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VERTEBRATE MICROSITE SAMPLING: HOW MUCH IS ENOUGH?

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ABSTRACT—Data from vertebrate microsites are important in paleoecological reconstructions, but their usefulness has been limited because of undemonstrated repeatability of sampling data and the time- and labor-intensive nature of their retrieval. Re-examination of a previously studied vertebrate microsite revealed that repeatable diversity and abundance data are obtainable using a controlled sorting methodology. It was found that a curve fitted to a plot of empirical diversity vs. sampling frequency will tend toward an asymptote as sampling frequency increases, indicating that the likelihood of discovery of new taxa having a major impact upon a paleoecological interpretation is diminishing. Rarefaction analysis was applied to the data obtained, and the rarefaction curve provided support for the behavior of the empirical diversity curve. It was also found that as sampling frequency increases, rank orders of relative abundance stabilize among the most common taxa in the sample, indicating that the likelihood of discovery of highly abundant taxa is diminishing. Adequate sampling of a vertebrate microsite can thus be achieved by dividing the original field sample into many small subsamples, and additively plotting diversity and relative abundance data. Once the diversity curve begins to tend toward an asymptote, and the abundance ranks among the most common taxa have stabilized, it is necessary to continue sampling only until double this number of subsamples has been analyzed in order to confirm the established patterns. Proceeding in this fashion will verify that ostensible exhaustion of the taxa present has been achieved. Standardization of sampling methodology will allow similarly compiled data to be compared, both from a single site and among multiple sites, improving the reliability of palaeoecological interpretations generated from vertebrate microsites.

INTRODUCTION

The reconstruction and understanding of ecological communities is an onerous task, and paleocommunities are no exception. Vertebrate microsites, as exemplars of thanatocoenoses, offer unique challenges to those attempting to glean information from them. Vertebrate microsites are accumulations of small, well-sorted remains of a large variety of taxa, dominated by teeth, dermal bone fragments, and scales (Wood et al., 1988). Microsite material in fluvial deposits accumulates as the result of channel lag deposits, point-bar accumulations, and vertically aggrading channel floor deposits (Koster et al., 1987). Taphonomy and other physical processes may influence the composition of a microsite during the transition of its components to the thanatocoenosis, and loss and breakage during collection along with the sorting methodology employed may also alter the results (Badgley, 1986). Similarly, the size of the sample analyzed will directly influence the amount of time and labor required to reach a conclusion and may also affect the nature of the reconstruction (Brinkman, 1990). Despite this, some of the most important sources of paleoecological data for vertebrate faunas are those derived from microsites. Several influential and valuable microsite analyses have been conducted, beginning with those of Shotwell (1955, 1958) and continuing to the present (e.g., Behrensmeyer, 1979; Dodson, 1987; Brinkman, 1990; Eberth and Brinkman, 1997). The relative usefulness and validity of microsite data have been called into question, however, due to the complex nature of these assemblages (Estes and Berberian, 1970; Blob and Fiorillo, 1996).

The study of vertebrate microsites can be likened to the study of extant ecological communities. In ecology, quadrat sampling is used to obtain an accurate estimate of species diversity and abundance. In this procedure, areas of known size are sampled to exhaustion, an average is taken, and these data are then used to estimate the population of the larger area under study (Krebs, 1985). Quadrat sampling is used extensively for communities whose members do not change position, such as extant plant communities. Microsite communities can be compared to extant plant communities, in that specimens are not constantly moving as in an extant animal community. The sampling of vertebrate microsites involves the observation of a fraction of the total community, and an estimation of species richness can be derived from this. Analyses of vertebrate microsites can be problematic when statements regarding the community they represent are made. In particular, a lack of standardized sampling methodology across various sites makes comparison among sites difficult, and the results of these types of analyses questionable.

Rarefaction is a statistical technique, also widely employed in ecology, that estimates the number of species one would expect to see represented in a random sample of individuals from a community; i.e., if a subsample n of a group of N individuals belonging to S species ($n < N$) was examined, how many species s ($s < S$) would be observed (Krebs, 1989)? Application of this methodology allows communities with different sample sizes to be compared, by standardizing all samples to a common size. The use of rarefaction requires that the communities under study meet several criteria, specifically that: (1) the subsamples in question are representative of the larger community; (2) individuals are homogeneously distributed within the community; (3) replicate samples can be shown to belong to the same community; (4) the communities under study are taxonomically similar; (5) standardized sampling procedures have been used; (6) the species under study come from similar habitats (Tipper, 1979). Rarefaction has been used in paleoecological analyses of invertebrate communities with some success (e.g., Stanton and Evans, 1972; Raup, 1975; Foote, 1992), and based upon the above requirements, it can be shown that vertebrate microsites lend themselves well to analysis using this technique. Microsites are generally considered to be representative of the communities from which they come (Brinkman, 1990). Microsites can also be considered to be taxonomically

TABLE 1. Summary of subsample study of Bonebed 105, Dinosaur Provincial Park, Alberta.

