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Abundance of "*Hipparion*"

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The "*Hipparion*" Datum in the Sinap Formation represents the novel meeting of representatives from two distinct but parallel radiations. Large hipparionines belonging to the ancient radiation of the Equidae became a part of a basal herbivore fauna that includes members of the more recent adaptive radiation of the Bovidae. Hipparion immigration into the Old World has implications for environmental change, faunal turnover, and large mammal evolution scenarios. A complete understanding of the impact of this immigration requires quantification of the contribution of hipparionine immigrants to both species diversity and herbivore biomass. We address the second issue here and quantify the abundance of hipparionines relative to ruminants at several localities in the Sinap Formation. Changes in hipparionine abundance immediately following the "*Hipparion*" Datum can be evaluated in the context of the well-controlled chronology for the Sinap fossil localities (Kappelman et al., chapter 2, this volume) and can be matched with the apparent changes in hipparionine diversity recorded by Bernor et al. (chapter 11, this volume).

Accurate estimates of hipparionine abundance are obscured by the various processes that transform living organisms into fossil assemblages. Biomass is often calculated by multiplying the estimated mean body mass of a taxon by its density (number of individuals per area). Biomass is even more difficult to estimate when taking into account the imprecision associated with estimating body mass for extinct taxa. However, body size remains perhaps the single most important parameter in the ecology of a particular species (Damuth and MacFadden 1990) and should be considered whenever possible. Body size influences the basic metabolic requirements of an organism (Kleiber 1932; McNab 1963, 1990); influences factors such as longevity and generation time; and determines much of an organism's interaction with various aspects of its environment, including locomotion, feeding (Kay 1984), and predator avoidance (Scott 1979; Maiorana 1990; Scott et al. 1999). Body size is fundamental when assessing the ecological position of a taxon and its relationship with other taxa. Thus, we present estimates of hipparionine relative abundance in conjunction with body mass estimates when possible. These, in turn, are used together to model the limits of immigrant hipparionine contributions to herbivore biomass following the "*Hipparion*" Datum.

Quantitative estimates of abundance are often given as number of individual specimens (NISP) or minimum number of individuals (MNI). These methods can give varying estimates of relative abundance, and one method may be more accurate than the other, depending on the specifics of the sampling and taphonomy of the fossil assemblage in question. Thus, estimates of relative abundance should be presented in conjunction with relevant taphonomic data whenever possible. Similarly, both NISP and MNI should be calculated for each fossil assemblage. Here, we present relative abundance estimates based on both NISP and MNI in conjunction with taphonomic data concerning the numbers of fragmentary and associated specimens for each assemblage studied.

The goals of this study are to describe changes in hipparionine abundance relative to ruminants in the Sinap Formation at several representative sites and to report body mass estimates for hipparionines and ruminants from these sites whenever possible. We assess the varying estimates of hipparionine relative abundance with respect to the available taphonomic data and report a best estimate of relative abundance for each site studied. Finally, equid abundance was expressed relative to ruminant abundance and changes in equid abundance were modeled using an iterative logistic curve fit in SAS (version 8.02; Cary, North Carolina: SAS Institute) and a simple quantitative model to convert within-locality relative abundance of equids to between-locality absolute abundance and biomass estimates.

Materials and Methods

Fossils collected by the Sinap project were identified by project members under the supervision of the principal investigators and cataloged using a laptop computer and a relational database (Johnson et al. 1996). This relational database was queried both during and at the end of the summer 1995 field season for all specimens identified as being either artiodactyls or perissodactyls from seven fossil collecting localities in the Sinap Formation.

A locality is a stratigraphically and laterally discrete site with fossils in situ; each locality is thought to represent a single depositional unit. The seven localities, reported in stratigraphic order here, are: Locs. 64, 4, 122, 121, 72, 91, and 12. These localities were selected for their stratigraphic significance and the size of their fossil sample. Loc. 64 was selected because it yields the largest pre-*"Hipparion"* large mammal assemblage in the Sinap Formation, whereas Loc. 4 was chosen because it records the earliest occurrence of hipparionines in the Sinap Formation. During June and July of 1995, specimens identified as being equid or ruminant by database queries were examined by R.S.S. and K.H. in Kazan, Turkey, where the Sinap collections are housed. These specimens were then further identified to the lowest possible taxonomic level and all equids and ruminants were then further examined. All of the ruminant and equid specimens were identified according to side, element, part (proximal or distal when applicable), completeness, association (i.e., whether they were associated and/or articulated with other specimens), size category (for ruminant specimens only), age (juvenile or adult), and lower taxonomic group whenever possible. These identifications were sometimes supplemented by ad lib notes and descriptions.

Specimen Definition

Various indices of faunal abundance all rely on counting specimens that belong to a particular group, usually a particular taxon. Even the most simplistic index of faunal abundance, NISP, relies on the identifications of the investigators and their definition of what constitutes a specimen. Thus, a practical, operational definition of the term "specimen" is crucial to any discussion of relative abundance.

Holtzman (1979) devotes some discussion to the issue of what constitutes a specimen and, while invoking "traditional paleontological usage," defines a specimen as "all the remains that can be shown to derive from a single once living individual, provided that the remains include at least one *identifiable element*" (p. 78; emphasis added). This definition contrasts with that of Shotwell (1958, p. 272), who uses the terms "element" and "specimen" interchangeably to refer to Holtzman's "identifiable element" or "finite [number of parts] that can be identified when isolated but cannot be further subdivided without a significant loss of identifiability" (Holtzman 1979, p. 78).

Claims of "traditional paleontological usage" notwithstanding, both definitions ignore the essential practicality that a specimen in paleontology refers to whatever fossil or fossils receive a single catalog or museum accession number. Fossils found in different field seasons may later be shown to derive from a single individual, but operationally, they remain separate but potentially associated specimens. Similarly, multiple associated elements that are each easily identifiable on their own may be given a single catalog number. Thus, for the sake of clarity, we refer to all fossils with a single catalog number as a single cataloged specimen. Cataloged specimens are not to be confused with identifiable specimens, which we used to derive estimates of relative abundance.

Simply counting the number of cataloged specimens attributed to a different taxon would give an unsystematic estimate of their relative abundance: relative abundance would be confounded by the vagaries of catalog number assignment. The definitions of specimen given by Holtzman and Shotwell are more sensitive to what is desirable in an estimator of relative abundance.

If a specimen is considered to be all the remains that can be shown to derive from a single individual (Holtzman 1979), then, at its very best, the number of specimens would be equal to the number of once living individuals preserved in an assemblage. At its worst, the number of specimens would be the number of individuals that one investigator believes are preserved in an assemblage. Multiple fossils would be counted as only one specimen when they are thought to derive from a single individual. As a systematic measure of relative abundance, this technique leaves much to be desired.

Alternatively, Shotwell's definition of specimen would potentially count single fossils as multiple specimens. For example, a complete long bone would be counted twice; once for the proximal end and once for the distal end. Neither Shotwell's nor Holtzman's definition of specimen would yield estimates of relative abundance that are both systematic and sensitive to the processes by which a fossil assemblage is formed.

Rather than use cataloged specimens as the basic unit when estimating relative abundance, we define an identifiable specimen as a single fossil that is identified as belonging to a particular group relevant to the question under study (in this case, a ruminant or a hipparionine). The two criteria used to define a specimen are (1) identifiability and (2) physical boundaries. Multiple bones are counted as multiple identifiable specimens, and single bones, whose respective parts may be further identified but remain complete, are identified as single identifiable specimens. Thus, an identifiable specimen is a discrete, easily recognizable skeletal part. Identifiable specimens can be easily recognized and counted and will simply be referred to as "specimens."

