8. The effects of collection strategy and effort on faunal recovery

A case study of the American and French collections from the Shungura Formation, Ethiopia

G.G. ECK
Department of Anthropology
University of Washington
Seattle, Washington, USA
ggeck@u.washington.edu

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Abstract

Although preserved by sediments that were contemporaneously deposited by the same river and lake system and exposed in contiguous areas, the American and French collections of fossil specimens from the Shungura Formation of southwestern Ethiopia produce differences in specimen counts that are surprisingly large. Some of these differences were caused by well-documented differences in geography and geology of the formation and the history of the research efforts of the two expeditions. Other differences apparently arose because of factors that are less well documented. The following paper briefly describes the well-documented factors leading to differences in specimen counts, including differences in the sizes of areas explored, months of active fieldwork, and numbers of sites excavated for the recovery of macro- and microfaunal remains. Further, it proposes methods for discovering factors that are less well documented, likely related to differences in research strategies and the inherent richness of the sediments explored. And finally, it suggests how the collections might be best used to avoid the effects of biases that they apparently contain.

Introduction

It is widely recognized that the analysis of counts and relative frequencies of individuals representing taxa provide much richer evidence for environmental interpretation and reconstruction than does analysis of simple presence and absence. Useful analyses of counts and relative frequencies in fossil assemblages, however, require that they represent these quantities in the living communities from which they derive and, as taphonomists regularly warn, the pathway between living individual and recovered fossil is a complex one that is affected by many factors both natural and human.

Using catalogs of fossil specimens collected from the Shungura Formation of southwestern Ethiopia, the following paper explores some of the natural and some of the human factors that affected the collection of these specimens and thus their counts and relative frequencies.

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These factors include the intrinsic richness of the sediments, their areas of exposure, and the collection strategies and effort used in the recovery of the specimens. Lessons are drawn as to how these effects might be better understood and the biases that they introduced into the collections minimized. Readers are directed to Alemseged et al. (2006) for additional analysis of this dataset and alternative interpretations of some of the patterns discussed.

Geographic, Geologic, and Historic Setting

The Shungura Formation is located in the lower Omo Valley of southwestern Ethiopia, west of the Omo River and north of Lake Turkana (Brown and de Heinzelin, 1983) (Figure 1). The composite stratigraphic section of the formation measures nearly 800 m and radiometric ages indicate that it covers the time span from 3.6 to 1.05 Ma (Feibel et al., 1989) (Figure 2). The sedimentary cycles of the formation are grouped into 12 members (Basal, A, B, C, D, E, F, G, H, J, K, and L), each (except the Basal Member) commencing with a volcanic tuff designated by the same letter. The sequence is typically composed of fluvial sediments, but episodes of lacustrine deposition also occurred, particularly in the Basal Member, upper Member G, and upper Member L (de Heinzelin and Haesaerts, 1983).

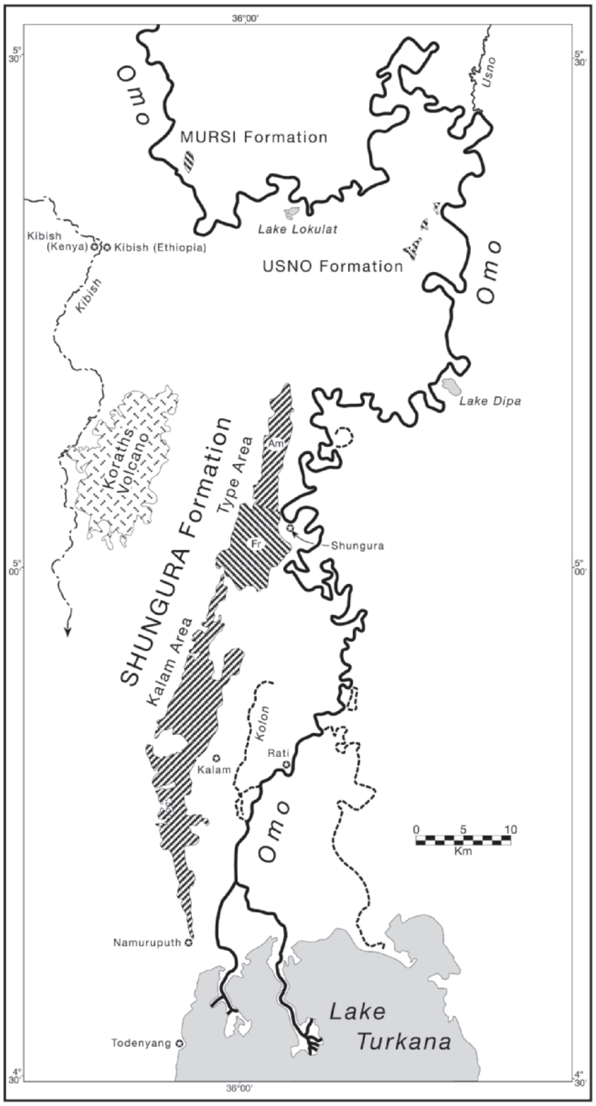
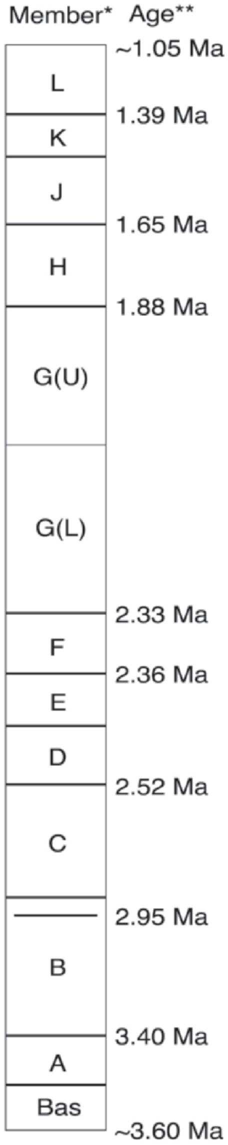


Figure 1. Omo Group formations of the lower Omo Valley.

The Mission Scientifique de l'Omo, led by C. Arambourg in 1932 and 1933, was the first expedition to conduct systematic paleontological work in the lower Omo Valley (Arambourg, 1947; Coppens et al., 1976). Heselon Mukiri, field assistant of L.S.B. Leakey, visited the exposures in the early 1940s and made unprovenanced fossil collections that were placed in the Coryndon Museum (now the National Museums of Kenya). In 1954, F.C. Howell examined these collections during a prolonged visit to eastern and southern Africa and discussed with Leakey the advisability of working in the lower Omo Valley one day. Howell then visited the Turkana Basin, during July of 1959, and collected vertebrate fossils from exposures of the Shungura Formation, which he left in the care of local authorities in southern Ethiopia. During this visit, Howell recognized the protracted sedimentary sequence, the volcanic ash accumulations, and intraformational faulting exposed in the lower Omo Valley. Seven years later, at the urging of the Emperor Haile Selassie, the Ethiopian Government gave permission for a joint international scientific consortium to work there. In 1966, the International Omo Research Expedition (IORE) was created



* Member thicknesses are scaled to stratigraphic thickness.
** Geologic ages are radiometric and from Feibel *et al.* (1989) except the first and the last, which are extrapolations.

