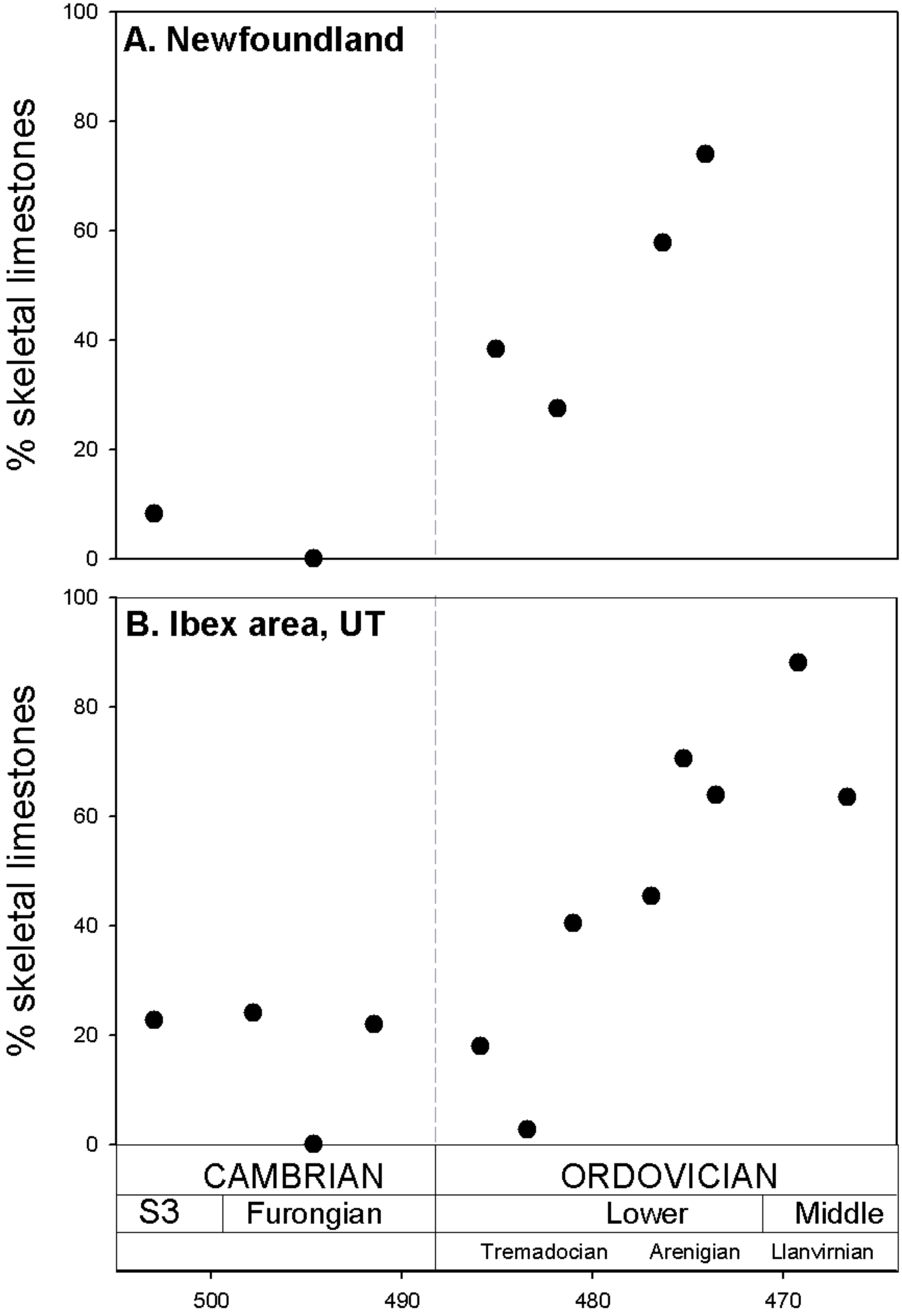

Ibex Area, Utah
paleoequator
Laurentia
western Newfoundland
~500 km

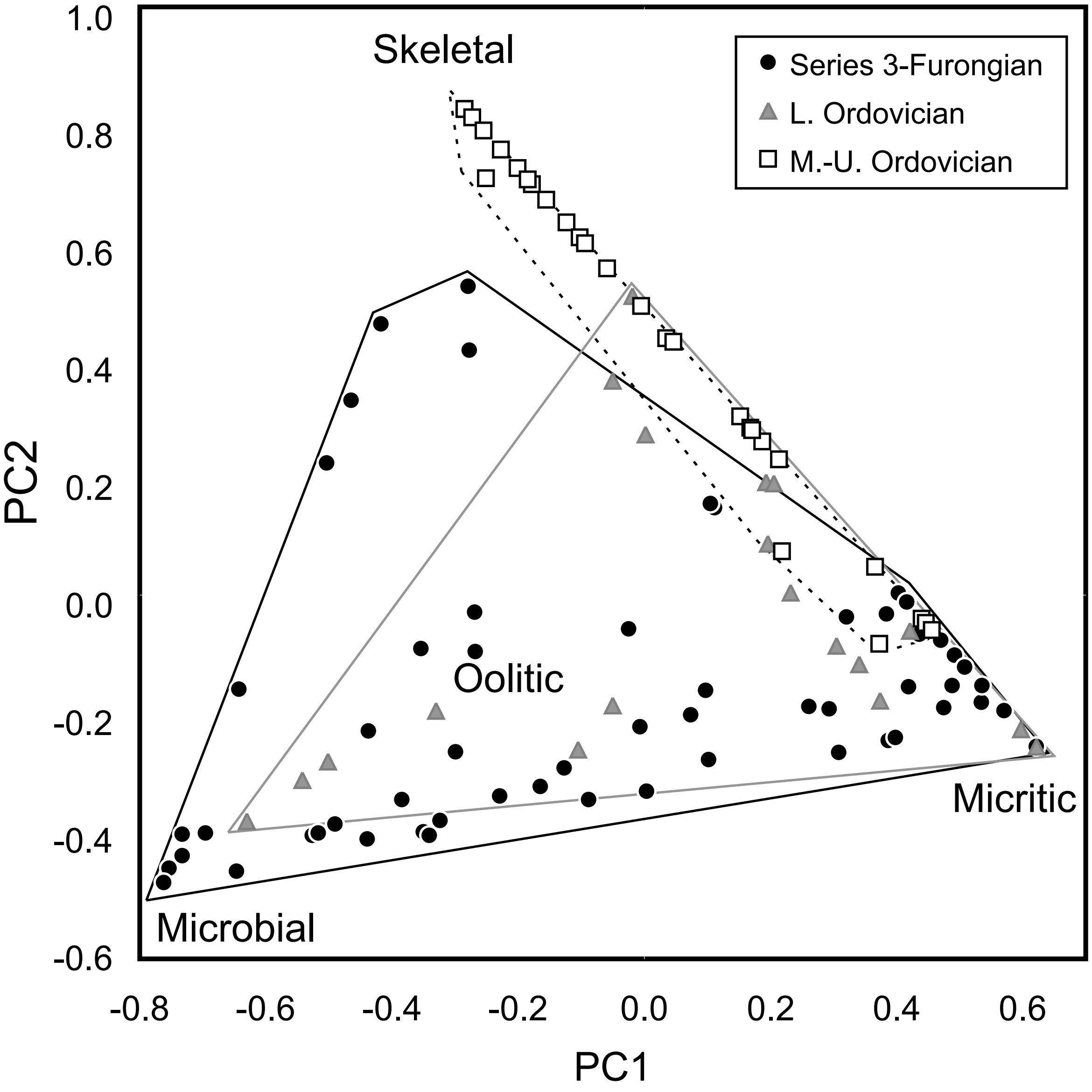

A Newfoundland
Samples
St. George Group
Lower Ordovician
Boat Harbour Formation
Watts Bight Formation
Port au Port Group
Furogian (Cambrian)
Berry Head Formation
Man O' War Member
Felix Member
Big Cove Formation
Campbell's Member
Cape Ann Member
March Point Formation
Series 3 Cambrian
50 m
BH78B
BH76B
BH72A
BH65B
BH64B2
BH63A,C
BH58A
BH41A
BH40B
BH35A
BH34A
BH26A
BH25MI
BH23A
BH17A, B, C
BH16A2
BHMI12B,12F
BH7A
MWU7
MWU6
BC4
BC2,BC3
BC1,A
CMU 28
CMCC 17
CMCC 1
CM 30
CM 29
CM 28MI3
CM 15
CM 3
MF 53
MF 41Th
MF 38
MF 36
MF 26
MF 18A
MF 17A,B,D,G
MF 11,A
B Ibex Area
Samples
Middle Ordovician (Whiterockian)
Lehman Formation
Kanosh Shale
Juab Limestone