Age and Size Categories

We followed the size categories for ruminants established by A. Gentry during the 1994 field season. Regression estimates of body weight derived from postcranial measurements

Table 16.1. Size Categories Used for Ruminant Specimens

Size Category	Description	Range of Estimated Body Weights (kg)
Very small	Smaller than *Gazella*	<15
Small	Size of *Gazella*	15–30
Medium	Larger than *Gazella*	30–75
Medium	*Prototoryx-Tragoportax* size	103
Large	Size of *"Hipparion" uzunagizli*	150
Large	Size of *Cormohipparion sinapensis*	200
Large	Size of *"Hipparion"* sp. 2	300
Very large	Giraffidae size	>500

Notes: Size categories were established by the authors during the 1995 field season based on notes by A. Gentry from the 1994 field season. Descriptions are based on A. Gentry's notes and body mass estimates reported here using the regression formulae of K. Scott (1990).

were later used to establish body mass means and ranges for each size category, and in a few cases, specimens were reclassified up or down one size category, based on regression estimates of body mass. In general, most initial subjective size category classifications were confirmed by body mass estimates indicating the robustness of the original framework. The size categories used in this chapter are shown in table 16.1.

Specimens were classified as belonging to a juvenile based on the presence of deciduous dentition, unfused epiphyses, or strongly visible lines of epiphyseal fusion (recently fused epiphyses). It is likely that specimens identified as juvenile encompassed a wide range of actual ages; hence these classifications are relative and probably not broadly applicable.

Fragmentation and Association Indices

In general, specimens were ranked as complete or fragmentary. Complete specimens were all specimens that constituted a complete or nearly complete element such that any missing piece of the element would be unidentifiable on its own. Fragmentary specimens refer to specimens in which a large part of the identifiable portion of the element is missing. Examples range from proximal and distal ends of long bones to other, more severely fragmented specimens. Teeth represent a unique category in terms of fragmentation and isolated teeth are often well preserved. A complete isolated tooth is not strictly comparable to a complete long bone as an indicator of the degree of fragmentation in a fossil assemblage. Often isolated teeth are very common in even the most fragmented fossil assemblages. Thus, teeth were scored separately as either isolated, fragmentary, or part of an incomplete mandible or maxilla. An index of fragmentation was calculated by dividing the number of fragmentary specimens by the total number of complete and fragmentary specimens and multiplying the result by 100. Dental specimens were excluded from this calculation.

"Association" refers to whether a specimen was found in articulation with another in the field and cataloged as being associated or was subsequently determined to articulate with another specimen. Thus the definition of association used in the catalog is expanded here to include all specimens that are determined to articulate with each other (the definition used in the catalog refers only to specimens found in association during excavation). Each element or partial element (proximal or distal end) that articulates with another element or is cataloged as associated was scored as "associated." Elements could be associated with more than one other element but were scored as associated only once. The number of associated elements was divided by NISP and multiplied by 100 to define an index of degree of association.

Relative Abundance Calculations

Relative abundance in this study is expressed as the abundance of one group relative to another. The two groups studied are the major basal herbivores—the ruminants and hipparionines. Thus, the relative abundance of the hipparionines is relative to the ruminants only and to not all of the specimens from the locality. The relative abundance of hipparionines is expressed as:

$$[\text{hipparionines} / (\text{hipparionines} + \text{ruminants})] \times 100$$

A number of different measures of abundance have been proposed, including NISP, MNI, and the weighted abundance of elements (WAE) (Shotwell 1955, 1958; Van Valen and Sloan 1965; Grayson 1978; Holtzman 1979; Gilbert et al. 1981; Badgley 1986; Marshall and Pilgram 1993). The abundance of hipparionines and ruminants was determined for this study using NISP, WAE, and two variants of MNI.

NISP is simply the number of specimens identifiable as belonging to a particular group (in this case, as hipparionines or ruminants). In some cases, and generally only in the

case of associated specimens, more than one identifiable specimen was given the same catalog number. In these instances, an alphabetical designation was added to each individual identifiable specimen and all identifiable specimens were used to determine NISP.

WAE was determined by dividing the number of identifiable elements (e_i) by the number of identifiable elements per individual (m_i). The quantity m_i was introduced by Shotwell (1955) and refers to the number of skeletal parts in a single living individual that have a reasonable probability of being preserved and identified. Ribs and vertebrae are generally excluded from this number (Shotwell 1955), and determination of identifiable elements per individual relies on the judgment of the investigator (Shotwell 1955, 1958; Holtzman 1979; Badgley 1986). The number of identifiable specimens per hipparionine individual and ruminant individual is shown in table 16.2. As noted earlier, e_i is not the same as NISP. For example, a complete femur constitutes a single specimen and adds one to NISP. In contrast, a complete femur can be divided into two identifiable elements and so adds two to e_i. Thus, WAE is designed to compensate for the effects of fragmentation and variable numbers of elements per individual.

MNI is simply the number of the most abundant element. An element may occur multiple times in a single individual, in which case it is first divided by its representation in a single individual. For example, MNI might be given by the higher of either the number of right astragali or the number of calcanei divided by two. MNI-G is a variant of MNI in which the MNI of each size category of ruminant was first determined and these MNI values were then summed to determine MNI-G cumulatively for all size categories.

Various workers (Grayson 1978; Hill 1979; Hanson 1980; Brain 1981; Badgley 1986) have noted that many factors influence the formation of fossil assemblages, which in turn influence different measures of relative abundance. Perhaps the most significant of these factors are sample size, association, fragmentation, and differential preservation.

MNI and MNI-G always reduce the effective sample size and therefore increase random error (Van Valen and Sloan 1965). Furthermore, MNI always overestimates the abundance of rare taxa (Grayson 1978). These tendencies have been confirmed by computer simulations of faunal assemblages (Van Valen and Sloan 1965; Holtzman 1979; Gilbert et al. 1981), although the errors are reduced when the number of taxa is small (Gilbert et al. 1981). For these reasons, NISP may be preferable as a measure of abundance. However, for cases in which there are many associated specimens or there is differential preservation of taxa, NISP overestimates the abundance of well-preserved taxa and MNI is preferable as a measure of abundance. In general, as association of specimens increases, so does the accuracy of MNI (Badgley 1986). Similarly, the accuracy of NISP drops as differential preservation increases.

Fragmentation may influence estimates of relative abundance in unpredictable ways. MNI has often been considered less biased by fragmentation because fragments from the same element (and hence the same individual) are less likely to be incorporated into the estimate of relative abundance. Marshall and Pilgram (1993) found that MNI decreases with increasing fragmentation. In contrast, they found that NISP first increases with increasing fragmentation and then decreases at the highest levels of fragmentation. NISP may be the best measure of relative abundance at high levels of fragmentation because of biased undercounting (Marshall and Pilgram 1993). This conclusion generally assumes that highly fragmented assemblages always derive from separate bones and distinct individuals. One exception to this assumption is assemblages accumulated in conjunction with a high degree of trampling. Trampling will pulverize single elements into many fragments. When available, evidence of taphonomic factors such as trampling will influence the choice of the best estimator of relative abundance.

WAE has the advantage of usually being intermediate between NISP and MNI. WAE theoretically corrects for some differential preservation but involves a partly subjective correction factor, m_i. Effective sample sizes are higher with WAE estimates, which reduces random error, but the use of a subjective correction factor may be inappropriate (Badgley 1986). Other factors may already counter the effects of differential preservation, making WAE less useful as a measure of abundance. For instance, differential preservation in favor of larger taxa at a site may be countered by differential deposition in favor of smaller taxa with shorter generation times.

The approach we adopted here is to calculate all of these estimates of relative abundance and examine them in relation to the taphonomy of the sites under consideration. Thus, MNI is preferred at sites with greater association, whereas NISP is often preferred at sites with very high fragmentation. If estimates are similar, it is possible to bracket probable relative abundance within a very narrow range.

Body Mass Estimation

Body mass was estimated based on the nonlength measurements of limb bones and regression formulae of K. Scott (1990). The measurements described by Scott (1990) were taken by R.S.S. on all ruminant and equid limb bone specimens whenever possible. Estimates from each nonlength measurement on a specimen were averaged to determine estimated body mass. We used the regression formulae for bovids and ruminants to derive two body mass estimates for each ruminant specimen measured. Body mass estimates for the hipparionine specimens were based on the equid regression.

