

Chapter 3

Combining Stratigraphic Sections and Museum Collections to Increase Biostratigraphic Resolution *Application to Lower Cambrian Trilobites from Southern California*

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Approaches in High-Resolution Stratigraphic Paleontology, edited by Peter J. Harries, © 2003 Kluwer Academic Publishers, Printed in the Netherlands

1. QUESTIONS OF PRECISION AND THOROUGHNESS

Range charts are the critical limiting factor for biostratigraphic resolution. High-resolution biostratigraphy requires detailed local range charts that resolve the first and last appearances of numerous fossil species with centimeter precision. Unless the fossil collecting is also extraordinarily thorough, range charts underestimate the full length of taxon ranges and miss rare taxa altogether. High precision involves collecting fossils from thin rock intervals and recording precisely the stratigraphic separation of these intervals. Thoroughness has two components: 1) collecting at many stratigraphic levels; and 2) processing enough rock at each level to find the local highest and lowest occurrences of both the abundant taxa and the rare taxa.

Field projects with realistic deadlines achieve precision more easily than thoroughness, especially in the collection of macrofossils. It may be feasible to excavate clean, continuous exposures and carefully measure the position of each sampled interval. Time will likely be inadequate, however, to examine as much rock as one would wish. Museum collections appear to offer an easy means to increase the thoroughness of a measured section. They often house rich faunas that combine decades of collecting by many individuals. Although museums might not retain all the mediocre specimens of common taxa, their selectivity may be expected to include several kinds of specimen that are important for range charts: rare taxa not seen in all measured sections; individual finds that extend the known taxon range; and fossils from nearly barren rock intervals. Unfortunately, the attractive taxonomic richness in museum collections is likely to be offset by accompanying records that are of variable quality and typically lack detail concerning the precise provenance of the specimens.

This chapter explores options for using rich, but loosely documented, museum collections to test and augment range charts from more precisely measured stratigraphic sections. After reviewing the types of essential information that range charts contain, we categorize museum specimens according to the aspects of this information that they can augment. Then we turn to computer-assisted methods of combining the information from museum collections and measured sections.

At each step, we illustrate the dilemma of precision and thoroughness with the real example of olenelloid trilobites from Lower Cambrian outcrops in two neighboring mountain ranges in the eastern Mojave Desert of southern California (Fig. 1), and from the reference collections of the Geology Museum at the University of California, Riverside (UCR). We

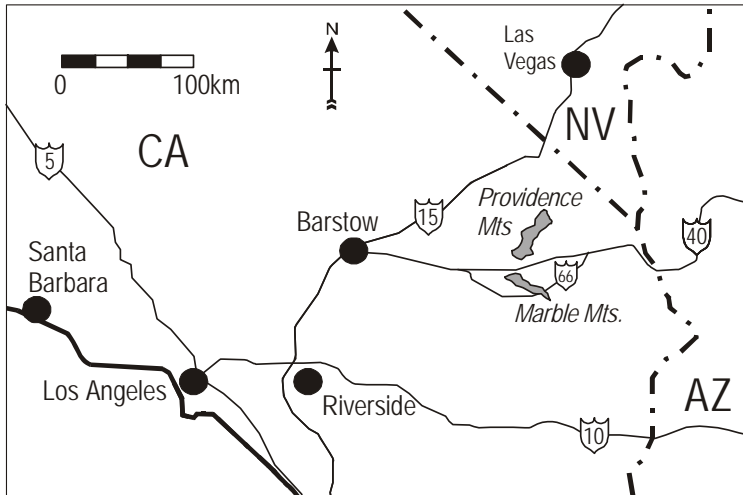


Figure 1. Location of the Marble Mountains and Providence Mountains.

combine the insights of a systematist (M.W.), a stratigrapher (P.M.S.), a museum curator (M.A.K.) and a fossil collector (E.F.), all intimately familiar with these outcrops and collections.

2. THE CRUCIAL CONTENTS OF RANGE CHARTS

Local range charts (e.g., Figs. 2, 3) depict the observed durations of fossil taxa against a scale of stratigraphic distance in a measured section of rock strata. The sequence and spacing of the stratigraphically lowest and highest finds of all taxa are sufficient primary information in the sense that nothing more is required to establish all the ranges; a taxon range connects the lowest and the highest finds. Nevertheless, any suite of ranges contains secondary pattern elements that, while not necessary to construct a range chart from a measured section, may be recognized in museum collections. A good range chart will also include ancillary information from the measured section that has bearing on the reliability of the observed range ends.

The pattern of a suite of ranges reveals the overlap of taxa. This secondary information can be tested and improved by the contents of museum collections, whether or not the museum specimens are accompanied by locality information that is precise enough to insert a specimen directly into the series of faunas from the measured section. In particular, consider whether two taxa can be shown to have coexisted and, if not, which is the younger:

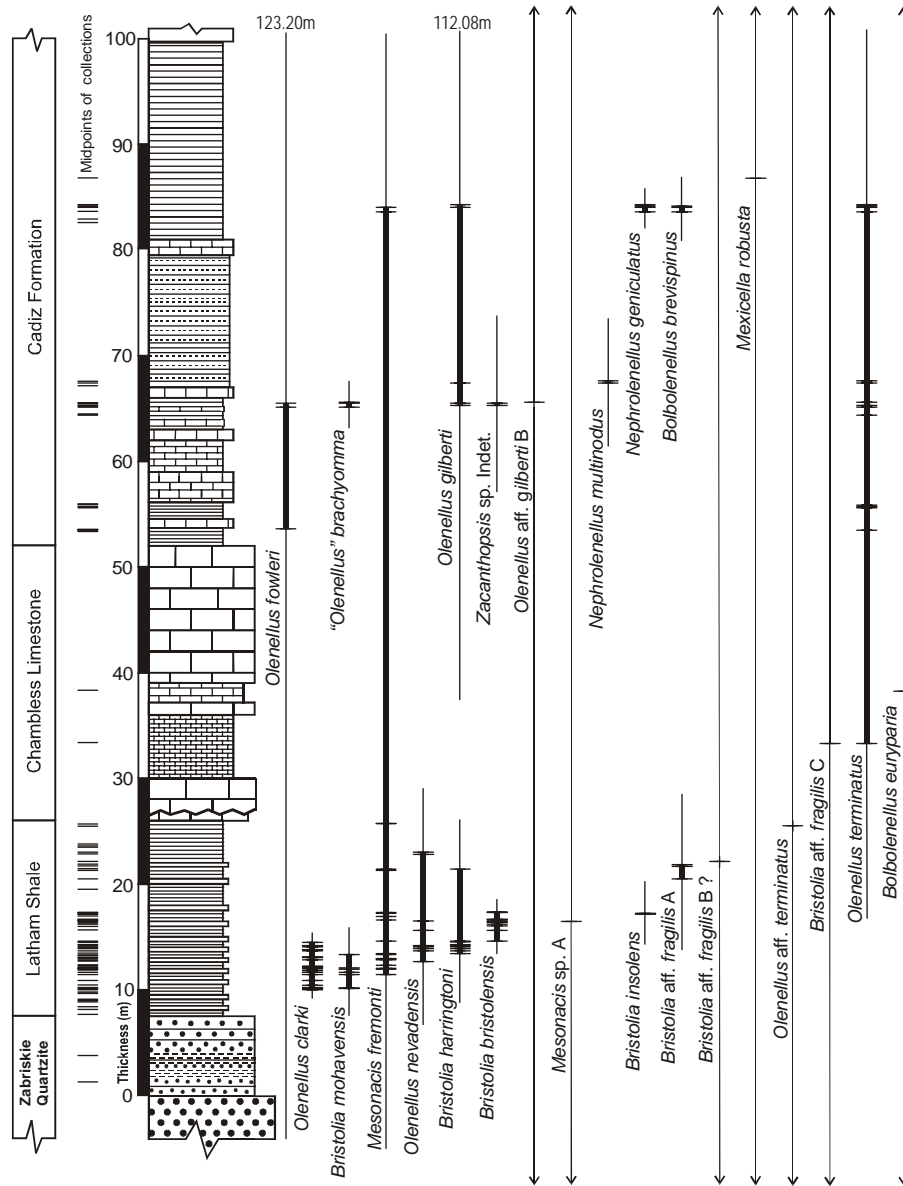


Figure 2. Range chart for trilobite-bearing Lower Cambrian and lowest Middle Cambrian strata of the southernmost Marble Mountains. Collections (second column from left) indicate fossiliferous levels whether or not the materials include identifiable trilobite species. The Latham Shale and Cadiz Formations were examined continuously. Thick vertical lines are observed species ranges drawn through all identifiable finds (horizontal cross bars). Thin vertical lines are 95% confidence intervals based on the number of finds in the range (two parameter case from Strauss and Sadler, 1989, Table 1). Infinite range extensions, which result from a single find, are terminated with arrowheads. Values in meters indicate the position of the ends of long finite extensions that lie beyond the figure.

- a) The *overlap* or conjunction (*sensu* Alroy, 1992) of locally observed ranges shows that the taxa coexisted at that location. Because the observation of a co-occurrence is positive evidence and independent of the sampling technique, this information is particularly worth seeking in museum collections. We refer here to physical co-occurrences at the same place, not the mere temporal overlap of ranges. The latter emerges when range charts from separate localities are correlated into one composite range chart. Physical co-occurrence data can be sufficient information to establish a temporal sequence of faunal assemblages (Guex and Davaud, 1984; Guex, 1991, Alroy, 1992). Such data alone do not indicate, however, which end of the sequence is youngest (polarity).
- b) The existence and duration of gaps between non-overlapping pairs of ranges (*disjunctions*, *sensu* Alroy, 1992) cannot be proved with complete certainty. They are likely to be exaggerated if the collecting was not thorough. Furthermore, they may be disproved by one isolated collection that demonstrates a co-occurrence.
- c) The *polarity* or superposition of two disjunct ranges indicates which taxon of a disjunct pair is the younger. If the ranges are truly disjunct, then two isolated faunas, each containing one of the pair, can be arranged in the correct order. Note that for taxa with overlapping ranges, the evidence of polarity rests in the sequence of their first- and last-appearance events and requires thorough collecting. We refer here to indications of polarity that might be gleaned from isolated finds of two taxa that are not sufficient to identify their range ends.