Wah Wah Limestone
Pogonip Group
Lower Ordovician (Ibexian)
Fillmore Formation
House Limestone
100 m
K5
K3,4
K1,2
J4,5
J3
J1, 2
WW7
WW4,5,6
WW2,3
WW1
UF1
H3
H2
H1


Cambro–Ordovician Thin Section Skeletal Abundances
○ % western Newfoundland
● % Ibex Area, Utah
☐ Average for each time bin
% skeletal material
0
5
10
15
20
25
30
35
40
45
Series 3–Furongian (Cambrian)
Tremadocian (L.Ordovician)
Arenigian (L.Ordovician)
Llanvirn (M. Ordovician)


Proportion of Facies in Cambro–Ordovician strata
A
Western Newfoundland
100%
80%
60%
40%
20%
0%
March Formation (MF)
Cape Ann Member (CA)
Campbell's Member (CM)
Big Cove Member (BC)
Felix Member (FM)
Man O' War Member (MOW)
Watts Bight Formation (WB)
Boat Harbour Formation (BH)
Series 3– Furongian (CAMBRIAN)
L. ORDOVICIAN
Ibex Area, western Utah
100%
80%
60%
40%
20%
0%
Lava Dam Member (LDM)
House Limestone (HL)
Filmore Formation (FLM)
Wah Wah Formation (WW)
Juab Formation (JU)
Kanosh Formation (KA)
Lehman Formation (LE)
L. ORDOVICIAN
M. ORDOVICIAN
Mudstone
Skeletal grainstone
Oolite
Carbonate-dominated
Oolite-dominated
Microbialite
Wackestone
Packstone
Flat-pebble conglomerate
Shale-dominated
B
WB
BH
LE
MOW
CM
FM
FLM
CA
LDM
HL
MF
BC
JU
WW
KA


Prop. Bioclastic
0.20
0.15
0.10
0.05
0.00
Cambrian
Ordovician


A. Newfoundland
B. Ibex area, UT
% skeletal limestones
% skeletal limestones
0
20
40
60
80
100
CAMBRIAN
ORDOVICIAN
S3
Furongian
Lower
Middle
Tremadocian
Arenigian
Llanvirnian
500
490
480
470


Skeletal
Oolitic
Micritic
Microbial
● Series 3-Furongian
▲ L. Ordovician
□ M.-U. Ordovician
PC2
PC1
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6