For purposes of estimating biomass, a parameter B was calculated for hipparionines and ruminants. In the case of hipparionines, $B_{\text{hipparionine}}$ was simply the mean of available body mass estimates for hipparionine specimens derived from all localities studied here. For ruminants, the mean of

Table 16.2. Identifiable Elements per Individual Used in the Computation of Weighted Abundance of Elements (WAE)

Identifiable Element	Number of Identifiable Elements per Ruminant Individual	Number of Identifiable Elements per Hipparionine Individual
Proximal humerus	2	2
Distal humerus	2	2
Proximal radius	2	2
Distal radius	2	2
Proximal ulna	2	2
Proximal femur	2	2
Distal femur	2	2
Proximal tibia	2	2
Distal tibia	2	2
Proximal metacarpal	2	2
Distal metacarpal	2	2
Proximal metatarsal	2	2
Distal metatarsal	2	2
Proximal accessory metapodial	0	8
Distal accessory metapodial	0	8
Phalanx 1	8	4
Phalanx 2	8	4
Phalanx 3	8	4
Accessory phalanx 1	0	8
Accessory phalanx 2	0	8
Accessory phalanx 3	0	8
Astragalus	2	2
Calcaneum	2	2
Cuboid	0	2
Cuneiform	2	2
Ectocuneiform	0	2
Entocuneiform	0	2
Lunar	2	2
Magnum	2	2
Navicular	0	2
Pisiform	0	2
Scaphoid	2	2
Trapezoid	0	2
Trapezoideum	0	2
Triquetrum	0	2
Unciform	2	2
Centrotarsale	2	0
Ectomesocuneiform	2	0
Malleolar	2	0
Molar	12	12
Premolar	12	14
Incisor	6	12
Canine	2	4
horn core	2	0
Total (m_{ii})	104	150

available body mass estimates was first determined for each size category across all seven localities. These values were then weighted according to the relative representation of each size category across all seven localities to yield a value for B_{ruminant}. The values of B were used in conjunction with a simplifying model of abundance to derive estimates of hipparionine biomass at each locality.

Abundance Model

Using the fossil record to model population changes first requires that there be a consistent relationship between the fossil assemblage and the life assemblage. Some fraction f of the life assemblage is preserved in the fossil assemblage. In practice, a model must assume that f is constant across the taxa preserved at each assemblage under consideration. Selecting the most appropriate estimator of abundance for a given assemblage's taphonomy is designed to increase the chances that this assumption is valid. The assumption of constant f is expressed below as Assumption 1. The variables referred to here are defined in table 16.3.

Assumption 1

The first assumption is:

$$f_q = \frac{N_{pq}}{n_{pq}} = \frac{\sum_p N_{pq}}{\sum_p n_{pq}}$$

When this assumption is valid, then:

$$n_{pq} = \frac{N_{pq}}{f_q}$$

The second assumption allows for the comparison of different fossil assemblages through time.

Assumption 2

Some component of the life assemblage under consideration must be constant through time. Thus, in the case of two taxa, at least one of the following three statements is assumed to be true:

n_{1q} is constant for all assemblages q

or

n_{2q} is constant for all assemblages q

or

$(n_{1q} + n_{2q})$ is constant for all assemblages q

The first two cases assume that changes in the population of one taxon do not affect the population of the other (i.e., taxon populations vary independently of each other). The third case assumes that the two taxa are in competition and there is a one-to-one correspondence such that an increase in the population of one taxon is balanced by an equal and opposite decrease in the population of the other. These assumptions are special cases of a more general statement:

$(i \cdot n_{2q} + n_{1q})$ is constant through time and between localities

(i.e., for all assemblages q).

When the parameter $i = 0$, then this assumption implies that n_{1q} must be constant; when $i = 1$, then $(n_{1q} + n_{2q})$ must be constant. Therefore, the parameter i expresses the degree to which a change in the abundance of one taxon must affect abundance of the other taxon: i can thus be referred to as a coefficient of infringement.

The hypothetical case $i = 1$ assumes that an individual of one taxon is competitively equivalent to an individual of

Table 16.3. Explanation of Variables

Variable	Explanation
N	Abundance in a fossil assemblage, arbitrary units
n	Abundance in a life assemblage, arbitrary units
f	Fraction of a life assemblage preserved in a fossil assemblage, unitless
p	Taxon, in this case p = hipparionines (h) or ruminants (r)
q	Fossil locality or assemblage, in this case q = Loc. 64, 4, 122, 121, 72, 91, or 12
i	Coefficient of infringement, unitless
C	Constant, expressed in $m$kg/km^2
m	Constant expressing units of abundance defined by a reference assemblage—in this case Loc. 64
B	Estimated body mass of a taxon, kg
A	Estimated density of a fossil taxon, m/100 km^2 or $m$kg/100 km^2
r	Intrinsic rate of population growth, m/1000 ky-km^2
K	Carrying capacity, m/100 km^2

the other taxon. This is quite clearly unlikely to be true and therefore a third assumption is actually implied in this case.

Assumption 3

The population density of both taxa under consideration is expressed in units that are competitively equivalent. A starting point here is to use units of biomass. Thus, N_{ij} and n_{ij} need to be expressed in biomass units.

Given the assumptions discussed above, we suggest the following:

$$n_{1q} = \frac{N_{1q}}{f_q}$$

$$f_q = \frac{N_{1q}(i) + N_{2q}}{n_{1q}(i) + n_{2q}}$$

$$n_{1q} = \frac{N_{1q}}{N_{1q}(i) + N_{2q}} (n_{1q}(i) + n_{2q})$$

$$C = (n_{1q}(i) + n_{2q})$$

$$n_{1q} = \frac{N_{1q}}{N_{1q}(i) + N_{2q}} C$$

As noted, C is a constant according to assumptions two and three. We may express C in terms of units of some multiplier of kilograms per square kilometer. Let this multiplier be m and let $n_{11} + n_{21}$ be equal to $100m$ kg/km^2. Thus, C is defined in terms of the first assemblage in a time series and is equal to $100m$ kg/km^2 when $i = 0$ or 1 or when $n_{11} = 0$.

We applied this simplifying model to the case of ruminants and hipparionines from the Sinap Formation as follows. The preferred abundance estimate for ruminants and hipparionines at each of the seven Sinap localities used in this study was multiplied by the body mass parameter (B) for ruminants and hipparionines and the results were saved as N_{hq} and N_{rq}, respectively. The constant C was set equal to $100m$ kg/km^2 at Loc. 64. Loc. 64 is a pre-"*Hipparion*" locality and therefore, $N_{h,64} = 0$. Estimates for $n_{h,64}$ and $n_{r,64}$ were therefore 0 and $100m$ kg/km^2, respectively. The model presented here was evaluated for the conditions $i = 0$ and $i = 1$ and the values of N_{hq} and N_{rq} based on the preferred abundance estimate at each locality. Thus, the absolute abundance of hipparionines at the other localities was estimated and expressed relative to the biomass of ruminants represented at Loc. 64, which is set equal to $100m$ kg/km^2. Dividing these biomass estimates by B_{ruminant} and $B_{\text{hipparionine}}$, respectively, yields abundance estimates in units of $100m$/km^2.

These abundance estimates were in turn entered into a NLIN routine in SAS and paired with age estimates from Kappelman et al. (chapter 2, this volume) for the seven localities under consideration. The NLIN procedure was used to fit a sigmoid curve expressed by the Lotka-Volterra equation (Wilson and Bossert 1971) to the data. The results included asymptotic 95% confidence levels on r, the intrinsic rate of population growth, and K, the carrying capacity for hipparionines.

Results

Loc. 64

Loc. 64 is dated to ~10.77 Ma (Kappelman et al., chapter 2, this volume). The fossil assemblage is clearly dominated by bovids. Giraffids are also indicated and a smaller member of the hyaenid genus *Ictitherium*.

A total of 175 cataloged specimens were collected from Loc. 64. Of these, 21 were cataloged as indeterminate. One hundred thirty-two cataloged specimens were identifiable as ruminants and made up 150 identifiable specimens. Thirty-five identifiable specimens were placed in the category Very Small, 73 were Small, 16 were Medium, and 2 were Very Large (fig. 16.1A). Twelve specimens were identified as juvenile. The MNI of adult specimens is 6 and that of juveniles is 2. When MNI is calculated first for each size and age category and then summed, the total MNI-G is 11 (table 16.4). Teeth, phalanges, and podials, all of which are dense and have a high preservation potential, are the most common element types at Loc. 64 (fig. 16.2A). The Loc. 64 ruminant assemblage had a relatively high degree of fragmentation, with a fragmentation index of 57 (table 16.5). The degree of association was correspondingly low, with the possibility of only a few associated teeth (table 16.5).