Because polarity depends upon the negative evidence of disjunction, however, false polarities may be indicated if collecting has not been thorough. The disjunctions that are least likely to be negated by new finds are those between pairs of abundant taxa that are routinely separated by gaps longer than the combined lengths of their observed ranges. Museum specimens that are merely referred to different lithostratigraphic formations may suffice to prove superpositional relationships for short-lived taxa with disjunct ranges.

- d) The *duration* of a taxon range is liable to underestimation. More thorough collection tends to lengthen the known ranges. Because longer ranges generate more overlaps, the duration of ranges will likely be related to the number of co-occurrences (Fig. 4).

Total observed ranges, from the lowest to the highest local find of a taxon, often pass through fossiliferous levels and barren strata. The interval of uncertainty between the highest find and the real range end is potentially as large as, or even larger than, the thickest barren interval within the range.

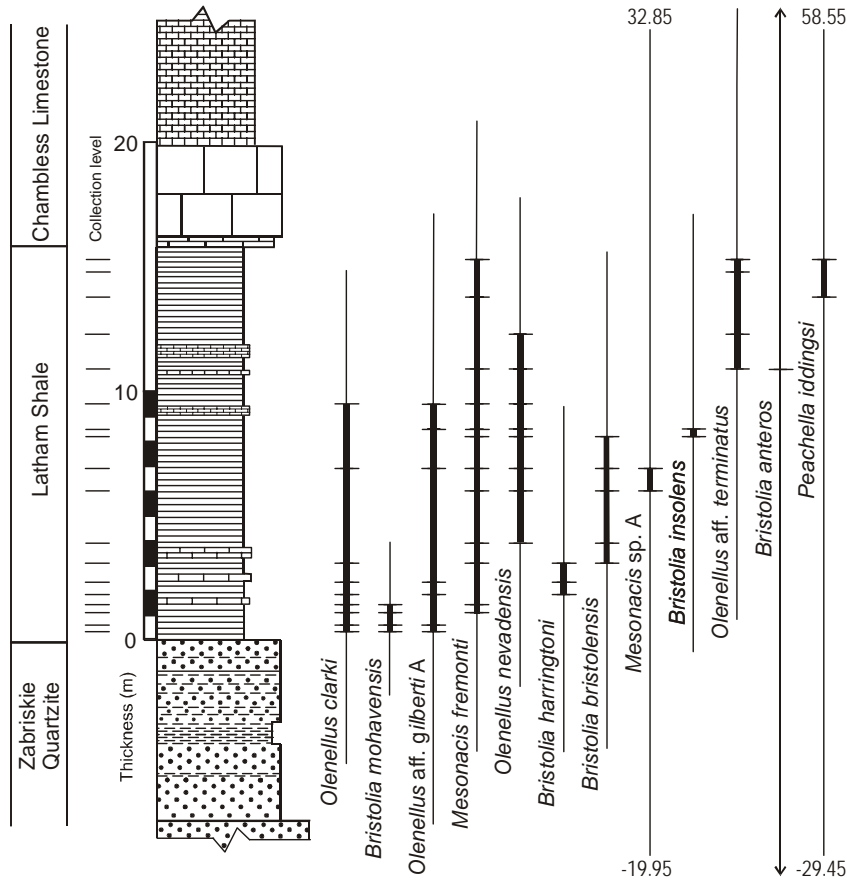


Figure 3. Range chart for olenelloid trilobites in the Latham Shale of the Summit Springs section in the Providence Mountains. Symbols as in Fig. 2. Collection was limited to excavations at the levels shown.

Museum collections have some potential to augment several kinds of information from observed ranges that provide better estimates of the reliability of range ends.

- a) The number and position of *finds* between the lowest and the highest may be used to place statistical confidence intervals upon the range ends (e.g., Paul, 1982; Strauss and Sadler, 1989; Marshall, 1990, 1994). Even if the formula for a confidence interval requires only the number of finds, the distribution of spaces between the finds will likely need to meet some preconditions. Confidence intervals spanning large stratigraphic distances indicate where collecting might not have been thorough enough (Figs. 2, 3).
- b) The stratigraphic position of all samples or *collecting levels* helps distinguish between gaps in a taxon range that result from “not-

looking” and those caused by “not-finding” the taxon. Figure 3 indicates the position of discrete sampling horizons; intervening levels were not searched. Figure 2 is based upon continuous searching in the shales; it indicates every level at which any fossil material was found.

- c) Sedimentary *facies changes* indicate levels at which the ends of observed ranges might result from changes in the habitat-related abundance of living individuals, The preservational mode of fossilized individuals, or the difficulty of collecting identifiable fossil specimens (e.g., top of the Latham Shale in Fig. 2).
- d) The *abundance* of taxa at each level indicates whether gaps and range ends are associated with intervals of low abundance. Relative abundance in measured sections and museum collections is a guide to the relative thoroughness of the collecting.

2.1 Observed Olenelloid Taxon Ranges

The collecting of Cambrian trilobites from the Marble Mountains began nearly a century ago (Darton, 1907; Clark, 1921; Resser, 1928; Hazzard, 1933; Crickmay, 1933; Mason, 1935; Hazzard and Mason, 1936; Riccio, 1952; Mount, 1974, 1976). The thoroughness with which these macrofossils can be collected varies with sedimentary facies. The following brief review of the mode of occurrence and our collecting strategies will provide essential preliminary insights into the distribution of gaps and fossiliferous horizons in the range charts (Figs. 2, 3).

The richest olenelloid faunas are preserved in the Latham Shale, a formation named by Hazzard (1954) for a topographically recessive unit of approximately 15 m of fine-grained, gray-green shale that is often obscured by large, fallen blocks of the overlying cliff-forming limestone. We prepared clean, continuous exposures by digging trenches between the fallen blocks. The individual trenches do not span the entire thickness of the Latham Shale; overlapping trenches were combined into a complete section by tracing thin marker beds of cross-laminated sandstone and limestone. In fewer than 12 months, natural movement of the shale talus significantly refills the trenches, reducing them to subtle swales. Detailed trench locality maps and logs are kept with our collections at the UCR Geology Museum. Most of the Latham Shale yields disarticulated trilobite remains. At rare horizons, however, the majority of specimens are partly articulated.

Lithologically indistinguishable Latham Shale crops out in the nearby Providence Mountains where one of us (E.F.) collected systematically in 1994. The UCR museum houses collections from both localities. The measured section from the Providence Mountains (Fig. 3) tests and amplifies

our attempt to add museum collections to the measured section from the Marble Mountains. Although collecting strategies in both mountain ranges processed unprecedented volumes of Latham Shale, they emphasize different aspects of thoroughness. Collecting in the long trenches in the Marble Mountains strove for stratigraphic continuity, trying to examine every parting; it generated relatively small, closely spaced faunas. In the Providence Mountains, the collecting effort concentrated upon large volumes of rock at discrete levels approximately 1 m apart. Sampled horizons in the Providence Mountains have produced 9 to 110 identifiable specimens each at 18 levels (chosen in advance), as contrasted with 1 to 41 identifiable specimens each at 54 levels (determined by the position of finds) from trenches in the Latham Shale of the Marble Mountains.

The Latham Shale overlies coarse, cross-bedded, trace-fossil-bearing quartz arenites of the Zabriskie Quartzite (Hazzard 1937) via a thin transitional interval of interbedded sandstones and shales that we interpret as a record of increasing depth of deposition. Although trilobites have not been recovered from the Zabriskie Quartzite, the olenelloids were likely extant at this locality before the quartz sands were deposited. Siltstones and quartz arenites of the underlying Wood Canyon Formation (Nolan, 1929) preserve rare *Cruziana* traces and have yielded a single poorly preserved specimen that Mount (1976) referred to the genus *Olenellus*.

Above the Latham Shale lies the distinctive, cliff-forming, oncolitic Chambless Limestone (Hazzard, 1954). The transition does not record a simple upward shallowing from the shale to the top of the limestone, as might be expected for a classic shale-limestone cyclothem. Rather, the shallowest conditions occur at the base of the oncolitic facies. The close of Latham Shale accumulation was marked by the deposition of less than 1 m of non-oncolitic, coarse, cross-bedded, bioclastic packstones which we interpret to have been deposited at a time of rapid shallowing. The upper surface of the cross-bedded packstone unit is a microkarstic erosion surface with up to 10 cm of steep castellated relief that records the maximum exposure. Subsequent drowning of this surface abruptly introduced coarse packstones, which are dominated by large, exquisitely detailed oncoliths and were once quarried from the Marble Mountains as an ornamental building stone. Smaller, less-well-preserved oncoliths, occur in the wackestones and mudstones that dominate most of the succeeding Chambless Limestone.

Both fresh and weathered surfaces of the Chambless Limestone reveal numerous disarticulated trilobite fragments in cross section. For most of these limestones, however, we have found no way to crack the rocks that separates the surfaces of the trilobite fragments from the matrix to reveal diagnostic features. Identifiable specimens have been recovered only from two non-oncolitic intervals in the Chambless Limestone. Both occur in the

lower half of the formation -- an interval of silty, calcareous, minimally fissile mudstones and a black oncolith-free interval of rubbly-weathering, dark, micritic, platy wackestones (Fig. 2). The former is well exposed only after rock-falls and yields sparse trilobite impressions when split. The latter reveals a few identifiable trilobites on weathered surfaces and the matrix breaks away from others when the mudstones are hammered perpendicular to bedding.