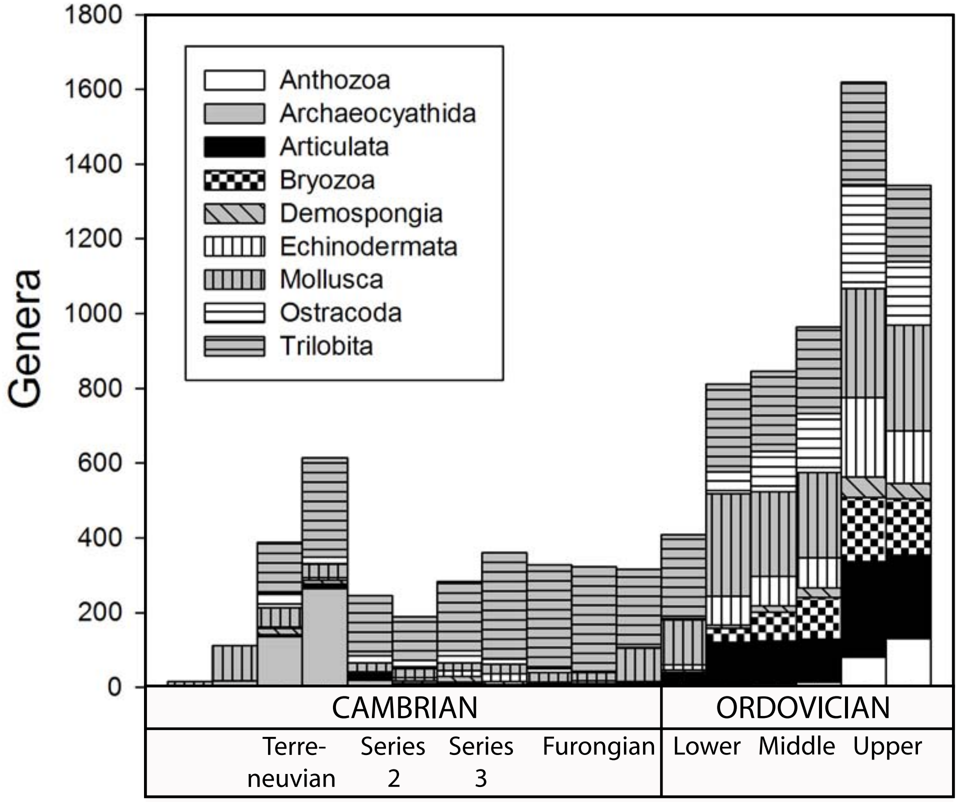

1800
1600
1400
1200
1000
800
600
400
200
0
Genera
Anthozoa
Archaeocyathida
Articulata
Bryozoa
Demospongia
Echinodermata
Mollusca
Ostracoda
Trilobita
CAMBRIAN
ORDOVICIAN
Terre-neuvian
Series 2
Series 3
Furongian
Lower
Middle
Upper

Table 1

Point Count Data from Middle Cambrian-Lower Ordovician Strata, western Newfoundland and Lower-Upper Ordovician strata, Ibex Area, Utah