Body mass estimates for Loc. 64 specimens were possible for 13 metapodials and tibiae (table 16.6). All but one of these estimates was <30 kg and most of these were <15 kg. This contrasts with the size category classifications of all Loc. 64 specimens, in which most specimens were classified as Small, corresponding to a body weight of ~15–30 kg. One specimen, AS92/581, a tibia, yielded a body mass estimate of 103 kg. Thus, larger bovids were present but probably rare or unpreserved due to a taphonomic bias.

Loc. 64 represents a small-bovid dominated assemblage that was probably accumulated after some degree of transport, leading to fragmentation and disassociation.

Loc. 4

Loc. 4 includes the earliest evidence for hipparionines in the Sinap Formation and dates to ~10.69 Ma (Kappelman et al., chapter 2, this volume). Like that of Loc. 64, the Loc. 4 assemblage is dominated by bovids. It also includes, in addition to hipparionines, giraffids, suids, rhinocerotids, felids, hyaenids, percrocutids, rodents, birds, and reptiles. There are 369 cataloged specimens from Loc. 4, and these yielded a total of 172 specimens that were identifiable as either ruminant or hipparionine. Of these, 169 were ruminants and three were hipparionines.

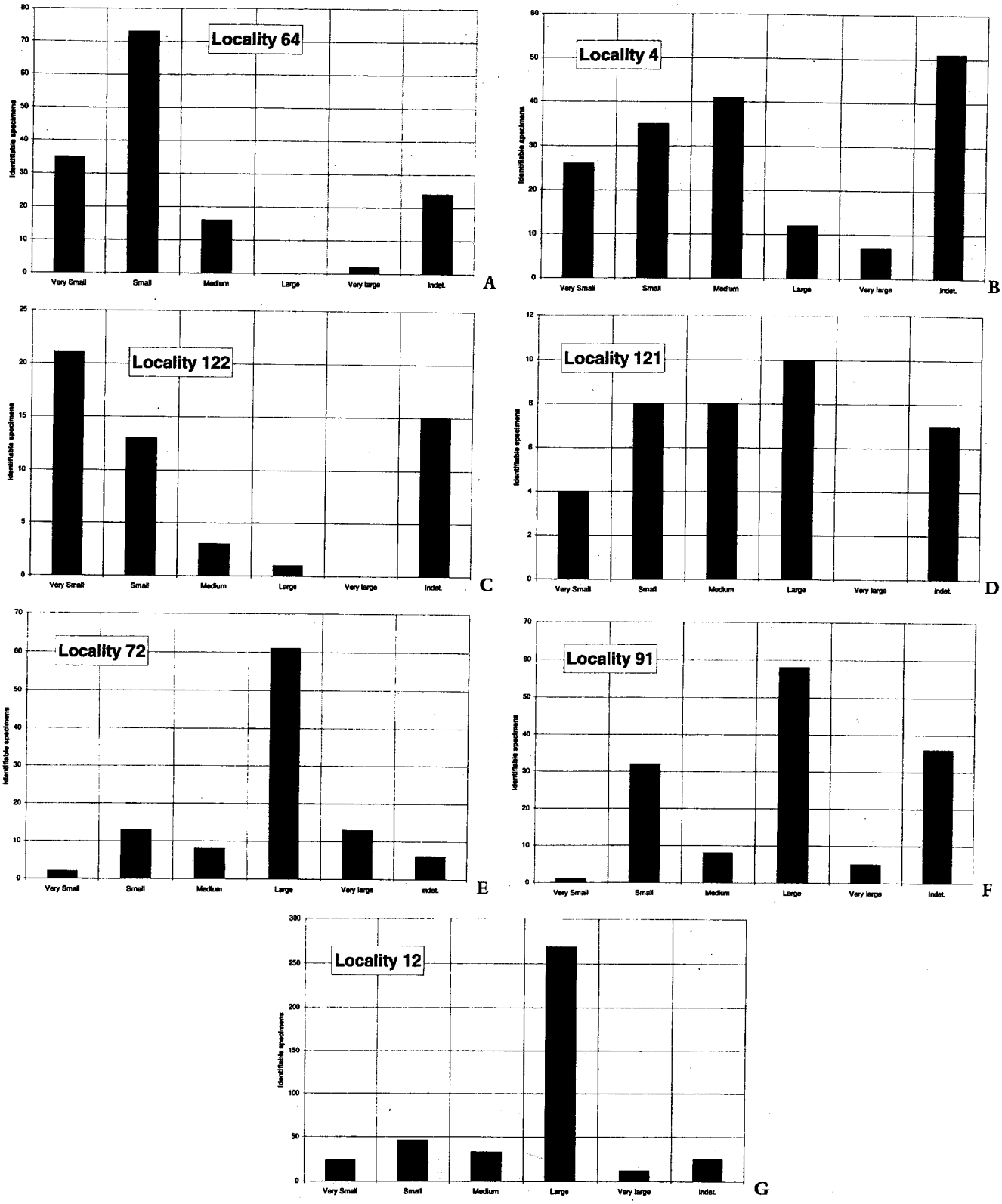

Figure 16.1. Frequency distribution of identifiable specimens by size category. (A) Loc. 64. (B) Loc. 4. (C) Loc. 122. (D) Loc. 121. (E) Loc. 72. (F) Loc. 91. (G) Loc. 12. Size categories are defined in table 16.1.