Taxon	Number of Specimens	Relative Abundance Rank	Mass (g)	Percent Composition by Number of Specimens
Salamander	197	1	1.71	29.62
Hadrosaur	145	2	8.23	21.80
Teleost	94	3	1.03	14.14
Holostean A	52	4	0.23	7.82
Gar	34	5	0.91	5.11
Frog	34	5	0.26	5.11
Coriops	17	7	0.14	2.56
Crocodile	12	8	0.84	1.80
Large theropod	10	9	0.82	1.50
Champsosaur	10	9	3.43	1.50
Mammal	9	11	0.28	1.35
Lizard	7	12	0.07	1.05
Small theropod	6	13	0.13	0.90
Eggshell	6	13	0.15	0.90
Troodon	5	15	0.27	0.75
Trionychid	5	15	5.14	0.75
Multituberculate	4	17	0.02	0.60
Chelydrid	4	17	2.25	0.60
Pachycephalosaur	3	19	0.02	0.45
Albanerpeton	3	19	0.005	0.45
Paralbula	2	21	0.003	0.30
Teiid	1	22	0.004	0.15
Saurornitholestes	1	22	0.12	0.15
Phyllodont	1	22	0.002	0.15
Myledaphus	1	22	0.01	0.15
Esocoid	1	22	0.001	0.15
Amia	1	22	0.01	0.15
Total	665	—	26.085	99.96

similar and ecologically homogeneous at the level at which they are examined, given that they are highly diverse collections of vertebrate taxa (Brinkman, 1990). Finally, as will be discussed below, sampling methodology can be standardized for the analysis of vertebrate microfossil localities.

Rarefaction analyses show that as sampling continues, the curve generated by plotting taxonomic diversity (*s*) vs. total number of individuals sampled (*n*) tends toward an asymptote, at which point completeness of sampling can be assumed to have been achieved. The goals of the present study were thus both to establish the potential for repeatability and reliability of diversity and abundance data obtained from microsite analysis, and to establish a methodology by which minimum sample size may be determined. Rarefaction analysis is applied to real microsite data as a model in the present study, in order to show that this tendency toward an asymptote exists when sampling a real community. The establishment of a methodology employing a minimum sample size will allow a reduced amount of material to be removed from the field and studied, while ensuring that the data obtained remain representative of the paleocommunity under investigation. In short, this will allow a determination of ''how much is enough'' with a minimum investment of time and labor. Further, the employment of a standardized methodology will allow comparisons to be made between samples taken from different localities and collected and analyzed by different workers.

METHODS

The sample under analysis was taken from Bonebed 105 (UTM coordinates 12; 464000; 5622500), in the Upper Cretaceous (Campanian) Oldman Formation of the Judith River Group of Dinosaur Provincial Park (DPP), Alberta, Canada. The region from which the sample comes is an estuarine channel-floor and channel-thalweg deposit from a slow-moving, meandering freshwater stream or river (Eberth, 1990). Bonebed 105 has been the subject of a previous study (Brinkman, 1990).

The present investigation was carried out in two phases. Thirty-three and one-half kilograms of sediment excavated from Bonebed 105 were subjected to underwater screenwashing through both coarse (1,110 μm) and fine (850 μm) screens. The remaining concentrated matrix was then divided into coarse aliquots weighing approximately 3 kg and fine aliquots weighing approximately 350 g. The first set of aliquots (one coarse and one fine) was divided into 61 equivalent subsamples, each with a coarse component weighing approximately 50 g and a fine component weighing 5.8 g. Each coarse component was manually sorted under a dissecting microscope to remove elements deemed uninformative, including large clay particles, ironstones, gastropod shell fragments, wood, and other debris. The weight of the initial discard was recorded for each subsample. Subsequently, the coarse component of each subsample was sorted a second time under a dissecting microscope. Any elements determined to be of vertebrate origin were placed into a vial for later examination. The weight of material retained from the coarse component was recorded for each subsample. The fine component of each subsample was sorted once, under a dissecting microscope, and vertebrate elements were placed into a vial and weighed in the same fashion. Coarse and fine elements were kept separate throughout this stage of the procedure.

Upon completion of manual sorting, the nature of the vertebrate material contained in each subsample was determined by comparison of each element with a set of representative specimens belonging to a wide range of expected taxa based on a previous study of this locality (Brinkman, 1990). Coarse and fine components continued to be kept separate. The number of elements belonging to each taxon, along with the number of taxa present, were recorded for the coarse and fine component of each subsample separately, as well as for the subsample as a whole. Diversity and both relative and absolute abundance were determined.