Recoverable olenelloids become more abundant again in the overlying Cadiz Formation (Hazard and Mason, 1936), a heterogeneous succession of micaceous shales, siltstones and sandstones with subordinate limestone beds. The upward transition from the Chambless Limestone occupies several meters of irregular and nodular beds of calcareous mudstones and wackestones, intercalated with siliciclastic mudstones. The trilobite-bearing shales of the Cadiz Formation are generally coarser and more micaceous than the Latham Shale. They likely represent shallower marine deposits. The Middle Cambrian portion of the Cadiz Formation begins near the top of our range chart (Fig. 2), with the appearance of *Mexicella robusta*. It includes distinctive oolitic limestone beds and brightly colored red, green and purple shales.

Our range chart for the Latham Shale and lower Cadiz Formation (Fig. 2) is the product of two years collecting through continuous artificial exposures in a suite of trenches dug into the shales. Near the surface, the shales disintegrate to splintery fragments, smaller than many of the trilobite cephalons. Our shallow excavations reached down to intact material that was split and searched layer by layer. Limestone and sandstone facies have been examined in natural outcrops between the trenches.

The trenching and bed-by-bed searching that led to Figure 2 are far more stratigraphically continuous and precise than any previous collecting in these formations. They have produced at least eight trilobite species from the Cadiz Formation and high in the Latham Shale that are not found in previous collections from the same area, now housed in the UCR Geology Museum. Nevertheless, the museum collections, which represent 55 years of relatively unsystematic collecting by many individuals, contain four species that we had not yet found in the trenches -- *Peachella iddingsi*, *Olenellus* aff. *gilberti* A and *Bristolia anteros* from the Latham Shale, as well as *O. puertoblancoensis* from the Chambless Limestone. It is these "missing" species that we particularly wish to incorporate into the range chart for the Marble Mountains.

The differences between our new collections and the museum holdings have quite straightforward origins. Material from a few pits in the Latham Shale, which are continually enlarged by amateur collectors and geology classes, dominate the museum collections. Our trenches tap into intervals

that are otherwise generally inaccessible. But the trenches typically excavate a swath less than 1 m wide; at no level does the volume of material we processed compare with that taken from corresponding intervals in the pits. Near the top of the Latham Shale, we had a single trench with relatively few fossiliferous levels. (The postscript summarizes results from an overlapping trench opened while this chapter was in review.) The less fossiliferous Cadiz Formation has attracted few casual collectors, especially in its Lower Cambrian portion. Museums hold correspondingly few Lower Cambrian fossils from the Cadiz Formation and our trenching there qualifies as the most successful collecting to date.

2.2 Internal Evidence of Shortfall in the Observed Taxon Ranges

Three lines of evidence indicate that some observed taxon ranges in the measured section from the Marble Mountains potentially fall short of the true local ranges; 1) the length of ranges relative to the nearby Providence Mountains section for the same stratigraphic interval; 2) the number of observed co-occurrences relative to the number of overlapping ranges; and 3) the size of gaps within the observed ranges. All three justify the appeal to museum collections to fill gaps in the coverage of the measured section.

Comparison of the two measured sections for the Latham Shale immediately reveals some shortcomings of thoroughness in collecting from the Marble Mountains. The relatively large volumes of rock processed at the fossiliferous levels in the Providence Mountains have yielded three species not yet found in the trenches in the Marble Mountains. *Bristolia anteros* and *Peachella iddingsi* are rare and probably short-ranged species. *Olenellus* aff. *gilberti* A is a long-ranged but even rarer species whose presence is recorded by only one individual in most samples. It would be possible to argue that the “missing” species reflect real discontinuities in the original geographic ranges, were it not for the fact that all three occur in the UCR museum collections from the Marble Mountains. This permits us to use the Providence Mountains to test the methods of incorporating museum collections into the measured section. Also, the trenches did yield one questionable specimen of *O. aff. gilberti* A.

Although greater ambiguity arises concerning differences in the lengths of ranges in the two sections, the much longer range for *Olenellus clarki* in the Providence Mountains is clearly also based upon recovering rare individuals. The species is 3 to 30 times more abundant in the lowest one-third of its range in the Providence Mountains than in the upper two-thirds. The length, position, and richness of co-occurring taxa for the lowest one-third seems to match the total observed range for the taxon in the trenches at

the Marble Mountains. It is reasonable to surmise that something resembling the sparsely populated upper two-thirds of the range also occurs in the Marble Mountains but was missed by the trenching strategy (see postscript). The pattern of abundance in some other taxon ranges supports this interpretation.

In spite of the disadvantages of sample size, the trenches in the Marble Mountains have yielded a single specimen of *Bristolia harringtoni* much higher in the Latham Shale than the apparent top of its range in the Providence Mountains. The ranges observed by continuous sampling in the Marble Mountains reveal a pattern of lower occurrence rates toward the top of observed ranges for *B. harringtoni*, *Olenellus nevadensis*, and *Mesonacis fremonti*. This is more than an artifact of sample spacing. It is reflected in failed co-occurrences -- within the gaps in these ranges are levels that yield other taxa. The sample spacing in the Providence Mountains is less likely to reveal such traits. Evidently, collections based upon large samples can usefully be incorporated into measured sections with relatively continuous sampling but smaller samples.

The observed taxon ranges in the measured sections fulfill the simple prediction that the number of overlapping ranges will increase with the length of the observed range (Fig. 4). Zero range length in Figure 4 means that the taxon was found at only one level. Any reasonable regression through the number of overlapping ranges intercepts zero range length at 3 to 5 overlaps because there are three to five long-ranging taxa at every level and even the shortest-ranged taxa must overlap with them. The large open symbols in Figure 4, which support such regressions, describe the properties of whole observed ranges as drawn through gaps in the ranges. The asterisks plot the significantly smaller numbers of overlapping ranges that can be shown by actual co-occurrences of fossil taxa at the individual collection levels. Most collection intervals have not yet yielded all the taxa that are known to range through them. Because the higher recovery rates are all from the Providence Mountains, we reasonably conclude that the pattern is an artifact of gaps caused by sample size, and does not record the genuinely patchy distribution of living taxa at the scale of tens of kilometers (see postscript for evidence of patchiness at the scale of hundreds of meters).

The gaps within a taxon range result from the same types of failures in fossil preservation and collection that explain the shortfall between the observed range and true range ends. Accordingly, the size distribution of these gaps have been used to construct 95% confidence intervals for the position of true range ends in Figures 2 and 3. The intervals are based on the average length of gaps within the observed range, using the formulae provided by Strauss and Sadler (1989). The total length of the observed

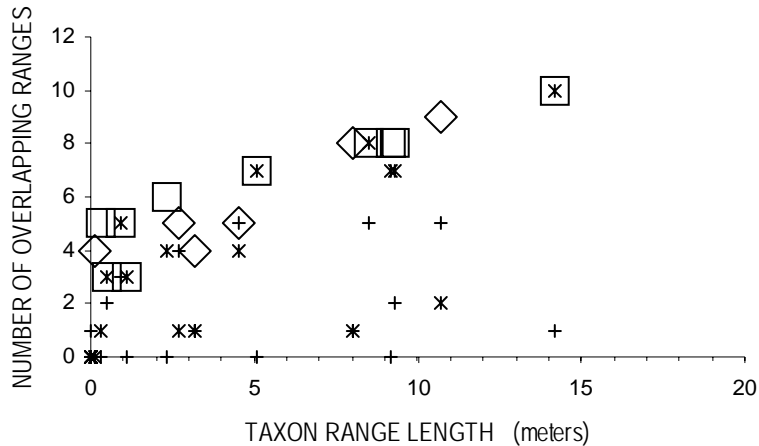


Figure 4. Number of overlapping ranges as a function of range length in the measured sections of Latham Shale in the Marble Mountains (diamonds) and the Providence Mountains (squares). The number of overlaps are underestimated by the actual co-occurrences at single levels in the measured sections (asterisks) and on slab-samples in the museum collections (crosses). Asterisks and crosses combine information from both localities.

range and the number of levels at which the taxon is found determine the average gap length; they are therefore the critical variables for length of the confidence intervals. Ranges based on a single find, for example, lead to infinitely long confidence intervals because they contain no information about average gap length.

As the number of finds increases, the confidence intervals shorten relative to the observed range length. For a range based on fewer than six finds, the combined length of the upper and lower confidence intervals exceeds the length of the observed range. For most taxa, the 95% confidence extensions on the observed ranges in the Marble Mountains are longer than the distance to the next closest range end (Fig. 2). *Olenellus clarki* appears to be an exception; but our previous comparison with the Providence Mountains indicates how badly misleading the confidence intervals become when critical assumptions are not satisfied.

The confidence intervals assume that the likelihood of finding a taxon is uniform within its range. As judged by the abrupt change in its abundance in the Providence Mountains, *O. clarki* violates this assumption. The tight confidence intervals on the range ends of *O. clarki* in the Marble Mountains result from many fossiliferous horizons which, as discussed above, may be restricted to the lowest one-third of the true range. Marshall (1994) explained how to relax the assumption that finds are equally likely at all

levels. His method depends upon approximating the tails of the real frequency distribution of gap sizes and assumes that gap size is not correlated with position in the range. Again, *O. clarki* violates the crucial assumption; significantly larger gaps characterize the upper two thirds of the range.

For the Latham Shale, comparison with independent collections allows the reliability of range ends to be assessed without making severe assumptions about randomness or estimating statistical parameters from the frequency distributions for the gaps in the observed range. The local shortfalls in range ends lead to contradictions between different sections. Resolving the differences compensates directly for shortfall. Rather than attempting to place a confidence interval on each local range, we seek the highest of the local last appearances and the lowest of the first appearances. We will show how museum holdings allow this strategy to be pursued further than measured sections alone would permit. As preparation, let us review the nature of museum holdings.