Sam.	Dunham	Age	Fmtion	Micr	Spar	Ooid	Trilo	Oncoid	Echino	Brach	Microb	FP	Unident	Mollusc	Peloids	Other
MF11	GS	S3	March	41	85	0	9	5	16	1	0	5	4	0	0	34
MF11A	GS	S3	March	39	24	0	33	0	0	0	0	0	0	0	0	104
MF17	FP	S3	March	19	54	0	6	0	0	0	0	122	14	0	0	0
MF17B	GS	S3	March	83	36	0	14	0	2	2	0	74	1	0	0	8
MF17D	GS	S3	March	92	95	0	3	0	1	0	0	0	0	0	0	9
MF17G	GS	S3	March	106	19	0	23	47	2	0	0	0	3	0	0	1
MF18A	GS	S3	March	95	6	0	38	0	0	1	0	57	1	0	0	2
MF26	MS/WS	S3	March	200	0	0	0	0	0	0	0	0	0	0	0	0
MF36	FP	S3	March	53	23	8	0	0	0	0	3	113	0	0	0	0
MF38	GS	S3	March	75	71	1	21	5	4	0	0	11	6	6	0	0
MF41Th	MIC	S3	Cape Ann	151	14	0	0	0	0	0	35	0	0	0	0	0
MF53	O	S3	Cape Ann	4	102	94	0	0	0	0	0	0	0	0	0	0
CMCC1	MIC/GS	FU	Campbell’s	114	8	0	0	0	30	0	43	0	5	0	0	0
CMCC17	O	FU	Campbell’s	11	53	134	0	0	0	0	0	0	0	0	0	0
CM3	FP	FU	Campbell’s	122	55	1	0	0	0	0	0	12	0	0	0	0
CM15	GS	FU	Campbell’s	3	98	82	0	2	15	0	0	0	0	0	0	0
CM28MI3	MIC	FU	Campbell’s	148	8	1	0	0	7	0	35	0	1	0	0	0
CM29	MS/WS	FU	Campbell’s	200	0	0	0	0	0	0	0	0	0	0	0	0
CM30	MIC	FU	Campbell’s	78	30	0	0	0	0	0	92	0	0	0	0	0
CMU28	GS	FU	Campbell’s	140	3	32	2	0	11	0	0	0	4	0	0	8
BC1	MS/WS	FU	Big Cove	200	0	0	0	0	0	0	0	0	0	0	0	0
BC1A	GS	FU	Big Cove	64	1	0	24	0	0	0	0	108	2	0	0	1
BC2	GS	FU	Big Cove	123	2	0	45	0	0	0	0	20	0	0	0	10
BC3	GS	FU	Big Cove	79	10	0	30	55	0	1	0	0	0	0	0	27
MWU6	O	FU	Man o’ War	62	34	87	1	0	8	0	0	0	8	0	0	0
MWU7	MS/WS	FU	Man o’ War	192	8	0	0	0	0	0	0	0	0	0	0	0
BH7A	FP	TR	B. Harbour	155	20	0	0	0	1	0	0	10	0	0	7	7
BH16A2	PS	TR	B. Harbour	125	30	0	0	0	0	0	0	15	0	1	20	9
BH17A	PS	TR	B. Harbour	19	91	0	4	2	24	0	0	2	5	3	32	18
BHMI7B	MS	TR	B. Harbour	17	35	0	0	0	0	0	137	0	0	0	11	0
BH17C	MS	TR	B. Harbour	93	31	0	1	0	0	0	0	4	0	0	19	52
BHMI12B	MIC	TR	B. Harbour	89	63	0	0	0	0	0	19	0	1	9	19	0
BH12F	GS	TR	B. Harbour	119	68	0	3	0	0	0	0	0	2	0	8	0
BH23A	GS	TR	B. Harbour	97	7	0	1	0	1	2	0	6	3	2	14	67
BH25MI	MIC	TR	B. Harbour	152	3	0	0	0	0	0	0	1	0	22	17	5
BH26A	MS	TR	B. Harbour	132	4	0	0	0	0	0	0	0	0	0	0	64
BH34A	WS	TR	B. Harbour	142	13	0	0	0	2	0	0	0	1	0	39	3
BH35A	FP	TR	B. Harbour	23	56	33	0	0	0	0	0	38	0	0	48	2
BH40B	WS	TR	B. Harbour	34	63	0	0	0	1	0	0	8	1	0	93	0

Sam.	Dunham	Age	Fmtion	Micr	Spar	Ooid	Trilo	Oncoid	Echino	Brach	Microb	FP	Unident	Mollusc	Peloids	Other
BH41A	MIC	TR	B. Harbour	105	5	0	0	0	0	0	0	0	3	0	0	87
BH58A	WS	TR	B. Harbour	116	21	0	0	0	1	0	0	18	2	0	29	13
BH63A	O	TR	B. Harbour	27	49	107	0	0	0	0	0	1	0	0	11	5
BH63C	O	TR	B. Harbour	42	56	42	0	0	0	0	6	0	0	0	54	0
BH64B2	MIC	TR	B. Harbour	6	30	0	0	0	0	0	150	0	0	0	0	14
BH65B	O	TR	B. Harbour	38	59	73	1	1	5	0	0	10	2	1	10	0
BH72A	GS	TR	B. Harbour	122	53	0	0	0	0	0	0	0	1	0	21	3
BH76B	GS	TR	B. Harbour	23	57	0	6	0	14	0	5	20	4	1	70	0
BH78B	GS	TR	B. Harbour	40	54	1	1	0	11	0	2	43	2	6	16	24