The number of taxa retrieved was additively plotted against

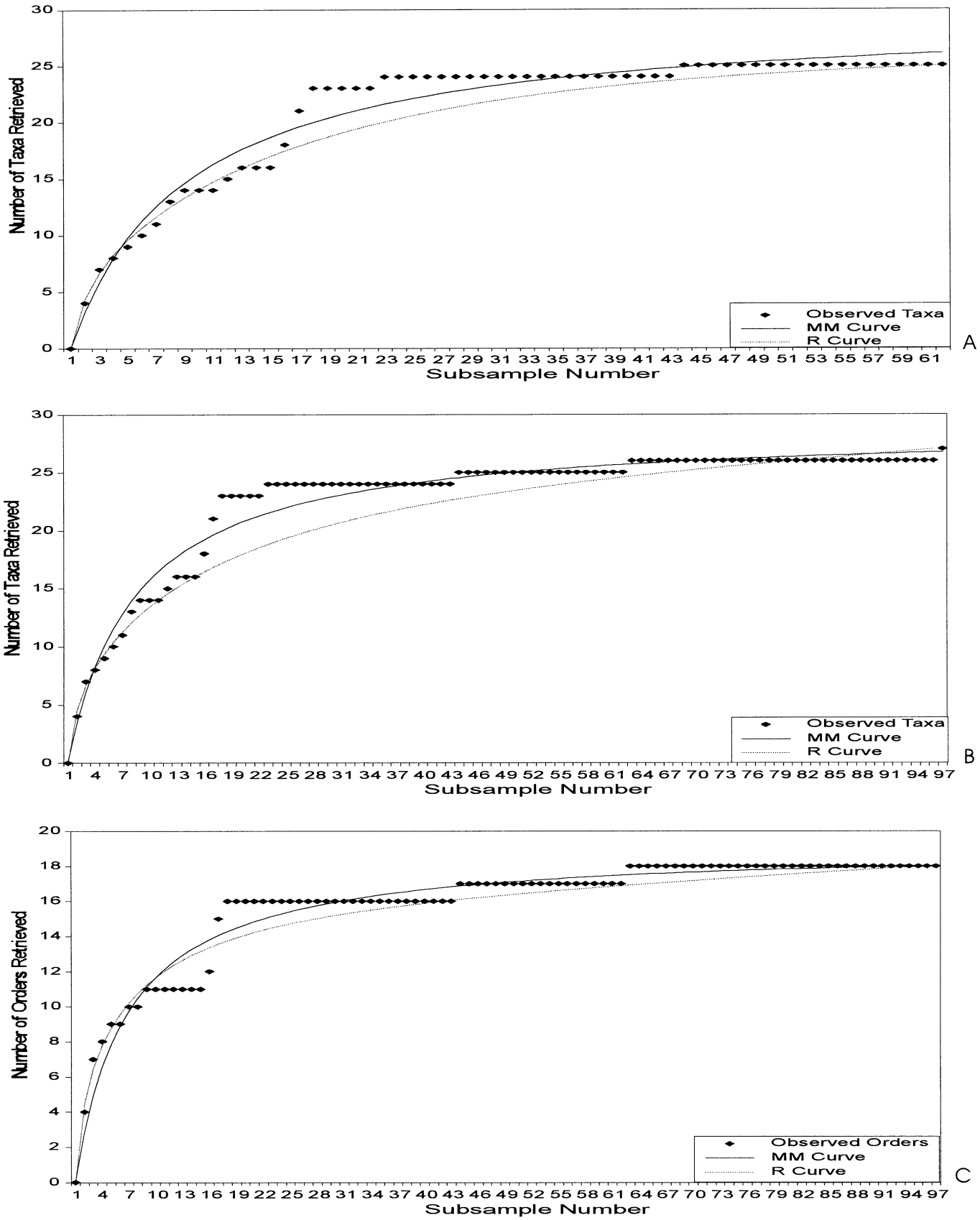
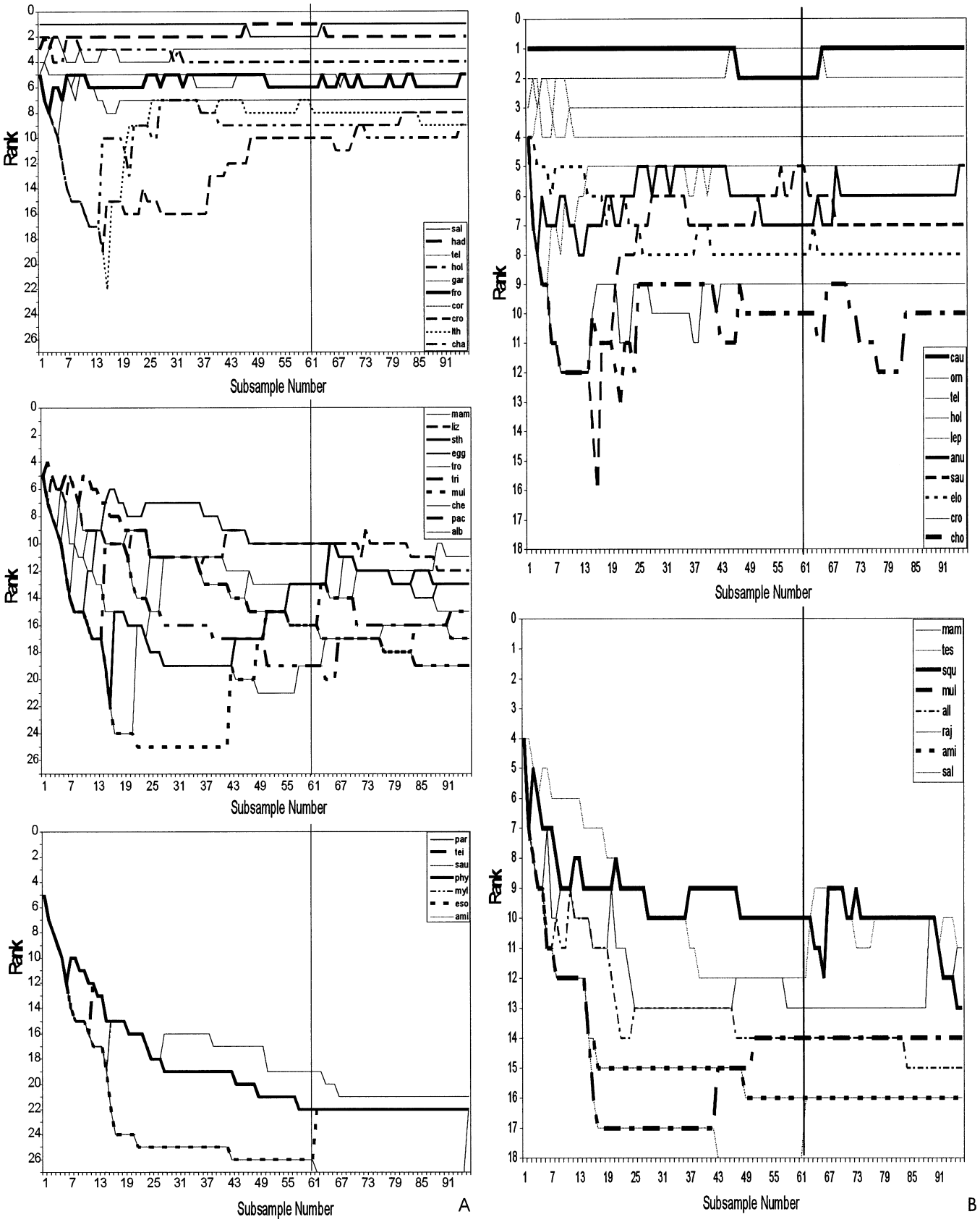


FIGURE 1. Additive empirical (observed) diversity curve, represented by a solid line, and analytical rarefaction curve, represented by a dashed line, for **A**, 61 subsamples, **B**, 96 subsamples, both at the lowest taxonomic rank assignable, and **C**, 96 subsamples at the ordinal level. Data from Bonebed 105, Dinosaur Provincial Park, Alberta.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total number of specimens as the study proceeded. A form of the Michaelis-Menten enzyme kinetics equation, useful in describing systems that tend toward an asymptote (Burton, 1998), was fitted to these data using a non-linear least-squares method. Rank order of relative abundance was also additively plotted to give an idea of the fluctuations in relative abundance that were occurring as sampling continued.