3. THE DOCUMENTATION AVAILABLE FOR MUSEUM COLLECTIONS

Museum collections consist of the specimens themselves, plus supporting documents concerning their taxonomic assignment, collecting locality, and other information related to their acquisition. The specimens can be re-examined and their taxonomy updated, if necessary. The geographic and stratigraphic descriptions of the collection locality cause far more difficulties than the original taxonomic identifications, because they can so rarely be improved.

Supporting documents do not often supply the precision that is needed to place a museum fauna into a more recently measured section. In a more likely best-case situation, the museum houses a series of faunas which are precisely stratigraphically located in an accompanying description of a different measured section. Computer algorithms can generate a composite of two or more sections, even if their individual sampled intervals cannot be manually interleaved into one section. Different problems arise where the documents describe a more restricted collection interval (a small excavation or a very short measured section), but leave the stratigraphic position lamentably loosely identified. Not all compositing algorithms can make good use of a "section" with only one collection level. In the worst instances, one locality number covers a blend of isolated material that was picked up across a wide stratigraphic interval. This creates a false impression of co-occurrences. Strong incentives to work with such

imprecisely documented parts of museum collections arise from the fact that they are numerous and may involve large and diverse faunas that include the rare taxa we wish to add to the range charts.

In order to examine the potential uses for faunas from the whole array of situations presented by museum documents, we must first distinguish geographic and stratigraphic aspects of precision. Geographic precision varies from coarse identifiers such as a county, a mountain range, or a nearby town, to precise map coordinates or marked maps and photographs. For the present purposes we consider only those museum materials that can be confidently placed within one kilometer of our measured section at the southernmost edge of the Marble Mountains.

Stratigraphic resolution entails questions of interval and position. The first question asks simply: how thick was the sampled interval? It is useful to distinguish four levels of decreasing resolution in the thickness of the sampled interval.

- a) A single bedding *surface*, interpreted with care, might provide reasonable indications of contemporaneous co-occurring individuals. Many shell pavements, however, almost certainly “time-average” (Walker and Bambach, 1971) individuals from a living community over a time interval longer than one generation. A few simple shell pavements occur within the Latham Shale. We accept their contents as evidence of co-occurring taxa, but not necessarily co-occurring individuals.
- b) A single depositional *bed*, properly interpreted, might reveal coexisting taxa for biostratigraphic purposes. For example, particular care is needed to tease apart the depositional history of shell beds (Kidwell, 1991) because they may contain significant condensation, mixing and hiatus surfaces. Turbidites exemplify short-lived deposits that can mix indigenous and transported trilobites (e.g., Babcock, 1994a,b). The Latham Shale, however, contains neither shell beds nor coarse turbidites capable of reworking fragments of trilobite large enough for olenelloid species to be identified.
- c) A measured *interval* that encompasses many beds is unlikely to be useful unless the information concerning position allows it to be associated confidently with a single sample in the measured section or positioned within a barren portion between samples.
- d) A wide collecting *area* and collections that include loose material from talus (or “float”) serve only to fill out faunal lists for whole formations and members.

The question about position asks: can the sampled interval be positioned relative to unambiguous lithostratigraphic coordinates that are recognizable

in the measured section? Consider three possibilities:

- a) Measured distances above or below a lithostratigraphic boundary may serve to place collections in stratigraphic order. But we note that some measurements made by different collectors or on different dates can be incompatible. In extreme cases, we have found reported distances above the base of a stratigraphic unit that exceed our estimates of the total thickness of that unit. Ranges of distances reported for two collections may overlap, leaving relative age unresolved.
- b) An assignment that only identifies the lithostratigraphic unit provides enough information to position the faunal list relative to those from underlying and overlying formations. The range chart for the Marble Mountains spans three lithologically distinct fossiliferous formations.
- c) A distinctive lithology may allow a museum specimen to be examined and assigned to a particular bed or member, in spite of less informative documentation. For example, the UCR collection contains *Olenellus puertoblancoensis* within a distinctive minimally fissile calcareous shale facies that is known only from one interval, low in the Chambless Limestone of the southern Marble Mountains.

Considering all of the preceding discussion, the following (italicized) categories of useful types of museum materials emerge. In the definitions, “specimens” are individual fossils. *Slab samples* present one or more rock surfaces that preserve specimens of two or more taxa on the same surface and (absent reworking) demonstrate their coexistence for biostratigraphic purposes. *Spot collections* consist of all the specimens from a single stratigraphic interval that is at least as finely resolved as those in the measured section. The necessary resolution for this category therefore varies from project to project. *Blended collections* mix all the materials from a wider interval, possibly including loose surficial “float,” and assign them all to one formation and location number. Within the blended-collections and spot-collections there may be slab-samples.

Collection series are suites of any of the previous categories that can be placed confidently in correct stratigraphic order. The best examples would be a series of spot-collections whose spacing is recorded in descriptions of a previous measured section. Some useful information may be extracted from much looser series, such as a suite of blended-collections, one from each of the successive stratigraphic formations, especially if they contain rare taxa not recovered from the measured section. For all the taxa contained in the faunal list for one unit, the sequence of first and last occurrences remains unknown. Nonetheless, a subset of taxa from the whole suite of blended-collections, one taxon for each lithostratigraphic unit, may be placed in true

stratigraphic order to build a *pseudosection* that summarizes the reliable information about sequence.

A pseudosection retains the sequence properties of a real stratigraphic section, but not the true interval spacing. The samples in a pseudosection are not necessarily from one single line of collections but they do still share geographic proximity. Where the unit thicknesses are known, it is possible to give the pseudosection some vertical scaling by placing faunas at the midpoints of their respective units -- this ploy increases the range of numerical methods that can be used to combine the pseudosections with real measured sections. Collection series that are built from the documentation of real museum holdings usually contain a mixture of spot collections and slab samples, in addition to blended collections. For them, the pseudosections gain significant detail because an ordered series of taxa or coexisting sets of taxa may be incorporated for a single stratigraphic unit.

The number of taxa in a single pseudosection is most severely limited by the constraint that it must not imply any unproven coexistences. Although each pseudosection contains few taxa relative to a real measured section, many different subsets of taxa may be extracted from one collection-series to build several pseudosections. The purpose is to combine all the rare taxa with others that are better represented in the measured sections.

With slab samples and spot collections from museums to demonstrate the coexistences and pseudosections to provide sequence information, it is possible to insert missing taxa into measured sections and to adjust the ranges of under-represented taxa. Of course, the insertion and adjustment process should apply the minimum changes necessary to bring the measured section into agreement with information gleaned from the museum collections. It should also provide rigorous quantification of the precision or confidence levels for the results. Automated numerical methods achieve these goals and allow large sets of data to be combined. Before turning to the numerical methods, however, it is worthwhile to question whether any information may be gleaned from the relative frequency of slabs that preserve different pairs of taxa. Are the most frequently encountered pairs those with the stratigraphically longest overlap between their ranges?

3.1 The Frequency Distribution of Slab-Samples

In UCR collections from the Latham Shale, some of the shale “slabs” that preserve identifiable parts of two different taxa are only a few square centimeters in area. In the field, the size of shale pieces appears to be determined primarily by depth of excavation below the weathered surface, rather than any stratigraphically distributed differences in shale lithology.

Accordingly, the frequency of different taxon pairs in slab-samples should relate to the patterns of overlap in the range chart, not variations in preservation. We compared the frequency of slab-samples in the museum collection with the range chart drawn independently from the measured section alone.

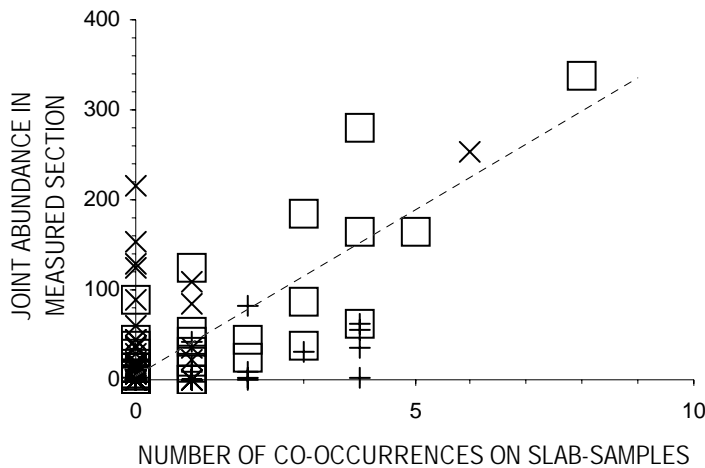


Figure 5. The frequency of coexisting taxon pairs, as proved by slab-samples from the Latham Shale in the Marble and Providence Mountains. Open squares and regression line: both localities. The regression has a correlation coefficient of 0.73. Crosses; values from the Marble Mountains only. X's: values from the Providence Mountains only.

Only one convincing empirical correlation emerges. It is the logical one between the frequency of museum slabs and the joint abundance of the two taxa at those levels in the section where both occur (Fig. 5); i.e., the product of the length of overlap of the two ranges and the average combined abundance of the two taxa at horizons in the overlap interval. Correlation coefficients are very weak between the frequency of museum slab-samples and all the simpler attributes of the range charts: the stratigraphic thickness of the interval in which the two taxon ranges overlap; the number of collection levels in the section that contain both taxa; and the abundance of the two taxa as estimated from their entire range (not just the interval of overlap). Therefore, museum slab samples alone do not provide a direct, reliable guide to the length of the overlap interval between taxon ranges. They need an independent measure of joint abundance in that interval. Spot collections would provide this measure and thereby the promise of reconstructing more of the pattern of ranges from isolated samples. Unfortunately, there are not enough spot collections in the UCR museum

holdings to permit reliable estimates of joint abundance of overlapping taxa.