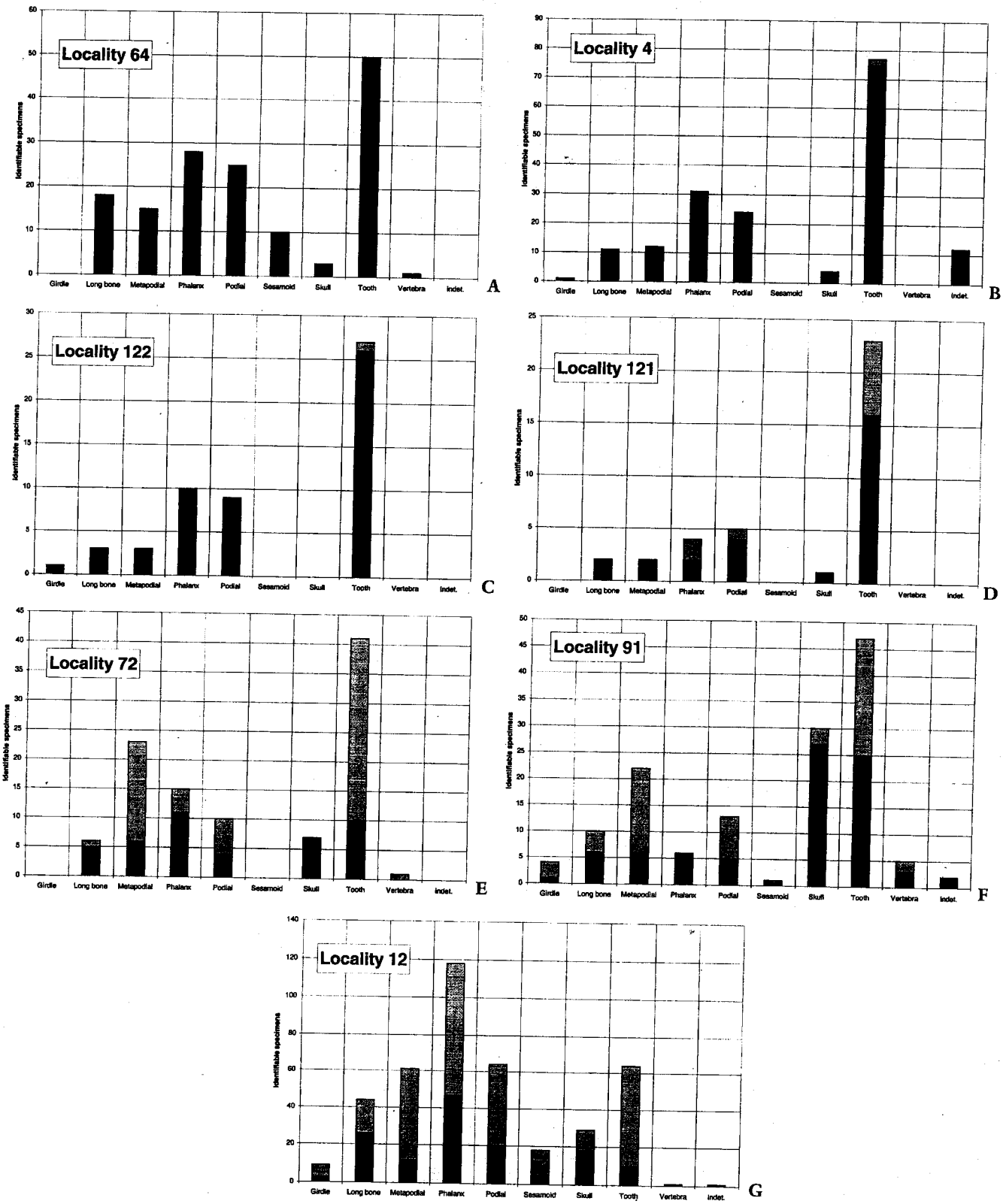

Figure 16.2. Frequency distribution of element types. (A) Loc. 64. (B) Loc. 4. (C) Loc. 122. (D) Loc. 121. (E) Loc. 72. (F) Loc. 91. (G) Loc. 12. Black denotes ruminants and grey denotes hipparionines.

Table 16.4. Raw Measures of Hipparionine and Ruminant Abundance by Locality

Locality	OTU	NISP	WAE	MNI	MNI-G
64	Ruminant	150	1.337	6	11
64	*Hipparionine*	*0*	*0.000*	*0*	*0*
4	Ruminant	169	1.404	4	9
4	*Hipparionine*	*3*	*0.013*	*1*	*1*
122	Ruminant	52	0.481	2	5
122	*Hipparionine*	*1*	*0.007*	*1*	*1*
121	Ruminant	27	0.260	1	4
121	*Hipparionine*	*10*	*0.067*	*1*	*2*
72	Ruminant	43	0.423	2	7
72	*Hipparionine*	*60*	*0.340*	*2*	*3*
91	Ruminant	82	0.760	11	6
91	*Hipparionine*	*58*	*0.493*	*3*	*4*
12	Ruminant	142	1.365	6	11
12	*Hipparionine*	*267*	*1.767*	*5*	*8*

Of the specimens identifiable as ruminants, 26 were categorized as Very Small, 35 as Small, 41 as Medium, nine as Large, and seven as Very Large (fig. 16.1B). Fourteen ruminant specimens were identified as juvenile. The MNI for adult ruminants is 4 and for juveniles is 1. The total MNI-G for ruminants is 9 (table 16.4).

The three specimens identifed as hipparionine are a deciduous premolar, a buccal tooth fragment (possibly of a milk tooth), and an accessory proximal first phalanx missing the epiphysis. These specimens suggest an MNI and an MNI-G of one juvenile.

The fragmentation and association indices for Loc. 4 were high and low, respectively (table 16.5), comparable to those for Loc. 64. Like Loc. 64, some degree of postmortem transport and breakage is probable for Loc. 4.

Body mass estimates for Loc. 4 specimens were possible for 12 ruminant specimens and range between 8 and 50 kg (table 16.6).

Locs. 122 and 121

Locs. 122 and 121 date to ~10.58 and ~10.53 Ma, respectively, and are separated by about 5 m. Both localities are just above the local *"Hipparion"* Datum and document an early increase in hipparionine abundance. The localities are situated on the same slope on the northeastern side of Sinap Tepe. *Hipparion* is present at both localities. However, in the case of the lower locality, Loc. 122, the only *Hipparion* specimen is AS95/684, a deciduous premolar and some associated tooth fragments. This specimen is a surface find and quite possibly may originally derive from Loc. 121, which lies directly upslope from Loc. 122. Thus, hipparionines appear to have been rare or absent at Loc. 122, but by the time of Loc. 121, they appear to have been more common. Indeed, Locs. 121 and 122 may record a period of rapid increase in hipparionine abundance.

The sample sizes at Locs. 122 and 121 are small, 123 and 57 cataloged specimens, respectively. Very Small, Small, and Medium bovids are the main groups represented in both assemblages (fig. 16.1C,D). Giraffids appear to be absent from both localities, possibly as a consequence of small sample size. Ten hipparionine specimens are identified from Loc. 121 compared with only one from the better-sampled Loc. 122 (table 16.4). As in Loc. 64, both localities are highly fragmented, showing a low degree of association,

Table 16.5. Fragmentation and Association Indices for Ruminant and Hipparionine Assemblages by Locality

Locality	OTU	Association Index	Fragmentation Index
64	Ruminant	Very low	57
64	*Hipparionine*	*Not present*	*Not present*
4	Ruminant	3	55
4	*Hipparionine*	*Three specimens only*	*Three specimens only*
122	Ruminant	4	73
122	*Hipparionine*	*One specimen only*	*One specimen only*
121	Ruminant	0	70
121	*Hipparionine*	*Very low*	*Mostly fragmentary*
72	Ruminant	0	79
72	*Hipparionine*	*0*	*52*
72	**Both**	**0**	**62**
91	Ruminant	26	54
91	*Hipparionine*	*9*	*62*
91	**Both**	**19**	**57**
12	Ruminant	27	47
12	*Hipparionine*	*45*	*37*
12	**Both**	**39**	**40**

Table 16.6. Estimated Body Weights of Ruminants from Selected Localities of the Sinap Formation

Specimen Number	Locality	Element	Estimated Body Mass (SD)
ST90-279	64	Tibia	8 (0.46)
ST90-268	64	Metapodial	13 (2.4)
ST90-269	64	Metapodial	20 (3.0)
ST91-274A	64	Metapodial	10 (2.0)
ST91-274B	64	Metapodial	10 (2.0)
ST91-488	64	Metapodial	7 (1.7)
ST91-489	64	Metapodial	8 (1.9)
ST92-1	64	Metapodial	22 (3.1)
ST92-11	64	Metapodial	25 (3.3)
ST92-20	64	Metapodial	12 (2.3)
ST92-28	64	Tibia	11 (0.21)
ST92-581	64	Tibia	103 (15)
ST93-429	64	Metapodial	13 (2.4)
ST94-753	4	Humerus	8 (2.4)
ST93-455	4	Metapodial	11 (2.2)
ST93-465	4	Metapodial	12 (2.3)
ST94-755	4	Radius	12
ST93-425	4	Humerus	13 (4.8)
ST94-768	4	Metapodial	15 (2.6)
ST94-25A	4	Metapodial	15 (2.6)
ST93-322	4	Metapodial	19 (2.9)
ST94-1	4	Metapodial	22 (3.1)
ST92-382	4	Radius	32
ST95-888	122	Tibia	8 (0.67)
ST95-649	121	Radius	35 (2.3)
ST95-650	121	Humerus	61 (6.6)
ST95-655A	121	Metatarsal	24 (15)
ST92-428	91	Metacarpal	24 (3.2)
ST92-448	91	Metapodial	19 (2.9)
ST93-10C	91	Tibia	27 (5.7)
ST93-10D	91	Metatarsal	26 (4.0)
ST93-13	91	Metapodial	34 (2.9)
ST93-2	91	Humerus	720[1] (1.5)
ST93-20	91	Metapodial	620[1] (146)
ST93-42A	91	Humerus	20 (5.2)
ST93-42B	91	Radius	22 (1.5)
ST93-838	91	Radius	649[1]
ST89-291	12	Radius	26 (2.6)
ST92-587	12	Humerus	22 (2.0)
ST93-913	12	Metatarsal	59 (26)
			144
ST95-1202	12	Tibia	44 (12)
ST89-290	12	Humerus	27 (8.1)
ST92-594	12	Metapodial	63 (3.4)
ST93-1181A	12	Metatarsal	29 (6.6)
ST93-1200	12	Radius	9
ST93-842	12	Humerus	217 (76)
ST93-903A	12	Tibia	48 (1.2)
ST95-163	12	Humerus	22 (3.5)

(continued)

Table 16.6. Estimated Body Weights of Ruminants from Selected Localities of the Sinap Formation *(continued)*

Specimen Number	Locality	Element	Estimated Body Mass (SD)
ST95-165	12	Metacarpal	32 (4.1)
			55
ST95-169/181	12	Radius	23 (2.2)
ST95-261	12	Metacarpal	15 (3.3)
			34
ST95-276A	12	Metapodial	12 (2.0)
ST95-311	12	Humerus	8 (1.9)
ST95-329	12	Metatarsal	40 (0.69)
ST95-337	12	Radius	42 (42)
			49
ST95-401	12	Radius	23 (0.33)
ST95-421	12	Metacarpal	19 (0.02)
ST95-574	12	Metatarsal	28 (2.3)
ST95-583	12	Radius	13
ST95-653	12	Radius	14 (0.66)
			17
ST95-663	12	Radius	748[1]

Notes: Estimated body mass is the mean of body mass predictions from nonlength measurements using the bovid regressions of Scott (1990). Standard deviations (SD) are shown when estimated body mass is based on more than one nonlength measurement. Body mass predicted by bone length is shown below the body mass estimate when available.