Subsequently, the data were rarefied by both analytical and jack-knife methods using the software package Rarefact 1.0 (Bennington, 1997). As mentioned previously, rarefaction answers the following question: if a subsample n of a group of N individuals belonging to S species ($n < N$) were examined, how many species s ($s < S$) would be observed (Krebs, 1989)? For the present investigation, N is the total number of elements identified, and S is the total number of taxa retrieved. In this analysis, total sample and subsample size, initially determined by weight, were converted into sizes by number of elements included. When given these data and the size of the subsample (n), Rarefact 1.0 provides the expected number of taxa in the subsample (s). The determination of s may be made using either analytical or jack-knife methods. Further details on rarefaction theory and analytical and jack-knife methodology are presented in Appendix 1.

Finally, all elements belonging to the same taxon were grouped and the percentage of the total mass of retained elements that were accounted for by each taxon was determined. Elements from both the coarse and fine parts of each subsample were combined at this stage.

Based upon an examination of the diversity curve and the relative abundance rank orders, it was determined that a further 35 subsamples should be examined to complete the study (see Discussion below). A second set of packets provided concentrated matrix for 35 more subsamples, each treated in an identical fashion to the first 61, with data collected in the same way.

RESULTS

Table 1 lists the 27 taxa retrieved from all 96 subsamples from Bonebed 105, including the percentage (by number) of the total number of elements retrieved. Some 61 subsamples were initially studied and the empirical relationship between diversity and sampling frequency was plotted with a solid line, using the Michaelis-Menten equation as described above, in Figure 1A. Relative abundance rank order in each subsample for each taxon is plotted in Figure 2A to the left of the vertical line. At the lowest possible assignable taxonomic level, the maximum diversity attained was 25 taxa at the 43rd subsample, and relative abundance rank order stabilized at the 48th subsample for the four most abundant taxa. These subsamples both fall within the region of the cumulative diversity curve that is tending towards its asymptote (Fig. 1A). Analytical rarefaction of the collected data using the hypergeometric distribution method (see Appendix 1) produced the curve shown by a dashed line in Figure 1A. The variables used to rarefy the first 61 subsamples were $N = 364$ elements and $S = 25$ taxa. Each subsample was given a size $n = 6$ (362 elements divided into 61 equally sized subsamples).

Based on these results, the study was continued until 96 subsamples had been examined, equivalent to double the number of subsamples required to reach stability in rank order and to reach the asymptotic region of the diversity curve (48). This decision was based upon the assumption that continuing to analyze an equivalent number of subsamples past the point of taxonomic stability indicated by constant rank orders and the asymptotic region of the diversity curve would reveal any major changes that may be occurring in the pattern. Had instability returned to the data, sampling would have continued even further (see Discussion below). The empirical diversity curve for all 96 subsamples is shown in Figure 1B by a solid line. The maximum diversity attained was 27 taxa in the 96th subsample (Fig. 1B), and the four most abundant taxa remained unchanged with relative abundance rank order stabilizing at the 64th subsample (Fig. 2A). Analytical rarefaction of the collected data using the hypergeometric distribution method (see Appendix 1) produced the curve shown by a dashed line in Figure 1B. The variables used were $N = 665$, $S = 27$, and $n = 7$. Comparison of the empirical diversity curve with the rarefaction model indicates that the empirical curve (solid line) is tending toward an asymptote as indicated by the rarefaction analysis model of the same data (dashed line).

All 96 subsamples were then re-analyzed at the ordinal level, or higher if ordinal classification was impossible, for comparison. Eggshell fragments were excluded from this appraisal, yielding a total of 659 elements subjected to analysis. The empirical diversity curve for all 96 subsamples, analyzed at the ordinal level, is shown by a solid line in Figure 1C. The maximum diversity attained was 18 orders at the 61st subsample (Fig. 1C), and relative abundance rank order for the four most abundant orders stabilized at the 66th subsample (Fig. 2B). Analytical rarefaction of the collected data at the ordinal level using the hypergeometric distribution method (see Appendix 1) produced the curve shown by a dashed line in Figure 1C. The variables used were $N = 665$, $S = 18$, and $n = 7$. Again, the trend toward an asymptote suggested by the rarefaction model is mirrored by the empirical evidence.