Figure 2. Composite stratigraphic section of the Shungura Formation.

under the direction of Leakey, Arambourg, and Howell (Coppens et al., 1976). In 1967, three contingents of the IORE independently explored the sedimentary exposures of the lower Omo Valley. The French one, under the direction of Arambourg and Coppens, worked principally in what came to be known as the "Type Area" of the Shungura Formation. The Kenyan contingent, under the direction of R.E.F. Leakey, and the American contingent, under the direction of Howell, worked further to the north, the Kenyans in the Kibish and Mursi Formations, and the Americans in the Usno Formation. In 1968, disappointed with the size or richness of the Mursi and Kibish Formations, Leakey moved to the eastern shores of Lake Rudolf (now Lake Turkana), which he had observed from the air-contained extensive sedimentary outcrops. For similar reasons, Howell arranged with Coppens to move south and jointly explore the Type Area of the Shungura Formation. It was agreed that the Americans would work the Type Area north of the "watering road," while the French would work south of it. This boundary would later be formalized by de Heinzelin and Haesaerts (1983), who drew the boundaries of Geological Sectors 15/16 and 17 generally along the watering road. Only in the later years of the expedition, mostly after 1972, did both the French and American contingents begin to explore the Kalam Area of the Shungura Formation, located to the southwest of the Type Area. The American contingent ceased work in the lower Omo Valley at the end of the 1974 field season, the French ended their work there in 1976. The two research teams conducted their research separately with little or no coordination of research strategies or collection methods, except for the watering road between them.

In the nine years of fieldwork between 1967 and 1976, neither contingent mounted an expedition in 1975, nearly 50,000 paleontological specimens were collected: 21,858 by the Americans and 27,409 by the French (Figure 3). Most of these were recovered during surface survey, but large paleontological excavations were also carried out, producing 6,692 American and 3,417 French specimens (see, for example, Johanson et al., 1976).

The vast majority of these are of mammals because neither contingent regularly collected lower vertebrates or invertebrates and plant specimens were very rare. Only 10% of the American collection comprises nonmammalian

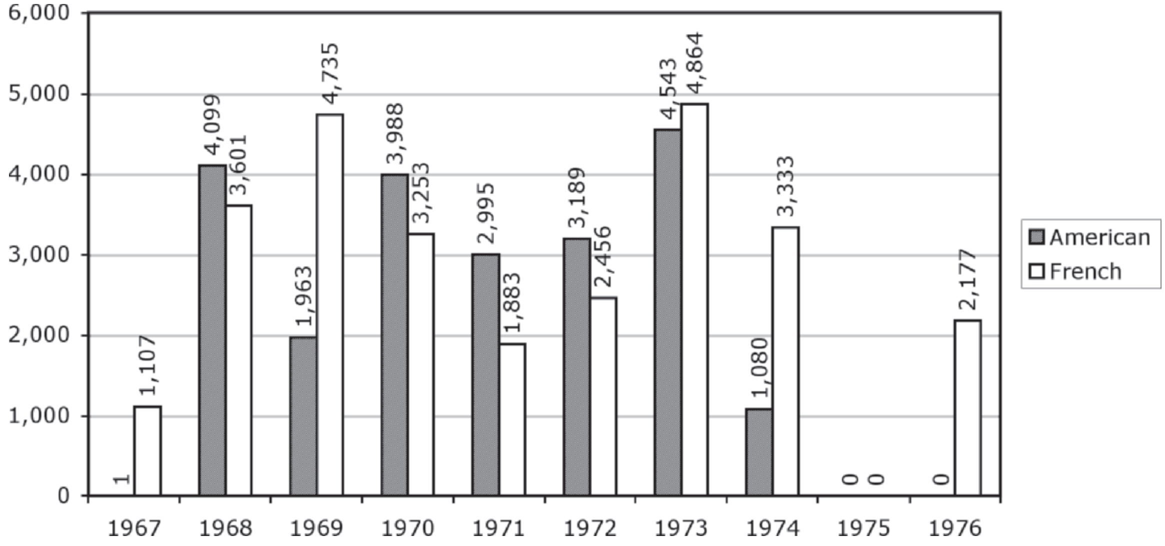


Figure 3. Numbers of specimens collected by each contingent by year.

specimens, while they constitute 6% of the French collection.

Among the 42,481 mammalian specimens that can be identified at the ordinal level, 11 orders are represented, with artiodactyls clearly predominating, primates making a surprisingly strong showing, and carnivores having the smallest numbers among the mammals of medium to very large body size, as is expected (Table 1).

Table 2 presents the numbers of mammalian specimens that have been identified at the family level.

Table 1. Numbers of specimens identified at the order level

	American	French	Total	Percentage
Artiodactyla	11,053	20,731	31,784	74.819
Primates	3,632	3,052	6,684	15.734
Proboscidea	743	1,259	2,002	4.713
Perissodactyla	390	510	900	2.119
Rodentia	724	96	820	1.930
Carnivora	149	113	262	0.617
Chiroptera	10	0	10	0.024
Insectivora	10	0	10	0.024
Lagomorpha	3	3	6	0.014
Hyracoidea	3	0	3	0.007
Tubulidentata	1	0	1	0.002
Total	16,718	25,764	42,481	

Factors Affecting the Numbers

DEPOSITIONAL AND EROSIONAL FACTORS

As noted above, nearly all of the richly fossiliferous deposits of the Shungura Formation consist of fluvial sediments laid down by a major river similar in size to the modern Omo River. These sediments consist of gravels and sands deposited in the river channel, light-colored silts deposited on the banks of the river near the channel, and dark-colored, silty clays deposited during periods of high water more distal to the channel.