Note that the relationship in Figure 5 weakens dramatically when the two Latham Shale localities are considered separately. For the Providence Mountains alone, there appear to be too few slab samples in the museum collections. For the Marble Mountains alone, there is a richer set of slab samples but, perhaps, some range lengths are underestimated in the measured sections and would benefit from augmentation by the museum collections. Which ranges should be adjusted and by how much? The most parsimonious solution would be the minimum set of range extensions necessary to satisfy all the additional coexistences demonstrated by museum slabs and observed in the Providence Mountains. Computer algorithms can find such solutions.

4. COMBINING INFORMATION

Museum collections provide two types of information that deserve to be combined with measured sections: 1) coexistences, as indicated by slab samples and spot collections; and 2) superposition, as indicated by partial sections and pseudosections reconstructed from collection-series. Two conceptually different tasks are involved: seriation and time correlation. Seriation places isolated samples into chronological order; e.g., ordering a suite of slabs. Time correlation matches levels of the same age between the parts of two or more sections or series that span the same time interval; e.g., combining the two range charts for the Latham Shale, one from the Marble Mountains and one from the Providence Mountains. Many practical problems are a combination of stratigraphic correlation and seriation in the sense that some pairs of the fragmentary sections do not overlap with one another; e.g., combining measured sections, partial sections, pseudosections, and spot collections. Pure seriation problems lack polarity -- seriation routines alone cannot determine which end of the series is younger. Adding a correlative section or pseudosection provides polarity. For both stratigraphic correlation and seriation there exist numerical methods that provide a reproducible objective basis and a means to automate the treatment of large data sets.

4.1 Seriating Isolated Slabs and Spot-Collections

Guex (1991), Guex and Davaud (1984), and Alroy (1992) have described numerical methods that seriate isolated faunas. Guex treated small data sets by manipulating the rows and columns in a coexistence matrix (Fig. 6). Because every taxon is assigned one row and one column, any pair of

taxa corresponds to two cells in the matrix that may be marked to indicate whether the two taxa coexist. Black and gray cells in Figure 6 tabulate coexistences proven by museum slab samples from the Marble Mountains. Of course, cells along the major diagonal of the matrix compare each taxon with itself; each half of the matrix on either side of this diagonal duplicates the information in the other half. For large data sets, Guex analyzed a coexistence map according to graph theory. Figure 7 illustrates the simple map that corresponds with the data in the matrix in Figure 6. For a full account of the graph theory, the reader is referred to Guex (1991). We will briefly describe his use of the coexistence matrix.

For the initial coexistence matrix, any sequence of taxa may be selected for the row labels; the columns must always be labeled in the same sequence as the rows. Subsequently the rows and columns in the matrix are rearranged so that cells which correspond to coexisting taxa become concentrated close to the diagonal of the matrix. The logic behind algorithms that can rearrange the matrix need not concern us here. It is sufficient to imagine a manual trial-and-error process. Figure 6 shows one possible solution for slab samples from the Marble Mountains. Some other arrangements are equally good. Notice, for example, that the first four row and column labels may be placed in any internal order without compromising the concentration of coexistences along the diagonal. Neither would it matter if they were moved, as a group, to the opposite end of the sequence. The slab samples tell us only that all four taxa coexist with one another and with no other taxa in the list.

Ideally, when the rearrangement is complete, no disjunct pairs (white cells in Figure 6) should remain embedded within the diagonal zone of dark cells that record coexistences. These embedded white cells are coexistences that are implied to exist but have not been observed. In analogous fashion, the ranges of two taxa may overlap when a range chart is drawn through all finds, even though the two taxa were never observed at the same level. If the slab-samples and the coexistence matrix drawn from them include no evidence of relative age or stratigraphic superposition, then the most parsimonious sequence must merely minimize the number of embedded white cells.

Once a parsimonious diagonal arrangement is achieved, each partial-row in the right-hand half of the symmetrical matrix (black cell rows in Figure 6) corresponds to a mutually coexistent set of taxa. Not every row is a biostratigraphically useful assemblage. We have already noted, for example, that the top four rows may be placed in any order and still represent the same single assemblage. Thus, the second, third, and fourth rows are merely subsets of the assemblage in the first row and do not represent “maximal

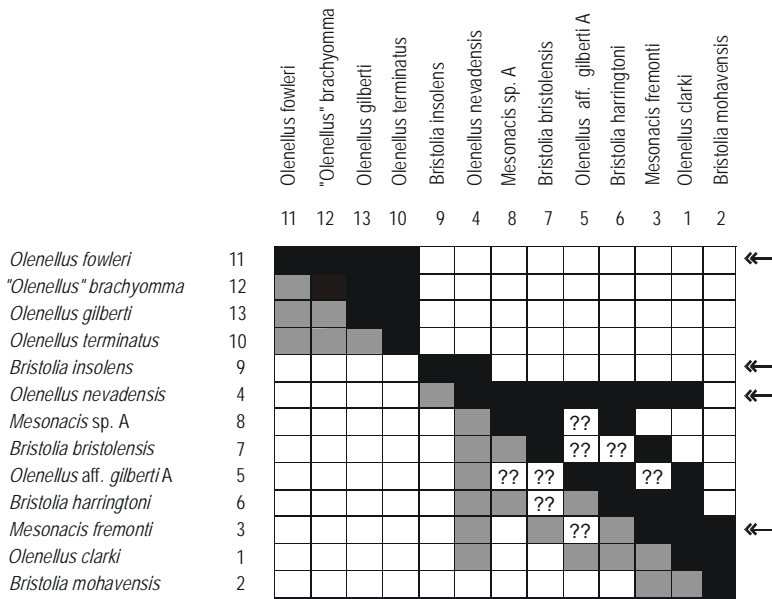


Figure 6. Coexistence matrix for olenelloid species on slab-samples and in spot-collections from the Marble Mountains in the UCR museum. Taxon numbers as in Figure 7 and Table 1. Black cells and gray cells indicate observed coexistences. The order of the rows and columns has been permuted according to the results of one 20-step reciprocal averaging run that led to the scores in Table 1. Question marks in embedded white cells indicate unsampled coexistences. Arrows locate biostratigraphically useful assemblages (“maximal unitary associations” of Guex, 1991). The gray cells lie in the redundant half of the matrix that is to be ignored when reading the assemblages by row. During the permutation process, however, cells may switch from the one half of the matrix to the other, and both cells need to be marked for each known coexistence of two different taxa.

unitary associations” (Guex, 1991). The Guex method eliminates all partial rows that contain only a subset of the coexistences in the half rows above, to leave a series of “unitary associations” that effectively provide a suite of assemblage zones in stratigraphic order.

For the Marble Mountains matrix in Figure 6, four assemblages remain: (10,11,12,13), (9,4), (4,8,7,5,6,3,1), and (3,1,2) in order from youngest to oldest. The matrix alone does not establish the polarity of the series. We chose Figure 6 rather than some other equally parsimonious arrangements by applying two additional pieces of information. The first is legitimately derived from the museum collections; museum labels indicate that taxa 10 to 13 occur in spot-collections from the Cadiz Formation whereas the coexistences for taxa 1 to 9 are established by slabs from the older Latham Shale.

Manipulation of the matrix soon shows that taxon 9 is best placed before

or after taxa 1 to 8, because the slab-samples prove only a single coexistence involving this taxon and the other eight from the Latham Shale. Similarly, taxa 9 and 2 are best placed at opposite ends of the Latham Shale group, because they share no coexistent taxa. But the museum information is inadequate to choose between the two options. Figure 6 also used the information that in measured sections taxon 9 has been found only in the upper half of the Latham Shale.

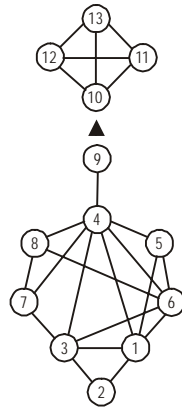


Figure 7. The matrix from Figure 6 recast as a semi-oriented coexistence graph in the sense of Guex (1991). Circled numbers at the vertices correspond to the taxa in Table 1 and Figure 6. Tie lines that connect vertices are edges that indicate observed coexistences in slab-samples and spot collections from the Marble Mountains. The arrow indicates stratigraphic superposition of four taxa from spot-collections in the Cadiz Formation (10-13) above nine taxa from slab samples in the Latham Shales (1-9). The arrow does not physically link vertices 9 and 10 because the corresponding taxa were not observed to coexist. The graph does not, therefore, indicate which taxa in the two clusters should be closest. The clusters are free to rotate relative to one another.

One semi-directional coexistence graph (Fig. 7) combines all the coexistence and superposition information from UCR's museum slabs and spot collections from the Marble Mountains. Figure 6 is one of several equally parsimonious permutations of the coexistence matrix. All include some embedded white cells that suggest unsampled coexistences. The coexistence graph in Figure 7 is more informative because it captures all the potential coexistence anomalies in one diagram. Any subset of four vertices, for example, with the property that they can be arranged into a quadrilateral that lacks diagonal connections, represents an impossible combination of coexistences for a range chart (Guex, 1991). Either the missing diagonals represent a real coexistence that has been missed (very likely in our slab-samples), or a pair of the quadrilateral edges are false coexistences, resulting from reworking or misidentification.

The quadrilateral formed by the taxa 6, 3, 8, and 7 is a good example. It is missing both diagonals. A trivial exercise confirms that no reasonable range chart can be drawn to reproduce this situation. Imagine any arbitrary range chart in which taxa 8 and 3 do not overlap with one another. Then add a range for taxon 6 that overlaps with both taxa 8 and 3; it must span the gap between them. Now it is clearly impossible to draw an uninterrupted range for taxon 7 such that it overlaps with taxa 3 and 8, but not taxon 6. Compare the matrix representation in Figure 6. Notice that the missing diagonal coexistence 6-7 corresponds to an embedded white cell. The 3-8 cell interrupts a row, but is not fully embedded in this matrix; alternative, equally parsimonious permutations do embed the 3-8 cell. Thus, Figures 6 and 7 demonstrate that the slab samples and spot collections do not represent all the real coexistences. The diagrams do not, however, indicate unambiguously which coexistences are really missing.