A comparison of the first 48 subsamples to the second 48 using a Kolmogorov-Smirnov Two-Sample Test revealed a significant difference between the cumulative diversity curves, both at the lowest possible assignable taxonomic level (Fig. 3A) and at the ordinal level (Fig. 3B). The relative abundance rank orders from each half of the study also showed slight differences in pattern. The additive diversity curve for the first 48 subsamples began to enter its asymptotic phase after 17 subsamples, at both lowest and ordinal levels of classification. The additive diversity curve for the second 48 subsamples began to enter its asymptotic phase after 20 subsamples, at both the lowest and ordinal levels of classification. Some 2,540 specimens were examined in the first 48 subsamples (1–48), with the asymptotic phase beginning after 1,013 specimens had been plot-

←

FIGURE 2. Relative abundance rank order diagram, based upon cumulative data, showing early fluctuation followed by stability for **A**, 96 subsamples at the lowest taxonomic rank assignable. **Abbreviations**: **alb**, *Albanerpeton*; **ami**, *Amia*; **cha**, champsosaur; **che**, chelydrid; **cor**, *Coriops*; **cro**, crocodylian; **egg**, eggshell fragments; **eso**, esocoid; **fro**, frog; **gar**, gar; **had**, hadrosaur; **hol**, holostean A; **liz**, lizard; **lth**, large theropod; **mam**, mammal; **mul**, multituberculate; **myl**, *Myledaphus*; **pac**, pachycephalosaur; **par**, *Paralbula*; **phy**, phylodont; **sal**, salamander; **sau**, *Saurornitholestes*; **sth**, small theropod; **tei**, teiid; **tel**, teleost; **tri**, trionychid; **tro**, *Troodon*. **B**, Relative abundance rank order diagram for 96 subsamples at the ordinal level. **Abbreviations**: **all**, Allocaudata; **ami**, Amiiformes; **anu**, Anura; **cau**, Caudata; **cho**, Choristodera; **cro**, Crocodylia; **elo**, Elopiformes; **hol**, holostean; **lep**, Lepisosteiformes; **mam**, Mammalia; **mul**, Multituberculata; **orn**, Ornithischia; **raj**, Rajiformes; **sal**, Salmoniformes; **sau**, Saurischia; **squ**, Squamata; **tel**, Teleostei; **tes**, Testudines. Data to the left of the solid vertical line from the first 61 subsamples. Figure 2A is divided into three groups of taxa and Figure 2B is divided into two groups of taxa, by rank, for clarity; i.e., Figure 2A (top) shows taxa ranked 1 through 10, Figure 2A (middle) shows taxa ranked 11–20, etc. Data from Bonebed 105, Dinosaur Provincial Park, Alberta.

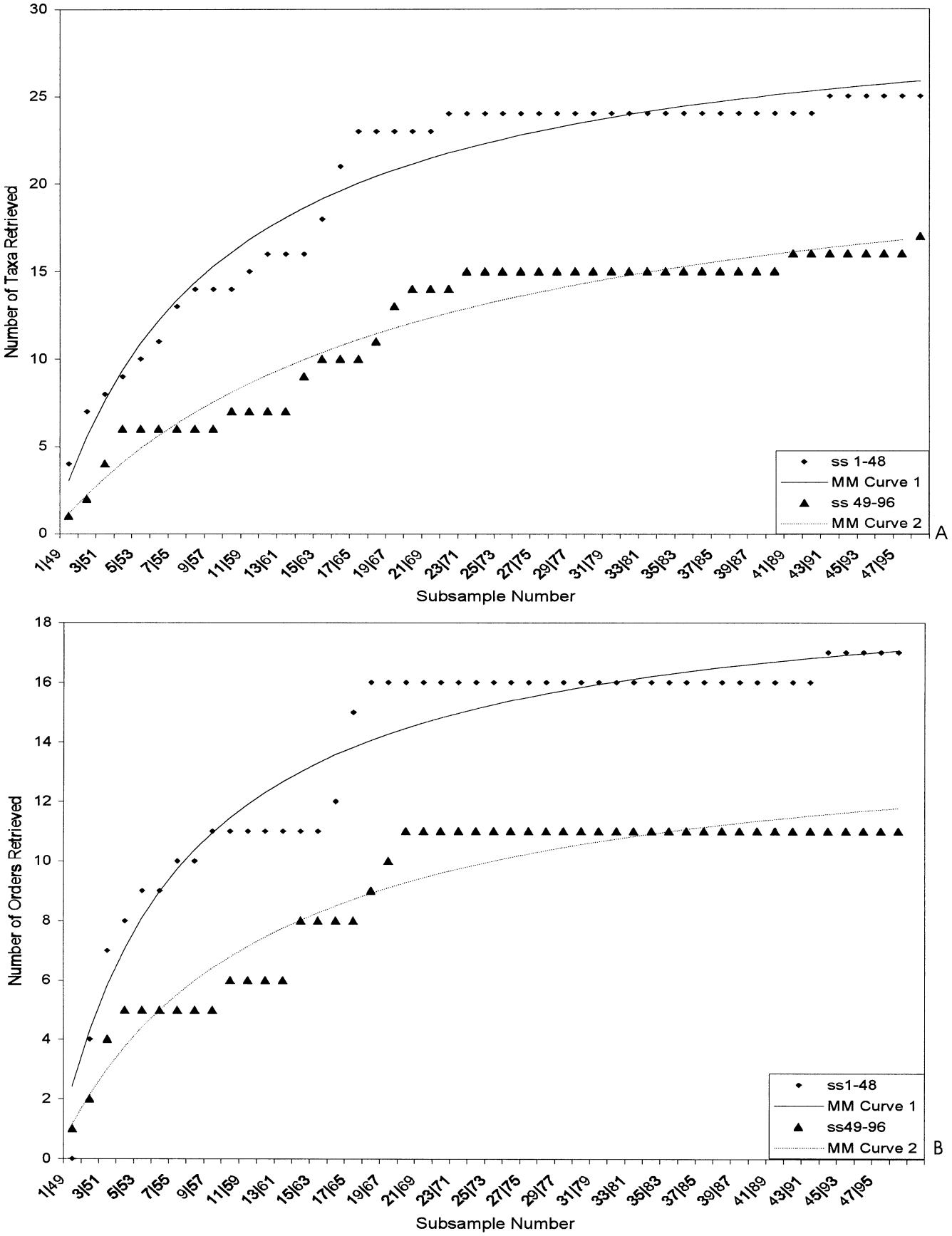

FIGURE 3. A comparison of additive empirical (observed) diversity curves for the first 48 subsamples, represented by a solid line, and the second 48 subsamples, represented by a dashed line, at **A**, the lowest taxonomic rank assignable, and at **B**, the ordinal level. Data from Bonebed 105, Dinosaur Provincial Park, Alberta.