Fossilization was clearly most complete in specimens from the channel sands and gravels. These were very well mineralized, hard, and resistant to breakage as they eroded onto the surface. Unfortunately, because they had in most cases undergone multiple episodes of burial and erosion and substantial transport by the river, they were already in a fragmentary state when they were deposited. Predepositional damage to specimens from the channel sands and gravels thus produced a strong bias towards the densest limb bones and limb bone parts, bovid horn cores, jaw

Table 2. Number of specimens identified at the family level

Macromammals	American	French	Total
Bovidae	6,295	11,007	17,302
Hippopotamidae	2,448	5,472	7,920
Cercopithecoidea	3,482	2,917	6,399
Suidae	1,770	3,087	4,857
Elephantidae	517	1,062	1,579
Giraffidae	535	1,007	1,542
Equidae	332	397	729
Deinotheriidae	225	196	421
Hominidae	147	13 5	282
Rhinocerotidae	55	109	164
Felidae	85	42	127
Hyaenidae	16	22	38
Hystricidae	15	10	25
Camelidae	5	16	21
Mustelidae	12	3	15
Chalicotheriidae	3	4	7
Procaviidae	3	0	3
Orycteropodidae	1	0	1
Total	15,946	25,486	41,432
Micromammals	**American**	**French**	**Total**
Muridae	611	60	671
Sciuridae	63	7	70
Viverridae	36	12	48
Cricetidae	23	6	29
Soricidae	10	0	10
Dipodidae	3	4	7
Bathyergidae	1	5	6
Thryonomyidae	5	1	6
Leporidae	3	3	6
Hipposideridae	5	0	5
Lorisidae	3	0	3
Emballonuridae	3	0	3
Pteropodidae	1	0	1
Total	767	98	865

fragments, teeth, and tooth fragments. Complete or partial crania and mandibles were rare and articulated or partially articulated skeletons or limbs were unknown from these sediments.

In contrast, specimens deposited in the near channel silts were less well mineralized and more subject to postdepositional damage as they eroded onto the surface. The erosional surface of silt deposits were thus often littered by a rich array of bone fragments, but only those of very dense foot bones, bovid horn cores, jaw fragments, and teeth were complete enough to identify to taxon and body part. Excavations into the silts carried out by the American contingent showed, however, that they often contained beautifully complete specimens, including complete crania and mandibles and partially articulated skeletons (see Johanson et al., 1976). Postdepositional damage typically occurred as the weathering front in the sediments, usually 10 to 15 cm below the surface, moistened the specimens, reducing them to the fragments noted above, which then dispersed as they eroded onto the surface.

The more distal over-bank deposits of dark-colored, silty clays rarely if ever produced fossil specimens.

It also seems that the teeth, especially isolated teeth, of large mammals suffered greater rates of fragmentation than did those of medium-sized animals. Impressions derived from surface survey suggest that a larger proportion of the teeth of the larger pigs, hippos, rhinos, deinotheres, and elephants occurred as fragments than those of smaller animals. This increased fragmentation might have resulted from the fact that the teeth of large mammals contain a greater proportionate volume of dentine and cementum. Especially their worn teeth, containing proportionately less enamel, may have been more subject to predepositional damage in the high-energy channel deposits. In the lower energy silts, dentine and cementum were poorly mineralized, leading to postdepositional damage. It thus may be that dental specimens of large mammals are underrepresented in the collections by comparison to those of the smaller animals. How large this disproportion might be is not known.

The sample of specimens scattered on the erosional surface of the Shungura was thus clearly biased towards those most resistant to damage: jaw fragments and teeth, dense postcranial elements, and bovid horn cores. It was also probably biased against the teeth of large mammals. Whether these biases differed between the American and French collections areas is not known.

FACTORS OF TIME AND SPACE

The French collection is substantially larger than the American, as noted above and shown in Figure 3. There are many reasons why this is so, but one is clearly the time spent searching for fossils. Although both contingents had field seasons of roughly the same length (about 10 weeks), the French had expeditions to the Shungura Formation in 1967 and 1976 when the American did not (see Figure 3).

In the Type Area, exposures of Members K and L do not occur in either the American or French areas, nor do exposures of Member J in the American area. Counts of fossils from these members in Table 3 and Figure 4 are of specimens recovered in the Kalam Area and, for reasons that will become clear below, they will not be considered further. The Basal Member is not exposed in the American area of the Type Area and the exposures of Member A are very small, explaining the big differences in numbers between the areas.

Also of importance is the fact that the French area of exposure in the Type Area is substantially larger than the American. Given the same numbers of specimens in the ground, larger areas of exposure will produce larger numbers during surface survey. This difference can be accurately measured on de Heinzelin's Geological Map of the Shungura Formation (de Heinzelin, 1983). I have done this by scanning the map to produce a digital image, separating the areas of the different members using Photoshop, and measuring the area of each member using NIH Image J. Because the Kalam Area of the Shungura Formation remains largely unmapped, I could make these measurements only for exposures of the members in the Type Area. I have followed de Heinzelin's (1983) convention of dividing Member G into

Table 3. Numbers of specimens found in each member

	American	French
Ba	2	34
A	60	429
B	2,118	1,637
C	3,821	3,414
D	993	540
E	3,814	2,026
F	4,473	4,585
G(L)	4,714	11,220
G(U)	503	1,549
H	499	695
J	222	150
K	287	447
L	361	492
Total	21,867	27,218

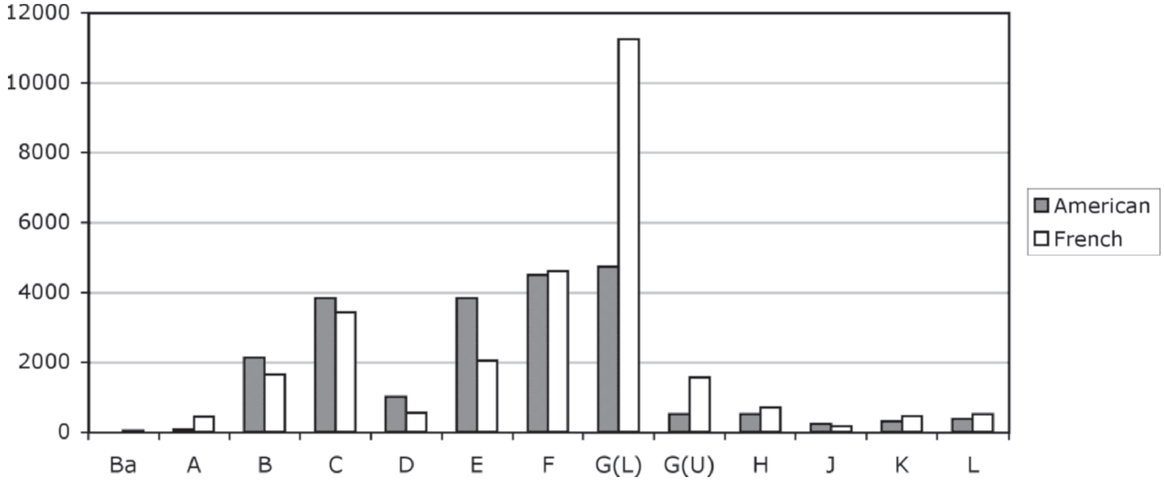


Figure 4. Numbers of specimens found in each member.

an upper and lower part because lower Member G (Member G(L)) consists mostly of fluvial deposits that are richly fossiliferous, while upper Member G (Member G(U)) is composed mainly of lacustrine deposits that are poorly so. My results can be seen in Table 4 and Figure 5 (note that this approach to data standardization differs from that of Alemseged et al., 2006).