Guex's (1991) book provides an excellent account of the different combinations of coexistence and superposition relationships, together with the parts of graph theory used to solve large instances of the seriation problem. For the handful of slab samples in the Latham Shale, the full Guex programs are not necessary. Alroy (1992) describes a simple iterative "reciprocal-averaging" method that solves the matrix permutation part of the problem numerically. Alroy's formulae are easily implemented on a spreadsheet. They generate numerical scores for each row that range from one to zero. After enough iterations, the scores converge on stable values that indicate a parsimonious order for the rows and columns of taxa.

Table 1 presents a typical set of results of reciprocal averaging that emerge, after 20 iterations, for the museum collections from the Latham Shale and the Cadiz Formation. The scores stabilize to four or more decimal places, but tend to converge on only two values; in the particular run summarized in Table 1, these values are exactly 0.0 for all the Cadiz taxa and approach 1.0 for the Latham taxa. Some runs stabilize with the scores for the Cadiz taxa at 1.0, because no polarity information is included. Because the calculations are very fast, it was a simple matter to wait for a solution that honored the polarity information used in Figures 6 and 7.

The tabulated scores for the Cadiz taxa indicate no preferred order, as is fitting for taxa all found in the same spot-collections. The numerical differences between the Latham taxa are vanishingly small and vary from run to run. No confident sequencing of these events is possible, except to note that *Bristolia mohavensis* and *B. insolens* likely appear towards the opposite ends of the sequence of Latham Shale taxa. As already noted, no evidence of the correct polarity within the Latham sequence has been found in the museum collections.

Table 1. One set of the typical results after 20 iterations of reciprocal averaging scores for olenelloid taxa in slab samples from the Marble Mountains (taxa numbered as in Figs. 6, 7)

TAXON NAME	TAXON NUMBER	RESCALED RECIPROCAL AVERAGE SCORE
<i>Olenellus fowleri</i>	11	0.00000
" <i>Olenellus</i> " <i>brachyomma</i>	12	0.00000
<i>Olenellus gilberti</i>	13	0.00000
<i>Olenellus terminatus</i>	10	0.00000
<i>Bristolia insolens</i>	9	0.99993
<i>Olenellus nevadensis</i>	4	0.99997
<i>Mesonacis</i> sp. A	8	0.99997
<i>Bristolia bristolensis</i>	7	0.99997
<i>Olenellus</i> aff. <i>gilberti</i> A	5	0.99998
<i>Bristolia harringtoni</i>	6	0.99998
<i>Mesonacis fremonti</i>	3	0.99998
<i>Olenellus clarki</i>	1	0.99999
<i>Bristolia mohavensis</i>	2	1.00000

Alroy (1992) does not extract assemblage zones from the optimized coexistence matrix. Where longer time spans and greater faunal diversity lead to numerical scores that are better differentiated than in our rather trivial example, he proceeds to use the individual taxon scores to rank the real faunal lists and from them generate range charts which predict the sequence of first and last occurrences. In other data sets, therefore, the process may have considerable potential for generating pseudosections from isolated spot-collections.

Unfortunately, reciprocal averaging achieves little more for the museum collections in the Marble Mountains problem than to confirm the formation-level faunal lists and indicate that the slab samples fail to capture all the coexistences. It does not enable us to build detailed pseudosections. Two factors that frustrate our attempt might not arise in other instances: 1) the separations of olenelloid first and last events are small compared with the lengths of the taxon ranges; and 2) there are too few spot collections that might provide more complete lists of conjunct ranges and constrain the number of range charts that can be built from a parsimonious co-occurrence matrix. Notice that the Marble Mountains reveal a general potential weakness of this use of slab samples and seriation; the Cadiz and Latham taxa are preserved in different sedimentary facies. If a section exposes an alternation of two facies that preserve different taxa, then there will be pairs of taxa, one from each facies, which cannot be found on slab samples whether or not their ranges overlap.

We could eliminate these frustrations by incorporating all the spot collections from the trenches. But reliance upon coexistence is then very conservative. Both the Guex (1991) and Alroy (1992) approaches to seriation would tend to waste some of the precise information about

sequence that is contained in the measured section. This information is better exploited by numerical *correlation* methods that can incorporate the isolated samples together with measured sections.

4.2 Correlating Museum Collections and Pseudosections

Correlation uses locally observed sequences of first and last appearance events as the primary information. The individual local sequences are provided by different stratigraphic sections. It is usually evident that they cannot all be entirely reliable indicators of the global sequence of events because they contradict one another in detail concerning the sequence of some of the first and last appearances. Good correlation algorithms resolve the contradictions to generate a more reliable composite sequence. They vary in their choice of models and assumptions. The RASC program (Agterberg and Gradstein, 1996), for example, assumes that errors in the stratigraphic position of observed events are normally distributed. Accordingly, its algorithms search for the most commonly preserved sequences of events. By contrast, graphic correlation (Shaw, 1964) assumes that reworking and caving problems can be identified in advance, leaving the true ranges systematically underestimated by observed ranges. Accordingly, its algorithms seek the earliest of the first events and the latest of the last events. For our macrofossil ranges, the assumptions of graphic correlation are preferable because reworking is highly unlikely. The observed taxon ranges will not overestimate true ranges unless fossils are misidentified.

Contradictory indications of the sequence of first and last appearance events are resolved by constrained optimization algorithms in the CONOP9 program (Kemple *et al.*, 1989, 1995; Sadler and Kemple, 1995; Sadler, 2000; Sadler and Cooper, this volume). The constraints require that any feasible sequence must contain all the observed overlaps between taxon ranges. Thus, this program has the advantage that it can seamlessly incorporate slab samples which are, in effect, one-level stratigraphic sections that record co-occurrences but do not reveal sequence. The optimal feasible sequence is one to which all the locally observed sequences can be fit with the minimum net extension of observed ranges. Kemple *et al.* (1995) explain in detail how the algorithms find an optimal sequence. The result is a parsimonious interpretation of the fossil record in the sense that it minimizes the failings in the collection process implied by the ad-hoc adjustments of observed ranges. The range extensions may be measured in different ways; the choice influences the outcome and should be based upon the nature of the stratigraphic sections. For the Marble Mountains problem, there are no lateral variations in lithology and the range extensions may safely be measured in rock thicknesses. When correlating sections from

contrasting facies it would be better to measure range extensions by the number of fossiliferous horizons or range-ends that must be crossed; this favors the sequences preserved in the more fossiliferous or intensely sampled sections.

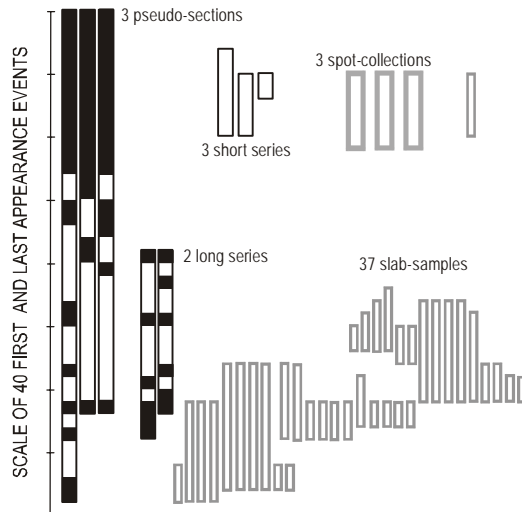


Figure 8. Seriation/correlation of slab-samples, spot-collections, pseudosections and collection series from the UCR museum holdings for the Latham Shale in the Marble Mountains. The vertical scale is derived from the optimal ordinal arrangement of all the included first and last occurrence events. Further explanation in the text.

Figure 8 summarizes how constrained optimization has fit all the UCR museum information from the Marble Mountains to a single ordinal time scale, with one unit for each first and last appearance in the data set. The ordinal scale is derived from pseudosections and collection series, with adjustments to ensure that it honors all additional co-occurrences preserved on the slabs. For pseudosections and long collection series with more than three levels, the rectangles in Figure 8 indicate the minimum span of contained events. Each solid black interval indicates a first or last appearance event that is observed in the series and not extended beyond the ends of the section by the constrained optimization. Blank intervals indicate that the series is lacking an intervening event that is known from other samples in the set. Shorter series have, at most, one collection level that is not terminal, so it is likely that all adjusted ranges will be extended to the limits of the series, leaving no black intervals. For spot collections and slab samples, the gray rectangles in Figure 8 indicate the maximum span of possible positions in the sequence that the fauna may occupy. The length of the gray rectangles varies with the length of the overlap between the ranges

of the preserved taxa, as implied by the optimal sequence.

CONOP9 can be made to optimize a set of slab samples and spot collections alone; simply set the optimization to find a sequence of events that minimizes the number of implied coexistences that have not been observed. Inclusion of the three pseudosections and the five collection series provides polarity for the optimization. Without them, the seriation of the slab-samples would provide many more equally well-fit solutions. Of course, the vertical scale in Figure 8 contains sufficient information to construct a range chart. Rather than pausing now to examine the order of events in this intermediate sequence derived from the museum collections alone, let us move on to add these results into the measured section and then construct the corresponding range chart.

4.3 Compositing Museum Collections and Measured Sections

Figure 9 displays the results of using CONOP9 to incorporate the museum collections into the measured section from the Marble Mountains. It uses the scale of stratigraphic thickness from the trenches. The extended ranges honor the additional proven coexistences. Several missing taxa have been inserted according to their coexistences and their position in pseudosections or collection series. Distinctive rock matrix on one museum specimen allowed *Olenellus puertoblancoensis* to be placed in a narrow interval in the Chambless Limestone. This was achieved by including an inferred co-occurrence with *Bristolia* aff. *fragilis* C and *O. terminatus*, recovered from that interval in the measured section.