TABLE 2A. Comparison of percent composition by number of Bonebed 105 in the present study and in a previous assessment of diversity and abundance of this site by DBB, at the lowest possible taxonomic level.

Taxon	Percent Composition (Present)	Percent Composition (Previous)
Salamander	29.62	33.40
Hadrosaur	21.80	23.50
Teleost	14.14	2.90
Holostean A	7.82	11.90
Gar	5.11	2.30
Frog	5.11	5.00
Coriops	2.56	2.60
Crocodile	1.80	1.70
Large theropod	1.50	0.17
Champsosaur	1.50	0.73
Mammal	1.35	1.50
Lizard	1.05	2.00
Eggshell	0.90	(not found)
Small theropod	0.90	1.60
Troodon	0.75	0.17
Trionychid	0.75	(not found)
Multituberculate	0.60	(not found)
Chelydrid	0.60	0.68
Pachycephalosaur	0.45	(not found)
Albanerpeton	0.45	(not found)
Paralbula	0.30	0.51
Teiid	0.15	(not found)
Saurornitholestes	0.15	(not found)
Phyllodont	0.15	(not found)
Myledaphus	0.15	1.10
Esocoid	0.15	(not found)
Amia	0.15	(not found)
Kindlea	(not found)	0.62
Platacodon	(not found)	0.90
Elopomorph	(not found)	0.28
Aspideretes	(not found)	0.79
Ankylosaur	(not found)	0.62
Dromaeosaur	(not found)	0.06
Thescelosaurus	(not found)	0.23

TABLE 2B. Comparison of percent composition by number of Bonebed 105 in the present study and in a previous assessment of diversity and abundance of this site by DBB, at the ordinal level.

Taxon	Percent Composition (Present)	Percent Composition (Previous)
Caudata	29.89	33.40
Ornithischia	22.46	24.35
Teleostei	14.26	3.80
Holostean	7.89	11.90
Lepisosteiformes	5.16	2.30
Anura	5.16	5.00
Elopiformes	3.03	3.39
Crocodylia	1.82	1.70
Saurischia	3.34	2.00
Choristodera	1.52	0.73
Mammalia	1.37	1.50
Squamata	1.21	2.00
Testudines	1.37	1.47
Multituberculata	0.61	(not found)
Allocaudata	0.46	(not found)
Rajiformes	0.15	1.10
Amiiformes	0.15	0.62
Salmoniformes	0.15	(not found)

ted. Some 2,453 specimens were examined in the second 48 subsamples (49–96), with the asymptotic phase beginning after 921 specimens had been plotted. A total of 4,993 specimens were examined from the 96 subsamples.

The findings of the present study were compared with data previously collected by Brinkman (1990) for Bonebed 105, by percent composition by number at the lowest possible assignable taxonomic level (Table 2A), and by percent composition by number at the ordinal level or higher (Table 2B). A Kolmogorov-Smirnov Two-Sample Test showed no significant difference in diversity between these two data sets.

DISCUSSION

An examination of the findings of the present study in comparison to a previous assessment of taxonomic diversity and abundance at this site by Brinkman (1990) (Table 2A, B), in which a much larger matrix sample was studied, shows that the information obtained from vertebrate microfossil localities is repeatable. The percent composition values shown in Table 2A and B are generally similar, with the exception of teleosts and salamanders. Those taxa that are most abundant, namely salamanders, hadrosaurs, teleosts and Holostean A, are ranked 1, 2, 3, and 4 respectively in terms of relative abundance in the present study. Brinkman (1990) ranked the same four taxa 1, 2, 3, and 5 respectively. This discrepancy is likely due to slight differences in sampling methodology, as a Kolomogorov-Smirnov Two-Sample Test revealed no significant difference between the two data sets. These four taxa are present in much larger numbers than other taxa present at the site (Table 1), and therefore in reconstructing the paleocommunity their relative significance should be considered to be greater. In addition, the lack of a significant difference between Brinkman's (1990) study and the present investigation, in which far less matrix was examined, indicates that analyses of smaller but appropriately documented quantities of material are equally meaningful.

The empirical curve shown in Figure 1A indicates that as the number of subsamples examined increases, the relative increase in diversity from one subsample to the next decreases. The early part of the curve shows a very rapid rate of increase between subsamples, but after 23 subsamples the slope of the curve begins to decrease and an asymptote is approached. The shape of the empirical curve indicates that continuing analysis of subsamples would be unlikely to alter interpretations of the relative abundance of the more common taxa in the assemblage, or of the paleoenvironment under study, in any major fashion.

The additive rank order diagram shown in Figure 2A provides information on the structure of the paleocommunity. In the first few subsamples, taxon rank varies markedly and there is no evidence of a pattern. After 33 subsamples, the majority of these fluctuations are no longer present and a general picture of the relative abundance of each taxon is obtained. After 48 subsamples the ranks of the four most common taxa have stabilized. The pattern shown in Figure 2A suggests that relatively few subsamples are necessary to achieve an accurate picture of relative abundance. Any further rank fluctuations are of only minor significance and will not affect the overall interpretation of the relative abundance of the more common taxa in the assemblage.