Although the absolute values cited in Table 4 are subject to some uncertainty because of the uncertainty in the scale of de Heinzelin's map, stated as approximately 1:10,000, the relative differences are very accurate because of the precision of the maps. The French area of exposure is substantially larger than the American, but much of the difference lies in Member G(U), which is poorly fossiliferous.

The factors of time and space probably explain much of the difference in the sizes of the American and French collections, but, as will be seen below, other factors play a role as well.

Table 4. Areas of exposure of members in the Type Area in km^2

	American	French
Ba	0.000000	0.021607
A	0.001545	0.078394
B	0.256655	0.272918
C	2.449999	1.281457
D	1.794332	1.048239
E	1.447085	1.179028
F	1.555917	1.607318
G(L)	3.807007	4.549295
G(U)	0.555443	4.250264
H	0.051012	0.588353
J	0.000000	0.026139
K	0.000000	0.000000
L	0.000000	0.000000
Total	11.918995	14.903012

THE FACTOR OF MULTIPLE SPECIMENS REPRESENTING SINGLE INDIVIDUALS

Fossil individuals can of course be represented in the record by a very large range of specimen counts, ranging from one to perhaps many thousands. Differential fragmentation rates of individuals, leading to widely ranging counts, obscure the more interesting variation in numbers of individual organisms. Given the fluvial environments of deposition, which are dominant in the Shungura Formation, it is likely that most surface specimens, derived from transported remains, came from different individuals and that specimen counts roughly represent individual counts. This was clearly, however, not always the case. During surface survey, one

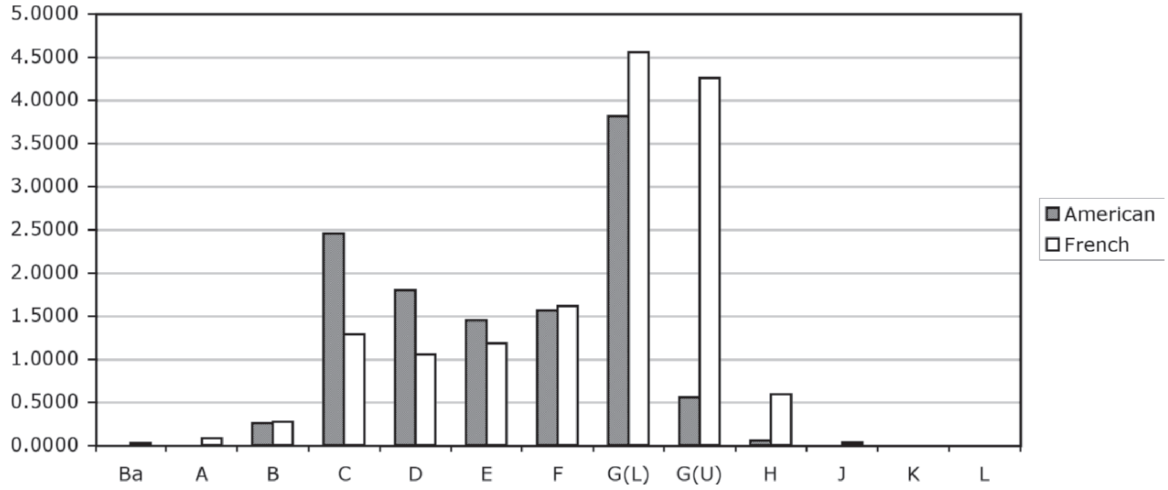


Figure 5. Areas of exposure of members in the Type Area in km^2.

often encountered patches of specimens that, based on similarity in preservation, individual age, and complementarity of elements, certainly or almost certainly belonged to single individuals. Beginning late in the 1968 field season, the American contingent began to enter into their field catalogs information indicating which specimens comprised single individuals, based on the above mentioned characteristics. This notation was later extended to the specimens collected in earlier 1968 as well. It is thus possible, in the American catalog, to remove multiple specimens representing single individuals, bringing the specimen counts more in line with the ideal individual counts. The French contingent did not regularly keep similar information and, as the French catalog now stands, it is less often possible to know which single specimens likely represent individuals and which ones do so as a group. In the analyses described below, it is assumed that the number of individuals represented by multiple specimens is essentially the same in the two collections and thus that this factor does not cause important differences in numbers. Whether or not this assumption is warranted can only be determined by future work on the French collection.

FACTORS OF COLLECTION STRATEGY AND EFFORT

The difference in numbers of excavated specimens occurring in the two collections is easily explained by the fact the Americans spent more time at excavation. Various members of the contingent, directed by M. Splingaer, D.C. Johanson, D.D. Dechant-Boaz, N.T. Boaz, H.B. Wesselman, D. Cramer, and myself, over several years carried out 17 excavations at 15 different localities producing 6692 specimens (see Johanson et al., 1976; Dechant-Boaz, 1994 for details). Some of these were only a few m^2 in extent, while the largest, in Locality 398, located at the bottom of Member F, covered 178 m^2 and produced 2642 specimens. In contrast, the French carried out one large excavation, directed by C. Guillemot, in Locality Omo 33, also located at the bottom of Member F, which produced most of the 3417 specimens recovered from the locality.

Differences in effort and probably luck explain the differences in micromammal recoveries too. Luck played a role in that concentrations of micromammals seem to be very rare in the Shungura Formation and their occurrence is very difficult if not impossible to predict. During the 1970 field season, J.J. Jaeger recovered modest numbers in the French area. In 1972 and 1973, H.B. Wesselman sampled many localities in the American area and recovered most of the micromammals in the American collection. Both used special techniques in excavating and wet washing sediments that are very different from methods used to recover the larger mammalian fossils (see Wesselman, 1984).