The range for *Olenellus* aff. *gilberti* A serves as an informative example for the entire optimization. Slab samples prove that the taxon coexists with *O. clarki*, *O. nevadensis*, and *Bristolia harringtoni*. Therefore, the algorithm inserted a short range that satisfies these three overlaps. Because *O.* aff. *gilberti* A is known only as a single questionable specimen in the trenches at the Marble Mountains it does not appear in the original range chart (Fig. 2). But the questionable specimen was found very close to the insertion level; therefore, Figure 9 was amended to show a find and a very short extension. The range of *B. insolens* was extended downward in order to fit with all the known coexistences at this level. These particular ranges change again with the inclusion of evidence from the Providence Mountains.

Figure 10 redraws taxon ranges in the Latham Shale after further adjustment by CONOP9 to accommodate the additional information in the measured section and museum specimens from the Providence Mountains. Notice, for example, that the last appearance of *Olenellus clarki* is extended

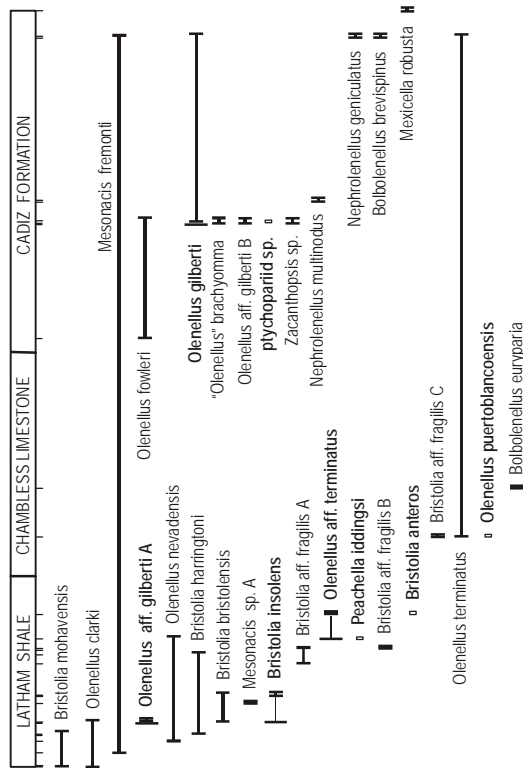


Figure 9. Range chart for the measured section in the Marble Mountains, after compositing with museum collections for the same locality. Vertical lines with short terminal bars = observed ranges. Bold taxon names indicate improvements to measured section. Vertical lines with long terminal bars = range extensions. Open rectangles = insertion of missing species.

significantly higher because, as previously noted, the large sample sizes in the Providence Mountains have captured late appearances of the taxon where its abundance is presumably low enough to be missed in the trench samples.

The adjusted position of the last appearance of *Olenellus clarki* is not determined directly by the stratigraphic thickness of its range in the Providence Mountains, or by reference to the lithostratigraphic boundaries that occur in both measured sections. Biostratigraphic evidence drives the constrained optimization and the algorithm extends the range to honor those additional coexistences that are known from the Providence Mountains. Furthermore, the algorithm extended the range of *O. clarki* upward instead of using the less parsimonious alternative that would have extended the ranges of several coexisting taxa downward. The alternative would have required a greater net adjustment to the range chart. Thus, the treatment of

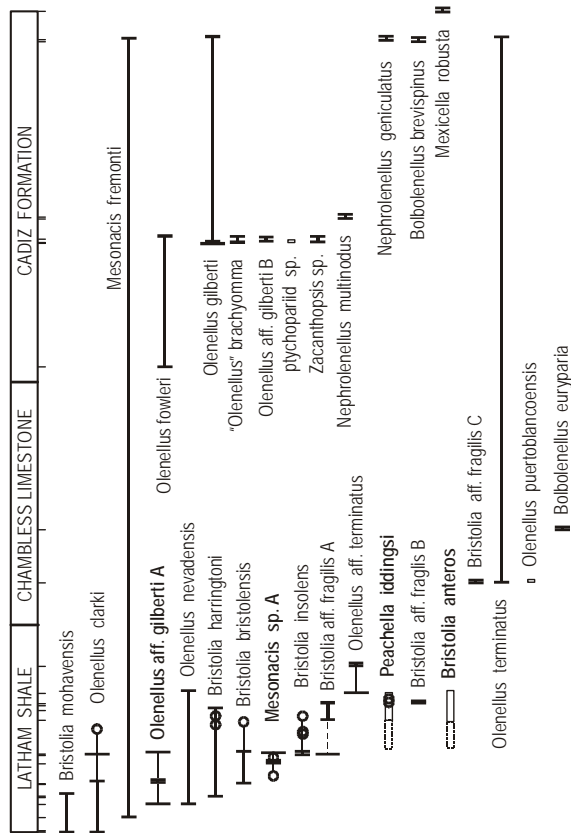


Figure 10. Range chart for the measured section in the Marble Mountains, after compositing with the section from the Providence Mountains and museum collections from both locations. Boldface indicates taxon ranges improved relative to Figure 9. Vertical lines with short terminal bars (that merge for short ranges): ranges based on information from the Marble Mountains. Lighter lines and longer terminal bars; range extensions fit by CONOP9. Open rectangles: taxon ranges inserted by CONOP9, dashed where shrunk by later finds (see postscript). Open circles; critical finds from most recent trenches in the Marble Mountains (see postscript).

this one range end illustrates both constraint (honors observed coexistences) and optimization (minimizes the required adjustments).

Notice also that the ranges do not simply lengthen from Figure 9 to Figure 10; some shorten. Even a single item of significant new information can change multiple components of the previously most parsimonious set of adjustments. For example, the upward extension of *O. clarki* and *O. aff. gilberti* A allows the previous downward extension of *Bristolia insolens* to be retracted; it now satisfies all proven coexistences without any extensions on the observed range. This is just one of the many interactions between the different sources of information that are best handled automatically rather

than juggled mentally. Besides guaranteeing to consider an immense number of possible arrangements, the benefits of automation include speed and reproducibility.

Figure 10 completes the process of combining all the information contained in specimens for which we have checked the taxonomic assignments. It might be improved by further trenching (see postscript), or recourse to more localities and museums. The next closest Lower Cambrian sections that we have measured reveal different sedimentary facies. Range charts for these sections need to be augmented separately with corresponding museum collections and then compared with the Latham Shale in order to reveal possible facies constraints on the paleogeographic distribution of taxa. There are other smaller, but relevant, museum collections, at the Los Angeles County Museum for example. It is an advantage of the automated compositing process that the range charts may be re-optimized and updated in a matter of minutes once the taxonomy of these other collections has been checked.

5. CONCLUSIONS

Composite sections that combine information from museum collections with range charts from measured sections yield encouraging improvements in resolving power. The composite sections can take advantage of decades of previous collecting without placing very exacting demands on museum documentation of the stratigraphic position of collecting sites. Our case history indicates that this extra effort can be worthwhile even for measured sections in which macrofossils have been collected with unusual thoroughness.

Even though the trilobite collecting associated with our two measured sections for the Latham Shale surely ranks among the most thorough for Lower Cambrian sections in the southwestern United States, the inadequacies of the individual sections are quite evident. Effort devoted to continuous sampling reduced the recovery of rare taxa at some levels. Apportioning more time for processing large volumes of rock at discrete sampling levels improves the recovery of rare taxa, but the reduced number of sampled intervals compromises the resolution of range ends for more abundant taxa.

It is obviously worthwhile to supplement continuous sampling by processing larger volumes of rock from the more richly fossiliferous intervals. Effective supplementary sampling, which recovers rare taxa and increases the number of proven co-occurrences, can be achieved by incorporating information from museum collections. Increasing the number

of known coexistences improves the results of correlation by constrained optimization. Although the optimization operates primarily on the observed sequences of first and last occurrence events, observed coexistences constrain the number of feasible sequences. Thus, observed ranges may be extended to accommodate additional coexistences.

Slab samples and spot collections that prove co-occurrences are the most reliable and readily exploitable of the isolated collections held in museums. Slab samples must be individually sought out to establish that a single piece of rock bears more than one taxon, but they place almost no demands on the stratigraphic precision of the museum locality records – geographic position may suffice. For spot collections, the locality records must confirm that all listed taxa were recovered from a narrow stratigraphic interval. Spot collections and single taxa from coarsely blended collections (one from each successive lithostratigraphic formation), may be combined into pseudosections. Thus, rare taxa that were not found in a measured section may be provided with sufficient coexistence and sequence information that a computer algorithm can insert them reliably into the composite section.

The notion of incorporating museum finds into range charts is not new. The keys to our successful compositing of these different types of data are two attributes of the computer algorithms. First, they can optimize large volumes of information with inter-relationships that are too complex for mental arithmetic (Sadler and Cooper, this volume); with their assistance it is feasible to add numerous separate items of information from museum collections. Second, the algorithms place stratigraphic correlation and seriation on an objective, reproducible basis; their rules for the compositing process are explicit and their results are reproducible and quantified. Comparable computer-assisted methods are already routine for related paleobiological tasks. The stratigraphic correlation and seriation algorithms in CONOP9 apply the rules of parsimony in a manner analogous to automated searches for most parsimonious cladograms. (Copies of the programs and sample data sets are available from P.M.S. on request.)

6. POSTSCRIPT

This chapter illustrated its methods using the current results of an ongoing investigation. While the manuscript was in review, we intensified the search for fossils in the upper portion of the Latham Shale in the Marble Mountains where the composite section indicates that additional taxa should be present. Targeting the level in existing trenches where *Peachella iddingsi* was predicted, we eventually found one individual of this taxon. A new set of trenches through the upper Latham Shale, opened 100 m away along

strike, revealed many richly fossiliferous horizons (LaGrange, 2002). The stark contrast with the earlier, less fossiliferous trench at this level reveals a small-scale patchiness in the distribution of trilobites within these shales. The new trenching confirms several predictions of the compositing exercise and adds new features to the range chart. Critical new finds are indicated by circles in Figure 10. Two fossiliferous levels, 1 m apart, establish the expected short range for *P. iddingsi* high in the Latham Shale. Finds of *Mesonacis* sp. A confirm the upward range extension indicated for that species.