Analytical rarefaction analysis of the data for the first 61 subsamples yielded the curve shown by a dashed line in Figure 1A. As the number of subsamples increases, the expected diversity of the sample also increases. The early portion of this curve increases rapidly, as seen in the empirical curve. The slope of the curve quickly begins to decrease, however, and tends toward a asymptote in a similar fashion to the empirical curve. The shape of the analytical curve demonstrates that as the number of subsamples increases, the expected diversity increases rapidly and then reaches an asymptote at which point no further diversity increases are expected. The empirical curve and analytical rarefaction model depicted in Figure 1A are similar. This suggests that the predictions of the rarefaction model are matched by the empirical data, and therefore the empirical curve itself is a useful predictor of the diversity pattern of the entire sample.

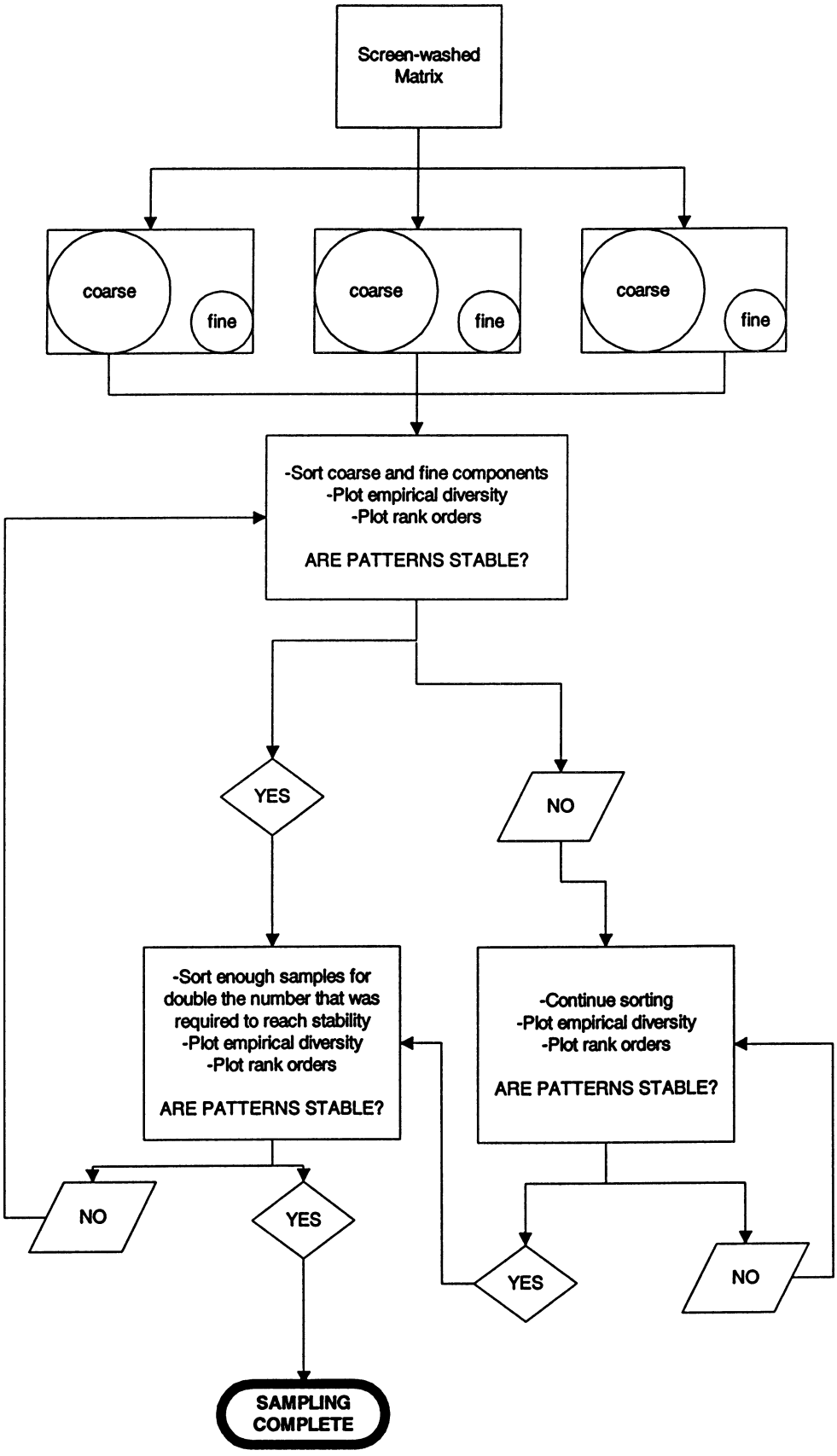

FIGURE 4. Flowchart of the vertebrate microsite sampling protocol developed in the present study.

Based upon the tendency toward an asymptote shown in the empirical diversity curve (Fig. 1A) and the reduction in fluctuation in the rank order diagram (Fig. 2A) for the first 61 subsamples, it was determined that 35 more subsamples should be examined. Taxonomic stability in both patterns was achieved at the 48th subsample, indicating that 96 subsamples would complete the study. The decision to expand to 96 subsamples was based on the assumption that analyzing the equivalent number of subsamples that led to the stable pattern would reveal the existence of underlying instability in the pattern had it existed. Sampling would have continued until the pattern stabilized again. At this point a 3rd phase would have been undertaken, in which another set of subsamples would have been analyzed to verify stability. In the present study, however, the stability achieved at the 48th subsample continued through to the 96th subsample and was concluded to be representative of the real pattern. The empirical diversity curve for the entire study (Fig. 1B) shows that only two additional taxa (each represented by only a single specimen) were discovered after the 61st subsample, and the relative abundance ranks of the most common taxa remained unchanged, with only minor fluctuations among these taxa (Fig. 2A).