Sam.	**Dunham**	**Age**	**Fmtion**	***Nuia***	**Unid.Alga**	**Brach.**	**Echino.**	**Gastro.**	**Biv.**	**Ostra.**	**Por.**	**Trilo.**	**Unid**	**Spar**	**Micr**	**?Carb.**	**Intra.**	**Pel.**
H1	MS	TR	House	0	0	0	0	0	0	0	0	0	0	18	182	0	0	0
H2	MS	TR	House	0	0	0	2	0	0	0	0	4	0	2	188	0	0	8
H3	MS	TR	House	0	0	0	0	0	0	0	0	0	0	0	200	0	0	0
L.NM1	WS	TR	Lower Ninemile	0	0	30	0	0	0	0	0	10	10	16	138	0	0	0
L.NM2	MS	TR	Lower Ninemile	0	0	0	0	0	0	0	0	6	2	6	188	0	0	2
LF1	GS	TR	Lower Fillmore	0	0	0	2	0	0	0	0	4	2	0	58	94	0	40
J1	PS	L.AR	Juab	0	0	0	2	0	0	0	0	26	4	12	158	0	2	0
J2	WS	L.AR	Juab	0	0	14	4	0	4	0	0	4	8	10	158	0	0	0
J3	WS-GS	L.AR	Juab	0	0	12	0	0	0	0	0	6	6	10	164	0	0	4
J4	WS-GS	L.AR	Juab	0	0	4	18	2	0	6	0	2	2	32	108	28	0	2
J5	GS-WS	L.AR	Juab	0	0	8	14	0	0	0	0	14	8	16	128	14	0	0
Sh/Ju	WS	L.AR	Shingle	0	0	6	2	0	0	0	0	8	4	40	142	0	0	0
UF1	PS	M.AR	Upper Fillmore	0	0	0	10	0	0	0	0	40	6	16	78	0	0	52
WW1	WS	M.AR	Wah Wah	0	0	4	0	0	0	0	0	8	2	4	178	0	4	0
WW2	MS	M.AR	Wah Wah	0	0	0	0	0	0	0	4	2	4	16	176	0	0	0
WW3	WS/GS	M.AR	Wah Wah	0	0	2	12	0	0	0	0	10	2	12	164	0	0	2
WW4	FPC	M.AR	Wah Wah	0	0	2	6	0	0	0	0	26	12	36	80	0	40	0
WW5	GS	M.AR	Wah Wah	0	2	2	34	0	0	0	0	34	14	32	42	0	38	4
WW6	WS	M.AR	Wah Wah	0	0	4	0	8	0	0	0	14	6	22	132	0	0	18
WW7	FPC	M.AR	Wah Wah	0	0	8	6	0	0	0	0	12	20	14	6	0	136	0
K1	WS-PS	LLA	Kanosh	0	0	6	0	0	0	6	0	4	2	44	132	0	0	8
K2	WS	LLA	Kanosh	0	0	2	0	12	4	0	0	4	4	24	154	0	0	0
K3	WS-GS	LLA	Kanosh	8	0	16	4	0	0	2	0	6	12	22	134	0	0	0
K4	MS	LLA	Kanosh	0	0	6	2	0	0	0	0	4	2	24	166	0	0	0
K5	GS-WS	LLA	Kanosh	0	0	10	4	2	0	14	0	26	8	64	64	0	0	14