Two rare occurrences of *Olenellus clarki* in the new trenches vindicate the upward range extension suggested by the composite section. The observed range now extends considerably beyond the abundant interval previously established lower in the formation (and beyond the range extension in the composite section). The range of *Bristolia bristolensis* is similarly extended upward by new finds. Sparse occurrences high in the range of these two olenelloids invalidate the short confidence intervals calculated for the previously-known ranges (Fig. 2) but match the pattern of finds of *O. clarki* in the Providence Mountains (Fig. 3).

Five new finds of *B. insolens* within an interval of 4 m extend the earlier solitary find from the Marble Mountains trenches into a range slightly longer than that in the Providence Mountains. New finds of *B. harringtoni* confirm the earlier observation that there are late occurrences of the species in the Marble Mountains significantly above the top of the range established in the Providence Mountains. The new trench adds five finds in an interval of approximately 1 m at a level where a single late occurrence previously established the top of the range. The new trench provides no mid-range finds, however, thus introducing the possibility that *B. harringtoni* is a Lazarus taxon with two disjunct ranges.

Even before *Bristolia anteros* was found in the new trenches, the other new finds permitted the projected positions of *B. anteros* to be more narrowly constrained. The observation of younger occurrences of *O. clarki* and *B. bristolensis* changes the impact of the known coexistences, allowing the lower half of the projected range of positions for *B. anteros* to be eliminated (dashed rectangle in Figure 10). After it was too late to redraw figure 10, specimens of *B. anteros* were recovered from the predicted interval (LaGrange, 2002). The previously suggested range extension for *B. aff. fragilis* A may also be removed. The ranges of *O. clarki* and *B. bristolensis* in the Marble Mountains had appeared to be reliable, because they were established on numerous closely-spaced finds with coexistences comparable to those in the Providence Mountains. The new finds indicate that these ranges should have been given more freedom to adjust during the compositing process.

The lesson from this postscript will be familiar to many: the goal of finishing a range chart is unreachable. Additional collecting may eliminate some gaps and discrepancies. But the same extra effort reveals new features in existing ranges and uncovers rarer taxa whose ranges remain poorly established, thus, inviting more collecting expeditions and repeating the cycle. Our own additions to the museum materials confirm that the augmented range chart from the Marble Mountains is still not exhaustive. Although specimens collected from talus in the Latham Shale include *Anomalocaris*, the genus has not yet been recovered *in situ* from any of our trenches.

ACKNOWLEDGEMENTS

This project is partially funded by NSF grant EAR-9980372 to P.M.S. Leslie Knox (now Mrs. Webster), Jennifer LaGrange, Jennifer Jones, Brenda Hunda, Sinnie Chen, Min-Hyoung Kim, and Jason Odell assisted in the collection of fossils from the trenches. Pete Palmer and Fred Sundberg identified Middle Cambrian trilobite material for us. Linda and Mike McCollum shared their measured sections and fossil locality information. Christian Gronau sent pictures of his collections from the Chambless Limestone. Art and Rosemond Riggle generously donated their trilobite collections from the Latham Shale in the Marble Mountains. Loren Babcock, Tim White, and Peter Harries helped us tighten the manuscript in many critical places.

REFERENCES

- Agterberg, F. P., and Gradstein, F. M., 1996, *RASC and CASC: Biostratigraphic Zonation and Correlation Software, version 15*.
- Alroy, J., 1992, Conjunction among taxonomic distributions and the Miocene mammalian biochronology of the Great Plains, *Paleobio*. **18**:326-343.
- Babcock, L. E., 1994a, Systematics and phylogenetics of polymeroid trilobites from the Henson Gletscher and Kap Stanton Formations (Middle Cambrian), North Greenland, *Grøn. Geol. Under. Bull.* **169**:79-127.
- Babcock, L. E., 1994b, Biogeography and biofacies patterns of Middle Cambrian polymeroid trilobites from North Greenland: Palaeogeographic and palaeo-oceanographic implications, *Grøn. Geol. Under. Bull.* **169**:129-147.
- Clark, C. W., 1921, Lower and middle Cambrian formations of the Mohave Desert, *Univ. Calif. Pub. Geol. Sci. Bull.* **13**:1-7.
- Crickmay, C. H., 1933, Paleontology, in: Hazzard, J. C., Note on the Cambrian rocks of the eastern Mohave Desert, California, with a paleontology report by Colin H. Crickmay, *Calif. Pub. Geol. Sci. Bull.* **23**:71-80.
- Darton, N. H., 1907, Discovery of Cambrian rocks in southeastern California, *J. Geol.*

15:470-475.

- Guex, J., 1991, *Biochronological Correlations*, Springer Verlag, Berlin.
- Guex, J., and Davaud, E., 1984, Unitary associations method: Use of graph theory and computer algorithms, *Comp. Geosci.* **10**:69-96.
- Hazzard, J. C., 1933, Note on the Cambrian rocks of the eastern Mohave Desert Mohave Desert, California, with a paleontological report by Colin H. Crickmay, *Calif. Pub. Geol. Sci. Bull.* **23**:57-80.
- Hazzard, J. C., 1937, Paleozoic section in the Nopah and Resting Springs Mountains, Inyo County, California, *Calif. J. Mines Geol.* **33**:273-339
- Hazzard, J. C., 1954, Rocks and structure of the northern Providence Mountains, San Bernardino County, California, *Calif. Div. Mines Bull.*, **170**:27-35.
- Hazzard, J. C., and Mason, J. F., 1936, Middle Cambrian formations of the Providence and Marble Mountains, California, *Geol. Soc. Am. Bull.* **47**:229-240.
- Kemple, W. G., Sadler, P. M., and Strauss, D. J., 1989, A prototype constrained optimization solution to the time correlation problem, *Geol. Surv. Can. Pap.* **89-9**:417-425.
- Kemple, W. G., Sadler, P. M., and Strauss, D. J., 1995, Extending graphic correlation to N dimensions: The stratigraphic correlation problem as constrained optimization, in: *Graphic Correlation* (K. O. Mann and H. R. Lane., eds.), *SEPM Sp. Pap.* **53**:65-82.
- Kidwell, S. M., 1991, The stratigraphy of shell concentrations, in: *Taphonomy; Releasing Data Locked in the Fossil Record* (P. A. Allison and D. E. G. Briggs, eds.), Plenum Press, New York, pp. 211-290.
- LaGrange, J. E., 2002, Biostratigraphy of Olenelloid Trilobites from the Lower Cambrian of the Southeastern Marble Mountains: Pushing the Limits of the Resolution of the Fossil Record, unpublished senior thesis, University of California, Riverside, Geology Museum, 44 p., 5 appendices.
- Marshall, C. R., 1990, Confidence intervals upon stratigraphic ranges, *Paleobio.* **16**:1-10.
- Marshall, C. R., 1994, Confidence intervals on stratigraphic ranges: Partial relaxation of the assumption of randomly distributed fossil horizons, *Paleobio* **20**:459-469.
- Mason, J. F., 1935, Fauna of the Cambrian Cadiz Formation, Marble Mountains, California, *S. Calif. Acad. Sci. Bull.* **34**:97-119.
- Mount, J. D., 1974, Early Cambrian faunas from the Marble and Providence Mountains, San Bernardino County, California, *Bull. S. Calif. Paleont. Soc.* **6**:1-5.
- Mount, J. D., 1976, Early Cambrian faunas from Eastern San Bernardino County, California, *Bull. S. Calif. Paleont. Soc.* **8**:173-182.
- Nolan, T. B., 1929, Notes on the stratigraphy and structure of the northwest portion of Spring Mountain, Nevada, *Am. J. Sci.* **17**:461-472.
- Paul, C. R. C., 1982, The adequacy of the fossil record, in: *Problems of Phylogenetic Reconstruction* (K. A. Joysey and A. E. Friday eds.), *System. Assoc. Sp. Vol.* **21**:75-117.
- Resser, C. E., 1928, Cambrian fossils from the Mohave Desert, *Smith. Misc. Coll.* **81**:1-14.
- Riccio, J. F., 1952, The lower Cambrian Olenellidae of the southern Marble Mountains, *S. Calif. Acad. Sci. Bull.* **51**:25-49.
- Sadler, P. M., 2000, *Constrained Optimization Approaches to the Paleobiologic Correlation and Seriation Problems: A Users' Guide and Reference Manual to the CONOP Program Family, Version 6.5*, University of California, Riverside.
- Sadler, P. M., and Cooper, R. A., this volume, Best-fit intervals and consensus sequences; comparison of the resolving power of traditional biostratigraphy and computer-assisted correlation.
- Sadler P. M., and Kemple, W. G., 1995, Using rapid, multidimensional, graphic correlation to evaluate chronostratigraphic models for the Mid-Ordovician of the Mohawk Valley, New York, in: *Ordovician Odyssey: Short Papers for the Seventh International Symposium on*

the Ordovician System (J. D. Cooper, M. L. Droser and S. C. Finney, eds.), *SEPM Pac. Sec. Book 77*:257-260.

Shaw, A. B., 1964, *Time in Stratigraphy*, McGraw-Hill, New York.

Strauss, D., and Sadler, P. M., 1989, Classical confidence intervals and Bayesian probability estimates for ends of local taxon ranges, *Math. Geol.* **21**:411- 427.

Walker, K. R., and Bambach, R. K., 1971, The significance of fossil assemblages from fine-grained sediments: Time-averaged communities, *Geol. Soc. Am. Abstr. Prog.* **3**:783-784.