Differences in the additive diversity curve and data for rank order of relative abundance between the two halves of this study can largely be explained by the presence of rare taxa. Eleven lower taxa and five orders are represented by fewer than five specimens out of a total of 4993. If emphasis is placed upon those taxa that are most abundant, the two halves of the study become nearly identical. The presence of six lower taxa and one order each represented by single specimens precludes the two halves of the study being exactly identical. Their presence reveals that the distribution of taxa throughout the matrix under investigation is not completely uniform. The rarity of these specimens suggests, however, that their value to an analysis of relative abundance in an attempt to reconstruct the paleocommunity represented by the microsite is dependent upon accurate documentation of abundance rank order. Further, although the two halves of the study were found to be significantly different, an examination of the number of elements attributable to each taxon reveals that the rank orders of the most abundant taxa are established by large differences in the number of elements identified (Table 1). Those taxa of low and intermediate rank differ from each other by only a few specimens. As a result, the examination of a single additional subsample could have a noticeable effect on the ranks assigned to these taxa. Care must be taken not to over-interpret the significance of the rank orders in this intermediate region, as they are subject to fluctuation. Only those ranks that stabilize relatively early in the investigation should be considered meaningful.

CONCLUSIONS

Three conclusions may be drawn from this investigation. Firstly, this study shows that repeatable diversity and abundance data can be gathered through controlled subsampling of vertebrate microsites. Secondly, the cumulative diversity plot generated from the subsamples has an initial region of rapid increase that levels off to an asymptotic phase. Once the curve has entered the asymptotic phase, and the relative abundance rank orders of the most abundant taxa have stabilized, the likelihood of the discovery of a numerically well-represented taxon can be assumed to be remote. Finally, controlled subsampling of vertebrate microsites will allow comparisons of relative abundance and diversity to be made across sites. It should be noted, however, that because distribution throughout the matrix is not random, some differences between data sets are expected. General patterns remain the same, however, and meaningful information can be derived from these. Care must be taken not to extrapolate beyond the scope of the data collected, and the general characteristics of microfossil assemblages must be kept in mind when drawing conclusions from microsite data.

The results obtained in the present study suggest that a standardized methodology for the examination of vertebrate microsites can be applied. In order to document a microsite, small subsamples should be analyzed sequentially, and diversity and relative abundance rank order should be cumulatively plotted. Once the diversity curve has entered the asymptotic phase and the rank orders have stabilized amongst the most abundant taxa, sampling should continue until an equivalent number of subsamples has been analyzed in order to ensure that the stability of the pattern holds. The second data accumulation phase will test the hypothesis that the first phase has yielded relative exhaustion of the taxa present, and has appropriately represented the rank order information. If the hypothesis is falsified, sampling should continue until the curve re-enters the asymptotic phase and the rank orders have once again stabilized.

A flowchart (Fig. 4) provides a synopsis of the vertebrate microsite sampling methodology proposed here. This methodology is applicable to comparisons of relative abundance and diversity data across sites. It provides a means whereby data collection can be standardized without dictating an absolute and uniform quantity of material to be analyzed from any given site. It should be noted that neither this, nor any other, method can provide a means for discovering the total diversity present in a given microsite in a statistically rigorous fashion. Only an exhaustive search can attain that goal. This study is intended only to provide a tractable methodology for the analysis of microsites in order to encourage their use as a valuable paleoecological resource.

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APPENDIX 1

Rarefaction is a deterministic transform of a collection's species-abundance distribution. Rarefaction is used in an ecological context to estimate the expected species richness *s* of a community of *N* individuals if its size were restricted to a subset *m* (Krebs, 1989). When individuals are sampled independently and randomly from a community, there is a direct relationship between the rarefaction 'curve' generated and the source community's species richness (Tipper, 1979). Vertebrate microsites are generally highly representative of the vertebrate fauna present in the paleocommunity (Brinkman, 1990) and provide a means by which the paleocommunity can be accurately sampled within certain limits (see Badgley, 1986, for a discussion of these). Vertebrate microsites allow for random and independent sampling of individuals from the community, and thus lend themselves well to analyses employing rarefaction.

In the present study, rarefaction analysis was conducted using both jack-knifing and analytical techniques. Jack-knifing involves repeated resampling of a data set to generate a diversity estimate for a smaller subsample. The actual subsample diversity can be compared to this. The analytical method involves the computation of *s* and its variance *v* using the following formulae:

$$s = \sum_{i=1}^{S} \left[1 - \frac{\binom{N - N_i}{m}}{\binom{N}{m}} \right] \cdots \tag{1}$$

$$v = \sum_{i=1}^{S} \left\{ \left[\frac{\binom{N - N_i}{m}}{\binom{N}{m}} \right] \left[1 - \frac{\binom{N - N_i}{m}}{\binom{N}{m}} \right] \right\} + 2 \sum_{j=2}^{S} \sum_{i=1}^{j-1} \left\{ \frac{\binom{N - N_i - N_j}{m}}{\binom{N}{m}} - \frac{\left[\binom{N - N_i}{m} \binom{N - N_j}{m} \right]}{\left[\binom{N}{m} \binom{N}{m} \right]} \right\} \cdots \tag{2}$$

Where

S is the number of species in the original sample
N_i is the number of individuals in the *i*th species
N is the total number of individuals in the original sample
m is the number of individuals in the rarefied sample

(Tipper, 1979)

Under both methodologies sampling is conducted without replacement. The above expressions therefore correspond to the hypergeometric distribution, which is known to be consistent with this type of sampling (Tipper, 1979).

A rarefaction 'curve' can be generated from both the jack-knife and the analytical methods, but it must be stressed that the only real values on the curve are the actual *s* values. A line may be fitted to these, but values along the line are not reliable (Tipper, 1979). The creation of a rarefaction curve allows the determination of the species-richness asymptote, at which the diversity of the subsample in question has reached the diversity of the original sample. The point at which this asymptote is reached predicts the subsample size necessary to achieve a representative description of the diversity of the original sample.