Differences in strategy and effort surely affected numbers of specimens collected during surface survey by both contingents, but these are more difficult to disentangle because neither contingent kept detailed records in this regard. From late in the 1968 field season until the middle of the 1972 field season, I directed crews that collected most of the surface specimens recovered from the American area. In late 1968, I decided, given the very large numbers of surface specimens, to collect only a limited set of those found, but to collect all of these. The collected set included: all recognized specimens of primates and carnivores, no matter how small or fragmentary; all complete or relatively complete crania and mandibles, all upper and lower jaw fragments with teeth, all complete or very nearly complete isolated teeth, and all astragali of other mammalian taxa. In addition, all bovid horn cores and all bovid and camelid distal metapodials were collected. Because of the seemingly disproportionate fragmentation of the teeth of large mammals discussed above, I collected teeth of large pigs, rhinos, deinotheres, and elephants that were more fragmentary than those of other mammals other than primates and carnivores. This surface collection strategy was also generally followed by American crews in the years after 1972. The American collection is thus clearly biased, in most cases, towards cranial specimens. Whether or not the French collection is similarly biased, but perhaps in other ways, is less well documented. I think there is a way to discover biases in both collections, as explicated below.

Differences in Numbers Caused by Differences in Collection Strategy and Effort

Of the major factors controlling specimen numbers—intrinsic richness of the sediments, areas of exposure, and collection strategy and effort—only areas of exposure are accurately enough documented, by de Heinzelin's Geologic Map, to allow numerical corrections for the specimen counts based on this factor. In the discussion below, I will thus investigate specimen densities, the number of specimens divided by the area of exposure of the member, rather than counts. Because the Kalam Area is essentially unmapped, Members J, K, and L, which principally crop out there, are excluded from further discussion. Similarly, because the Basal Member is not exposed in the American portion of the Type Area and the exposures of Member A are very small, these members too will be excluded. I will thus investigate specimen densities only from Members B through H. Excavated specimens, both micro and macro, have also been excluded because of the known differences in collection effort between the areas or rates of pre- and postdepositional damage between surface and excavated specimens.

Calculation of the densities of specimens of macromammals recovered on the surface of the two parts (American and French) of the Type Area gives the values presented in Figure 6 (counts of specimens used to calculate the densities can be found in the Appendix).

An intriguing pattern is apparent, one in which the highest density alternates between the American and French areas as one moves from Members B to H. Although the absolute values vary greatly from highs in Member B and lows in G(U) and the differences vary greatly as well, with the biggest in Member C and the smallest in G(U), I think that the

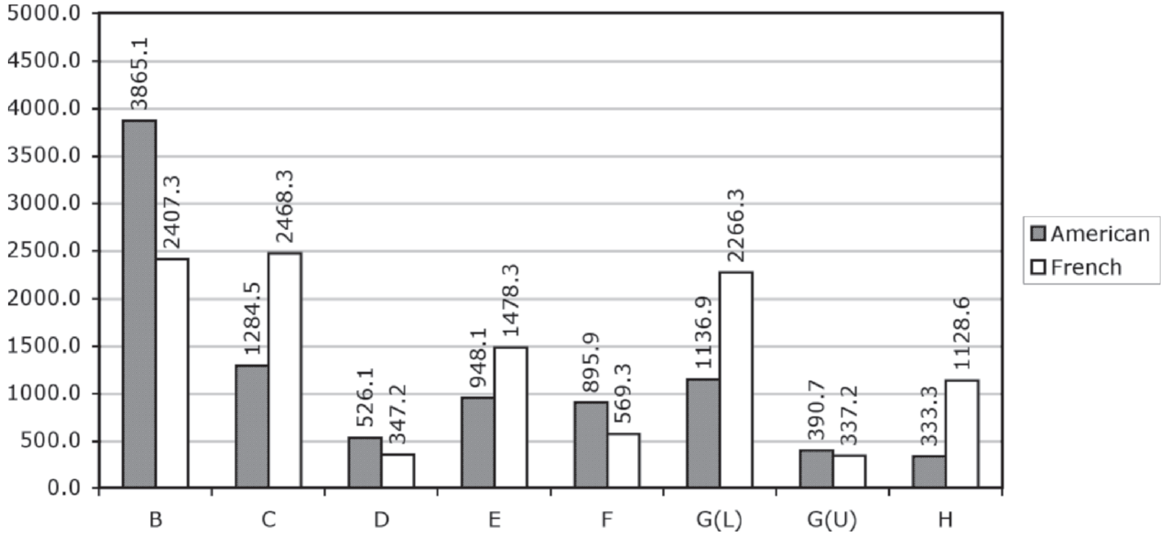


Figure 6. Densities of macromammal specimens (specimen count/exposure area).

important pattern is seen in the simple alternation of highest densities. I argue below that it is caused by intrinsic differences in numbers of fossil specimens preserved in the two areas of each member and by the differential distribution of especially rich surface occurrences of specimens. I further argue that significant differences in numbers caused by differences in collection strategy or effort produce a different pattern that will become apparent below. Because I know, as explained above, or suspect that different families of macromammals experienced different collection intensities, the following analyses are organized by family, beginning with the Hominidae.

HOMINIDAE

I choose to begin this discussion with the Hominidae because of all the mammals they were certainly the most sought after. Howell had come to the Omo to find hominids, among other things. The French clearly recognized their importance as well. Competition between the two camps in the hominids they found was clear. They were also egged on by Leakey's successes at Koobi Fora. I think that the effort to find hominids was great on both sides and the strategy clear, collect them all.

The densities of hominid specimens are shown in Figure 7. In both the American and French collections, one hominid individual is represented by a large number of fragments, the American specimen, L894–1, with 31 fragments from Member G(U) and the French specimen, Omo 323–896, with 21 fragments from Member G(L). In these cases, the counts for the specimens have been reduced to one in Figure 7. Importantly, the densities of hominid specimens show the alternating pattern seen in the macromammals as a whole. These densities are principally determined by the numbers of isolated teeth, but even the densities of jaw fragments, based on a total of only 15 specimens, show the pattern as seen in Figure 8.