[1]Estimates based on the ruminant regressions of Scott (1990).

(table 16.5) and are dominated by denser element types (teeth, phalanges, and podials) (fig. 16.2C,D).

Some body mass estimates were possible for specimens from Locs. 122 and 121 (see table 16.6). Three specimens from Loc.121 yield estimates of 61, 35, and 21 kg. The only body size estimate available from Loc. 122 is 8 kg. These estimates confirm the importance of smaller body sizes at both localities (fig. 16.1D), although the increase in hipparionines at Loc. 121 adds a number of Large individuals to the size distribution at the site.

Loc. 72

Loc. 72 dates to ~10.08 Ma (Kappelman et al., chapter 2, this volume). The fossil assemblage includes hipparionines, bovids, giraffids, suids, hyaenids, rhinocerotids, oryctero-podids, and chelonians. Hipparionines are more common here than in earlier localities, with relative abundance estimates ranging from 30.0% (MNI-G) to 58.2% (NISP) (table 16.7).

There are 183 cataloged specimens from Loc. 72, yielding a total of 43 and 60 identifiable specimens for ruminants and hipparionines, respectively. Ruminants were assigned to size categories as follows: Very Small (two), Small (13), Medium (eight), Large (one), and Very Large (13) (fig. 16.1E).

Six hipparionine specimens were juveniles, yielding an MNI of 1 for juveniles. The MNI for adult hipparionines is 2, and the MNI-G for all hipparionines is 3. Ruminants had an MNI of 2 for adults and 1 for juveniles and a total MNI-G of 7 (table 16.4).

Body mass estimates were possible for two hipparionine metapodials from Loc. 72: 172 kg and 234 kg (table 16.8).

Fragmentation was high for both ruminants and hipparionines at Loc. 72 and no associated specimens were identified among the ruminant and hipparionine specimens (table 16.5). The taphonomy of Loc. 72 appears similar to that for the earlier localities.

Loc. 91

Loc. 91, located on the east side of Sinap Tepe, is dated to ~9.98 Ma (Kappelman et al., chapter 2, this volume), and is only slightly older than Loc. 12. The Loc. 91 fossil assemblage

Table 16.7. Relative Abundance of Sinap Hipparionines by Locality

	Relative Abundance (%)			
Locality	NISP	WAE	MNI	MNI-G
64	0.0	0.0	0.0	0.0
4	1.7	0.9	20.0	10.0
122	1.9	1.4	33.3	16.7
121	27.0	20.4	50.0	33.3
72	58.2	44.6	50.0	30.0
91	41.4	39.4	21.4	40.0
12	65.3	56.4	45.5	42.1

Table 16.8. Estimated Body Weights of Hipparionines from Selected Localities of the Sinap Formation

Specimen Number	Locality	Element	Estimated Body Mass (SD)
ST93-289	72	Metacarpal	234 (47)
ST93-509	72	Metatarsal	172
ST92-419	91	Humerus	222 (24) 322
ST92-426	91	Radius	199 (36)
ST93-9	91	Metacarpal	182 (49) 283
ST93-11	91	Metatarsal	171
ST93-27	91	Femur	262
ST93-52	91	Metatarsal	210 (33) 262
ST93-56	91	Metacarpal	170 (35)
ST93-6	91	Metatarsal	183 (4)
ST93-7	91	Metatarsal	221 (79) 262
ST91-373	12	Metatarsal	160 (15) 240
ST95-422	12	Tibia	295 (46)
ST91-367	12	Metatarsal	180 (8)
ST91-419	12	Femur	227 (40)
ST91-420	12	Metacarpal	139 (9) 240
ST91-780	12	Metatarsal	206 (16) 276
ST93-1185A	12	Tibia	176 (19)
ST93-1193A	12	Metatarsal	164 (25) 269
ST93-1207A	12	Metatarsal	153 (15) 262
ST93-1213A	12	Metatarsal	219 (66) 279
ST93-1213A	12	Tibia	200 (27)
ST93-840A	12	Metacarpal	205 (49) 261
ST93-841A	12	Radius	184 (22) 186, 170[1]
ST93-860B,A	12	Humerus	176
ST93-860B,A	12	Radius	163 (31)
ST95-1054A	12	Metatarsal	291 (62) 322
ST95-131A	12	Metacarpal	154 268
ST95-149	12	Metacarpal	175 (36)
ST95-161	12	Metatarsal	175 (36)
ST95-418	12	Radius	160 (50)
ST95-513	12	Metacarpal	175 (28) 283
ST95-513	12	Radius	165
ST95-514-63	12	Metacarpal	187 272
ST95-603	12	Humerus	187 (6)
ST95-606	12	Humerus	194
ST95-615	12	Metatarsal	147 (20) 276

Notes: Estimated body mass is the mean of body mass predictions from nonlength measurements using the equid regressions of Scott (1990). Standard deviations (SD) are shown when estimated body mass is based on more than one nonlength measurement. Body mass predicted by bone length is shown below the body mass estimate when available.

[1]Estimate based on length including the ulna (measurement U1 of Scott 1990).

includes hipparionines, bovids, giraffids, hyaenids, rhinocerotids, and chelonians. Hipparionine relative abundance is similar to that determined for Loc. 72, with relative abundance estimates ranging from 21% (MNI) to 41% (NISP) (table 16.7).

There are 139 cataloged specimens from Loc. 91. These yielded 140 specimens that were identifiable as either ruminant or hipparionine. Of these, 82 were ruminants and 58 were hipparionines.

Ruminants belonging to the Very Small size category appear to have been rare; only one specimen classified as Very Small. The remainder of the ruminant specimens were either Small (32), Medium (eight), Very Large (five), or Size Indeterminate (36) (fig. 16.1F). The large number of Size Indeterminate specimens was probably due to the number of horn cores that were not possible to categorize according to relative size. Teeth and skull elements (mostly horn cores and partial mandibles) were the most commonly preserved ruminant elements (fig. 16.2F).

Of the 58 hipparionine specimens, one was classified as juvenile. Metapodials and teeth were the most common elements in the Loc. 91 hipparionine assemblage (fig. 16.2F). The abundance of hipparionine metapodials is unsurprising, given that the third metapodial is dense and large and hence more likely to be preserved than the smaller, more fragile bovid metapodials. The presence of accessory metapodials in hipparionines may also inflate their abundance relative to ruminants. Most surprising at Loc. 91 is the complete absence of hipparionine phalanges.

For the purposes of assessing degree of fragmentation and association (table 16.5), the Loc. 91 fossils were divided into ruminant and hipparionine assemblages. This was done for two reasons: (1) because ruminants and hipparionines have a different number of bones and elements with dissimilar physical attributes, the two groups will have different preservation potentials; and (2) ruminants and hipparionines may have exploited different habitats, possibly influencing their deposition after death. The first of these two factors is taphonomic whereas the second is paleoecological and taphonomic. Regarding the second factor, Shotwell (1955, 1958) speculated that multiple biotic communities might be preserved at a single site of deposition and be represented differentially based on their distance from the depositional setting. Thus, Shotwell divided fossil assemblages into distal and proximal communities. Fragmentation and association are relevant to this question, because differential fragmentation and association across taxa suggest degree of postmortem transport and hence membership in a proximal or distal community.