That the hominids, surely the most intensely searched for of all the mammals, share the alternating density pattern with the total macromammal sample, even though they consti-

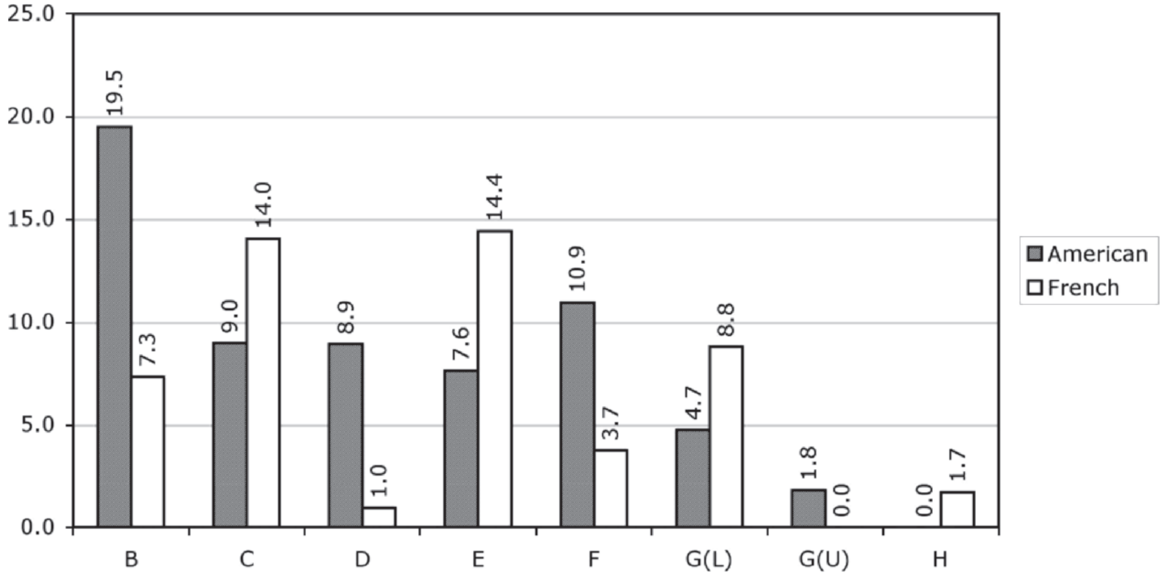


Figure 7. Densities of hominid specimens.

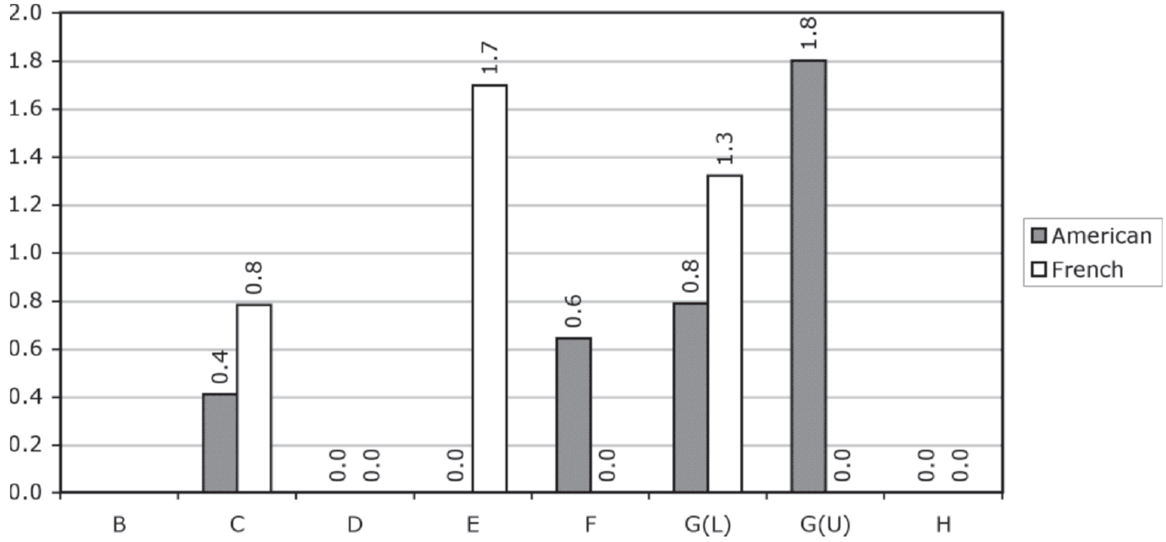


Figure 8. Densities of hominid jaw fragments.

tute only 0.5% of it, suggests to me that the alternating pattern results from factors other than differences in collection strategy and effort between the two contingents.

CERCOPITHECIDAE

Because of Howell's and my interests in monkeys, they too were collected with great effort, as noted above. One might expect a strong bias in the counts and densities of monkey specimens towards the American collection. This expectation is partially met in that the differences in monkey densities in Members E and G(L) are not as great as they are for the macromammals as a whole, and they are reversed in Member H, as can be seen in Figure 9. The bias towards the American collection is not as strong, however, as one might have expected.

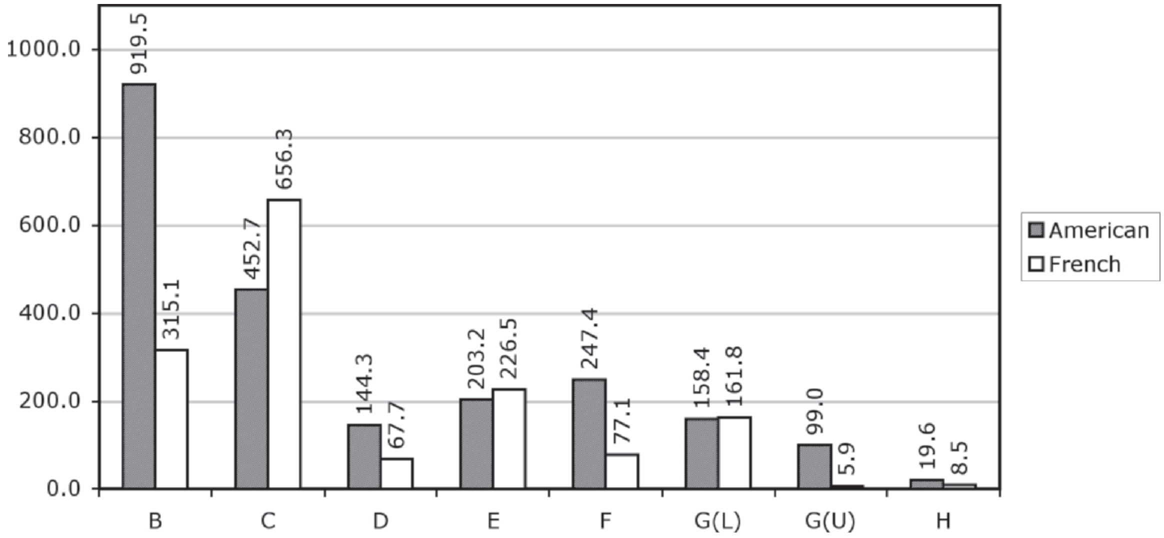


Figure 9. Densities of monkey specimens.

A weak bias towards the American collection is also seen in the densities of all monkey dental specimens, both complete and fragmentary teeth. The differences are small in Member E and the pattern is reversed in Member G(L) and H, as can be seen in Figure 10.

The bias towards the American collection is weaker yet, or perhaps disappears, if one looks only at the densities of complete teeth, removing all fragments from the counts (Figure 11). Only Member H is now out of alternating pattern and its densities are determined by a total of only four specimens. That the French were less compulsive about collecting tooth fragments is also suggested by the fact that 47% of their dental sample is composed of fragments, compared with 55% of the American sample.

The alternating pattern of high densities is again well established in the combined

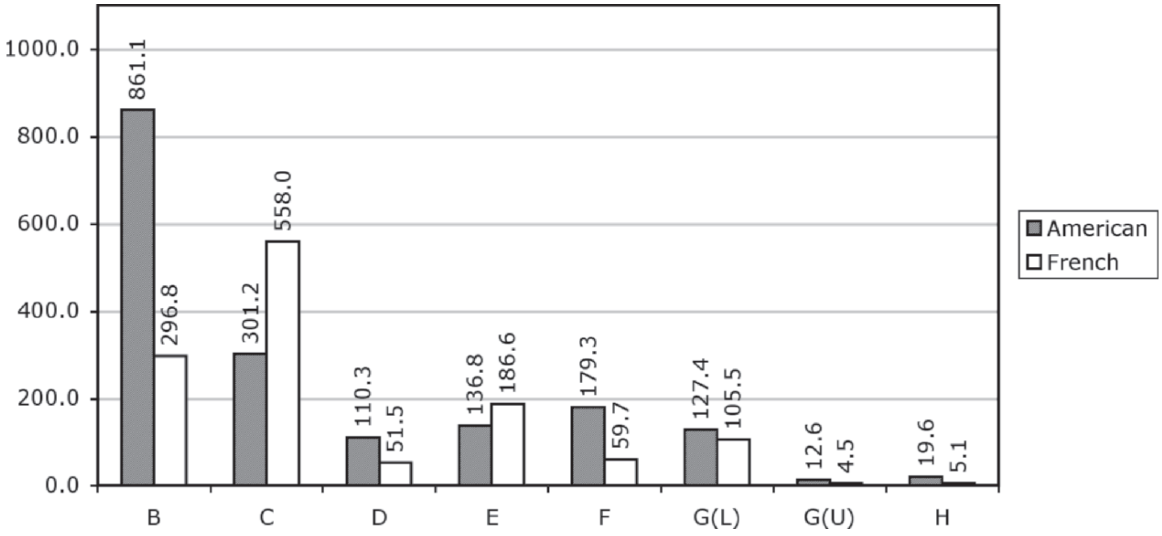


Figure 10. Densities of monkey complete and fragmentary isolated teeth.

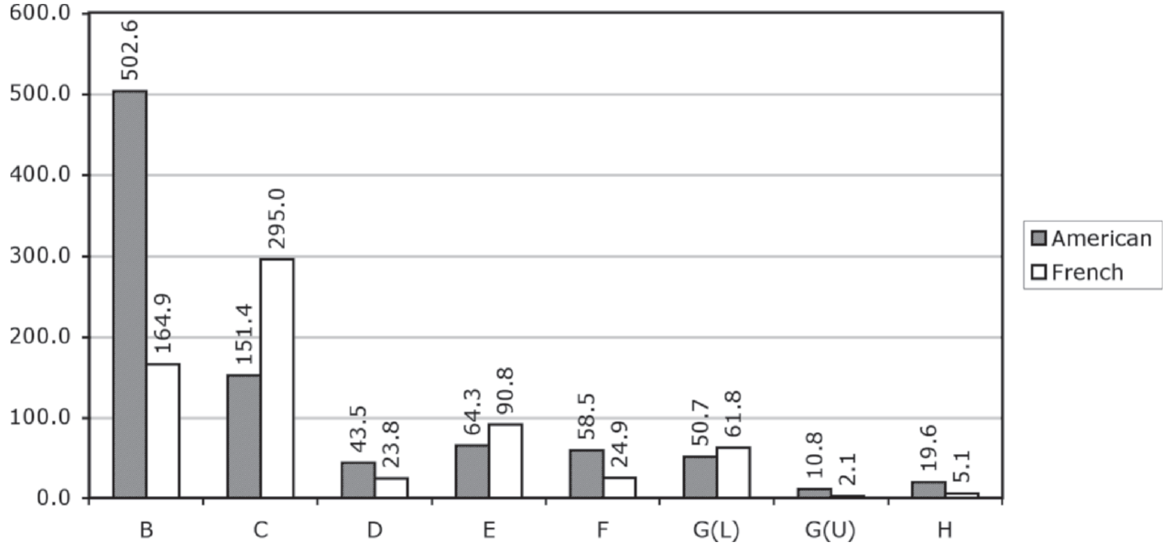


Figure 11. Densities of complete monkey teeth.

densities of complete teeth, jaw fragments, and complete and partial crania and mandibles. Only Member H is reversed, but the densities are determined by only four specimens (Figure 12). It would seem then that when it came to well preserved parts of monkey skulls the French were just as intense in their collecting as the Americans were. Only tooth fragments are biased in the American favor.

The same cannot be said when in comes to monkey postcrania. Here there is a very clear and strong bias in the American favor. Americans consistently collected more and a wider variety of postcranial elements (Figure 13), collecting more than twice as many as the

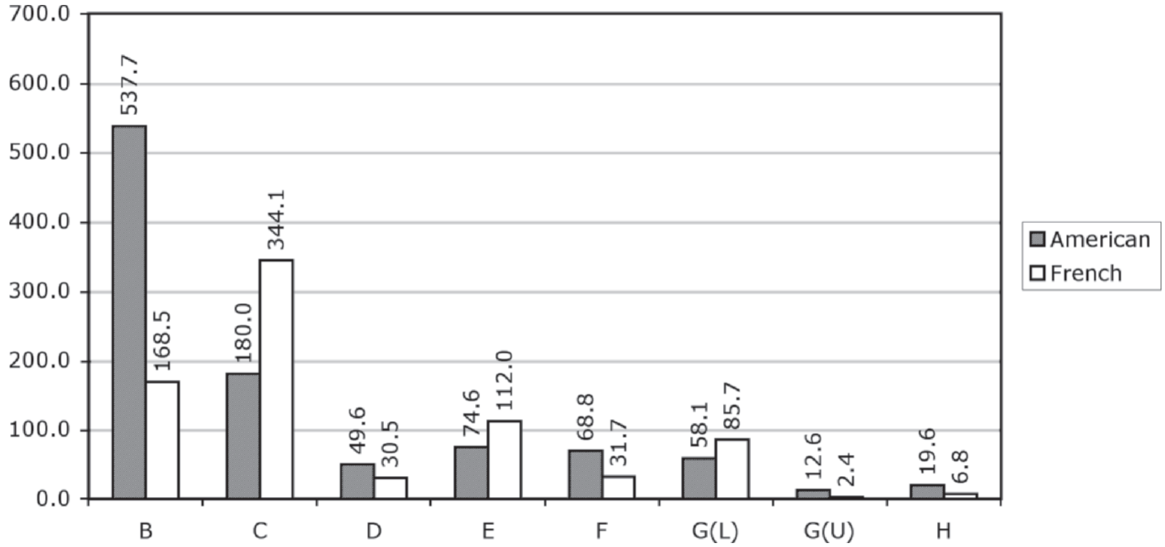


Figure 12. Densities of monkey complete teeth, jaw fragments, and complete and partial crania and mandibles.