Fragmentation was greater and association less among the 58 hipparionine fossils identified from Loc. 91 than among the 82 identifiable specimens in the ruminant assemblage from Loc. 91 (table 16.5). The fragmentation index of hipparionines from Loc. 91 was 62, as opposed to an index of 54 for the ruminants. Even greater was the contrast in degree of association: the association index for the hipparionines was 9 compared with 26 for the ruminant specimens.

Figure 16.1F shows the distribution by body size category for Loc. 91. None of the Loc. 91 ruminant specimens yielded a body mass estimate <15 kg, and two Very Large specimens (presumed giraffids) exceeded 600 kg (table 16.6). The hipparionines from Loc. 91 range between 165 and 285 kg (table 16.8).

Loc. 12

Loc.12 (~9.6 Ma), located on the top of Delicayincak Tepe to the east of Sinap Tepe, is the best sampled and most diverse fauna of the localities we studied and includes hipparionines, bovids, giraffids, rhinocerotids, proboscideans, carnivorans, orycteropodids, and chelonians. The hipparionines, bovids, and rhinocerotids (in that order) dominate the assemblage in terms of number of specimens. Relative to the ruminants, hipparionine abundance at Loc. 12 ranges from 42% (MNI) to 65% (NISP) (table 16.7). Even by the lowest estimate (42%), hipparionines have increased to high levels of abundance in the approximately 1 m.y. between their first appearance and Loc. 12 times.

Most of the specimens from Loc. 12 were excavated during the 1995 field season and came from two distinct bone pockets. Trenches between these bone pockets revealed a low to zero bone density. Within these pockets, bone density was high and many associated elements were impressively preserved. For example, entire distal limbs of hipparionines were preserved intact and still articulated: even tiny sesamoids were preserved in articulation.

The taphonomy of Loc. 12 appears unique. The hipparionine assemblage has a high association index of 45 and a low fragmentation index of 37. The degree of association among the ruminant fossils is also high (association index of 27), comparable to that of the Loc. 91 ruminants. Similarly, fragmentation is also low (47) for the Loc. 12 ruminants, but is not as low as that for the Loc. 12 hipparionines (table 16.5).

Loc. 12 is an assemblage characterized by an abundance of hipparionines, a diversity of taxa, and by high levels of association and low levels of fragmentation, suggesting minimum postmortem transport.

Body mass estimates for a number of ruminants (table 16.6) and hipparionines (table 16.8) were derived for Loc. 12 specimens. Ruminants spanned all five size categories (fig. 16.1G) from Very Small (<15 kg) to one Very Large individual (presumably a giraffid) with an estimated body mass of 748 kg. One bovid specimen classified as Large yields a body mass estimate of 217 (standard deviation, 76) kg. This specimen establishes the presence of large bovids at Loc. 12; the large standard deviation suggests complex scaling relationships among different postcranial dimensions.

The body mass distribution of hipparionines from Loc. 12 ranges from <150 kg to nearly 300 kg (table 16.8). On the basis of body size alone, it is not unreasonable to argue that multiple hipparionine taxa were present at Loc. 12 (see Bernor et al., chapter 11, this volume).

Discussion

The oldest localities in the Sinap Formation are dominated mainly by small bovids, whereas subsequent localities record the first appearance and subsequent increase in abundance of the three-toed horse, *"Hipparion."* Estimates of relative abundance of hipparionines vary, depending on the specific measure used. For example, at Loc. 12, NISP gives a relative abundance estimate of 65% for hipparionines; in contrast, MNI-G yields an estimate of 42%. The WAE estimate suggests an intermediate abundance of 56%. Based on these varying estimates, multiple interpretations are possible for the Loc. 12 fauna. Hipparionines may be either the dominant basal herbivore (according to NISP) or a common and significant basal herbivore still outnumbered by ruminants (according to MNI and MNI-G). In either case, hipparionines are a critical element of the fauna, but the choice of relative abundance measure has implications for the precise role of hipparionines as well as for interpretations of faunal change.

This sensitivity of interpretation to the choice of abundance measure is particularly evident when Loc. 12 is compared to Loc. 91. According to NISP, hipparionine relative abundance increases from 41% to 65% over the short stratigraphic interval from Loc. 91 to Loc. 12. A very rapid increase in hipparionine numbers is implied by NISP. In contrast, according to MNI-G, hipparionine abundance remains stable from Loc. 91 to Loc. 12 (table 16.7). The choice of relative abundance measurement is essential to understanding faunal change and our study illustrates the importance of exercising caution when estimating relative abundance. We recommend the use of multiple measures of relative abundance.

In cases where different relative abundance measures are in significant disagreement, it is necessary to select the best measure of relative abundance based on sample size and taphonomic data. For example, in the cases of Locs. 121 and 122, the fossil sample size is small and the MNI and MNI-G estimates clearly appear to overestimate the abundance of hipparionines. NISP and WAE estimates are probably preferable. Association of specimens is low and there is no reason to argue for the higher hipparionine abundances indicated by MNI and MNI-G.

The situation is very different at Loc. 12, where high levels of association suggest that MNI or MNI-G may be the most appropriate estimate of relative abundance. Thus, based on taphonomic information such as the number of associated specimens and considerations of sample size, it is possible to suggest a probable best estimate of relative abundance drawn from among the four measurements of relative abundance calculated here.

We selected the best estimators of hipparionine and ruminant relative abundance from among NISP, WAE, MNI, and MNI-G for the localities included in our study. In the cases of Locs. 4, 122, and 121, NISP is likely the best estimate of relative abundance. No evidence of associated specimens at these localities argues against the use of either MNI or MNI-G. Instead, the small sample sizes at Locs. 121 and 122 suggest that NISP is likely the best estimate at these localities. Loc. 4 is probably best represented by either NISP or WAE, with NISP preferred for sake of consistency. At Loc. 72, the low rate of associated specimens disallows the use of MNI or MNI-G as a preferred estimate, but the very high estimate (58%) given by NISP compared with the other estimates suggests that WAE may be a better estimator for this locality. The larger number of hipparionine elements with a likelihood of being preserved could be responsible for an inflated estimate of abundance if NISP were used. The higher rates of associated specimens at Locs. 91 and 12 suggest that MNI-G may be the best estimate in these cases. Thus, the best estimators of relative abundance appear to be NISP at Locs. 4, 122, and 121; WAE at Loc. 72; and MNI-G at Locs. 91 and 12 (table 16.9).

Using the probable best estimates of relative hipparionine abundance, it is possible to assess the rate of increase in hipparionine abundance following the *"Hipparion"* Datum. We applied the abundance model described in the Methods section to the probable best estimates of relative abundance and evaluated for the conditions $i = 0$ and $i = 1$. These results are shown in table 16.9. The condition $i = 0$ corresponds to the hypothetical case in which ruminants and hipparionines do not compete. The results in table 16.9 suggest that biomass would have increased over 250% if hipparionine immigrants did not compete with established ruminant taxa. It would seem unlikely that such a change would occur in the absence of a major environmental change. Alternatively ($i >> 0$ or $i = 1$), ungulate herbivore biomass may have remained relatively constant, with the increase in hipparionines coming at the expense of ruminant taxa. The apparent increase in hipparionines reflected at the localities studied here would be due in part to a decrease in ruminant numbers. Immigration of a hipparionine species that was either competitively superior to Old World bovid or ruminant taxa or preadapted ("exapted" in Gould and Vrba 1982) to concurrent environmental change is then implied.

The density estimates for the case $i = 1$ (shown in shaded cells of table 16.9) were entered into a NLIN routine in SAS with age estimates for the seven localities under consideration from (Kappelman et al., chapter 2, this volume). As mentioned earlier, the NLIN procedure was used to fit a sigmoid curve expressed by the Lotka-Volterra equation (Wilson and Bossert 1971) to the data. The results included asymptotic 95% confidence levels on r, the intrinsic rate of population growth, and K, the carrying capacity for hipparionines. The results are shown in figure 16.3. The density estimates of abundance for each locality are plotted alongside their best fit Lotka-Volterra curve. The increase in hipparionine numbers recorded at the Sinap Formation clearly fits a sigmoidal pattern, indicating a good fit between the Lotka-Volterra model and the late Miocene *"Hipparion"* Datum data from the Sinap Formation. The theoretical predictions of the Lotka-Volterra model would thus appear applicable to the *"Hipparion"* Datum natural experiment.

A nonsigmoidal (and gradual) pattern of increase for hipparionines would imply a slow process of adaptation

Table 16.9. Estimated Absolute Abundances Calculated for Two Hypothetical Cases

Locality	Probable Best Estimate	$N_{hipparionine}$	$N_{ruminant}$	$N_{hipparionine}$ (kg)	$N_{ruminant}$ (kg)	Coefficient of Infringement (i)	$A_{hipparionine}$ ($m$kg/km)	$A_{ruminant}$ ($m$kg/km)	$N_{hipparionine}$ (m/100km)	$N_{ruminant}$ (m/100km)
64	NISP	0	150	0.0	12680.7	1	0.0	100.0	0.00	118.29
4	NISP	3	169	573.5	14286.9	1	3.9	96.1	2.02	113.72
122	NISP	1	52	191.2	4396.0	1	4.2	95.8	2.18	113.36
121	NISP	10	27	1911.8	2282.5	1	45.6	54.4	23.84	64.37
72	WAE	0.340	0.423	65.0	35.8	1	64.5	35.5	33.74	41.98
91	MNI-G	4	6	764.7	507.2	1	60.1	39.9	31.45	47.17
12	MNI-G	8	11	1529.4	929.9	1	62.2	37.8	32.53	44.73
64	NISP	0	150	0.0	12680.7	0	0.0	100	0.00	118.29
4	NISP	3	169	573.5	14286.9	0	4.0	100	2.10	118.29
122	NISP	1	52	191.2	4396.0	0	4.3	100	2.27	118.29
121	NISP	10	27	1911.8	2282.5	0	83.8	100	43.81	118.29
72	WAE	0.340	0.423	65.0	35.8	0	181.8	100	95.08	118.29
91	MNI-G	4	6	764.7	507.2	0	150.8	100	78.86	118.29
12	MNI-G	8	11	1529.4	929.9	0	164.5	100	86.03	118.29

Notes: Hypothetical cases are coefficient of infringement (i) = 1 or = 0. C = 100 *m*kg/km; body mass (*hipparionine*) = 191.2 kg; body mass (ruminant) = 84.5 kg. See table 16.3 for explanation of variables.

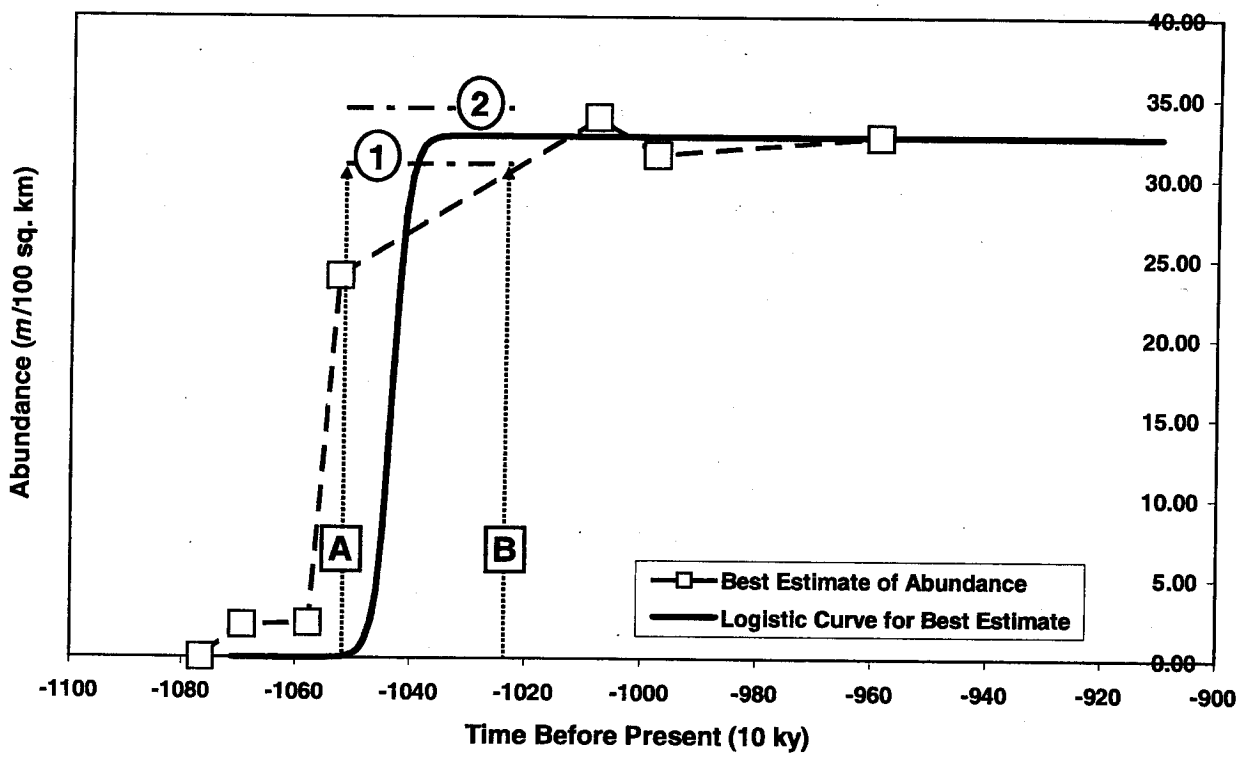

Figure 16.3. Plot of the best estimate of hipparionine abundance from each locality expressed in the units $m/100$ km^2 using the best-fit logistic growth curve. Symbols: [A] marks the time at which $N = K/2$ for the upper asymptotic 95% confidence limit for r and the best-fit estimate for b ($r = 1.0356$ $m/1000$ ky-km^2; $t(K/2) = 10.52$ Ma); [B] marks the time at which $N = K/2$ for the lower asymptotic 95% confidence limit for r and the best-fit estimate for b ($r = 0.4195$ $m/1000$ ky-km^2; $t(K/2) = 10.23$ Ma); (1) indicates the lower asymptotic 95% confidence limit for K ($K = 30.9$ $m/100$ km^2); (2) indicates the upper asymptotic 95% confidence limit for K ($K = 34.3$ $m/100$ km^2).

after immigration from the New World. Instead, the rapid and apparently sigmoidal increase of hipparionines after immigration suggests either open ecospace rapidly occupied by immigrant hipparionines and an accompanying explosive increase in basal herbivore biomass or the entrance of a competitively superior basal herbivore. It is worth noting that the peak of apparent hipparionine density is reached by ~10 Ma at Loc. 72. It is only after this time that the apparent diversification of *"Hipparion"* in Turkey ensues (see Bernor et al., chapter 11, this volume). Together, these events—the rapid increase to carrying capacity followed by a pulse of diversification—support a model of hipparionine diversification driven by competition and leading to niche separation and speciation.

Conclusions

An evaluation of the degrees of fragmentation and association of fossil specimens from seven localities in the Sinap Formation suggests preferred methods for estimating how taxonomic abundance varies between localities. An approach using a simplifying model allows estimates of hipparionine abundance relative to ruminants to be expressed in units of biomass and density. These estimates permit initial tests (using a nonlinear curve fitting procedure) of the patterns of increase in hipparionine numbers following their immigration from the New World. The results presented here suggest:

1. The increase of equids following the Old World *"Hipparion"* Datum fits a sigmoidal pattern (such as the Lotka-Volterra model);
2. The carrying capacity of immigrant equids depends on the degree to which *"Hipparion"* competed with the established ruminant dominated fauna at Sinap; and
3. If competition between ruminants and equids approached zero, large herbivore biomass at Sinap would have had to increase by >250% to accommodate the increase in equid abundance suggested by the data.

Thus we present for future study the hypothesis that hipparionine diversification was driven by competition leading to niche partitioning following a period of rapid population increase to a high carrying capacity.

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