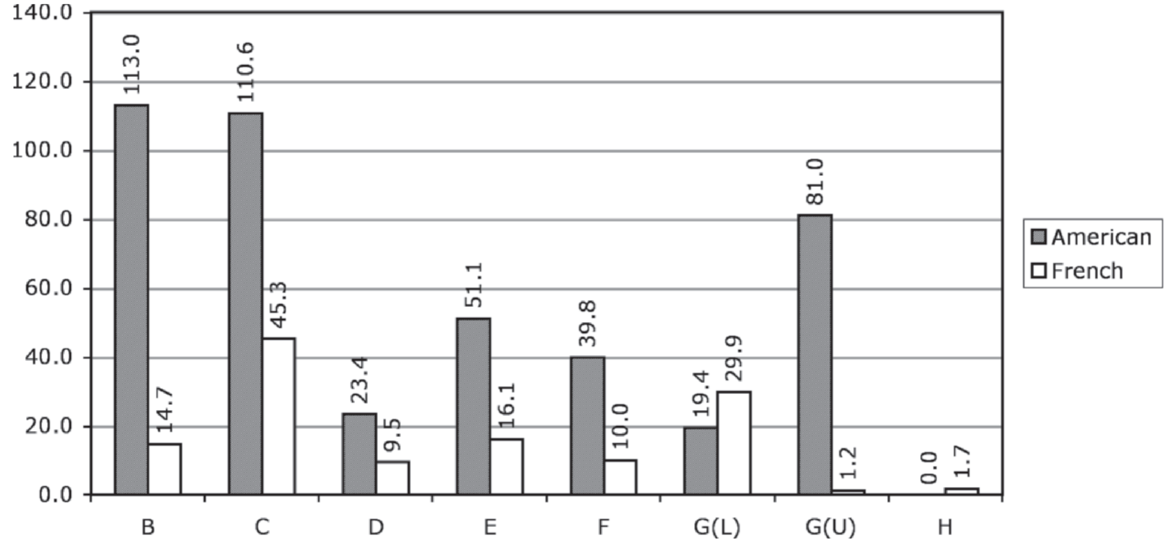


Figure 13. Densities of monkey postcrania.

French did, with average density three times that of the French. Clearly the Americans were much more compulsive than the French when it came to monkey postcrania.

The monkey densities suggest, that when high densities alternate between the two collections as one moves from Member B to Member H, they do so because of differences in intrinsic numbers of specimens within the sediments of the American and French areas. I think it highly unlikely that either the Americans or the French would have left undiscovered or uncollected the large numbers of highly valued specimens required to produce the observed differences in surface densities. The alternating pattern of high densities signals similarity in collection strategy and effort. When, however, densities are clearly biased towards one collection or the other, as they are for monkey postcrania, this signals differences in strategy and effort.

CARNIVORA

Even as early as 1968, Howell had long harbored a strong interest in the evolution of carnivores and encouraged the American survey teams to intensely search for and collect carnivore specimens of medium to large body size. One might thus expect that the American collection would be biased towards these very rare taxa (a total of only 181 specimens were collected by both teams from the surface of Sectors 1 though 27). The expected bias does not appear though, for, except for Member C, the alternating pattern of densities is seen (Figure 14).

ELEPHANTIDAE

Elephants are big and thus have the fortune of being easy to find, but the misfortune of being hard to carry and to store. The French had special interests in them because Coppens was writing a dissertation on elephant evolution. The Americans had a somewhat different interest because of their known potential for dating sediments. Specimens of elephant teeth were apparently equally sought by both contingents as can be seen in their alternating densities, being information rich and easy to carry (Figure 15).

The Americans were not as diligent, however, when it came to the heavier and more cumbersome cranial, maxillary, and mandibular specimens. The densities of these have a distinct French bias (Figure 16).

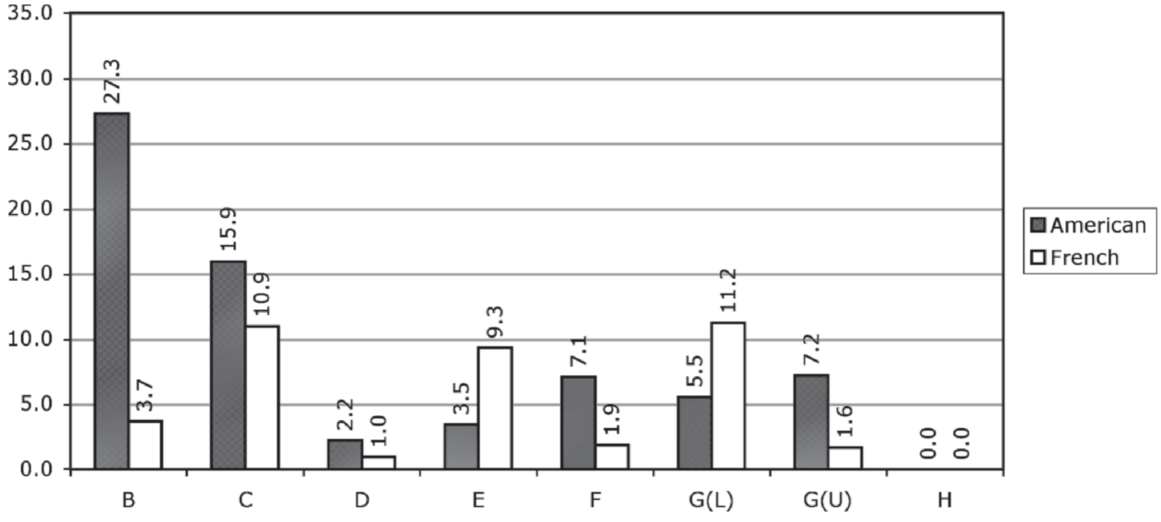


Figure 14. Densities of carnivore specimens.

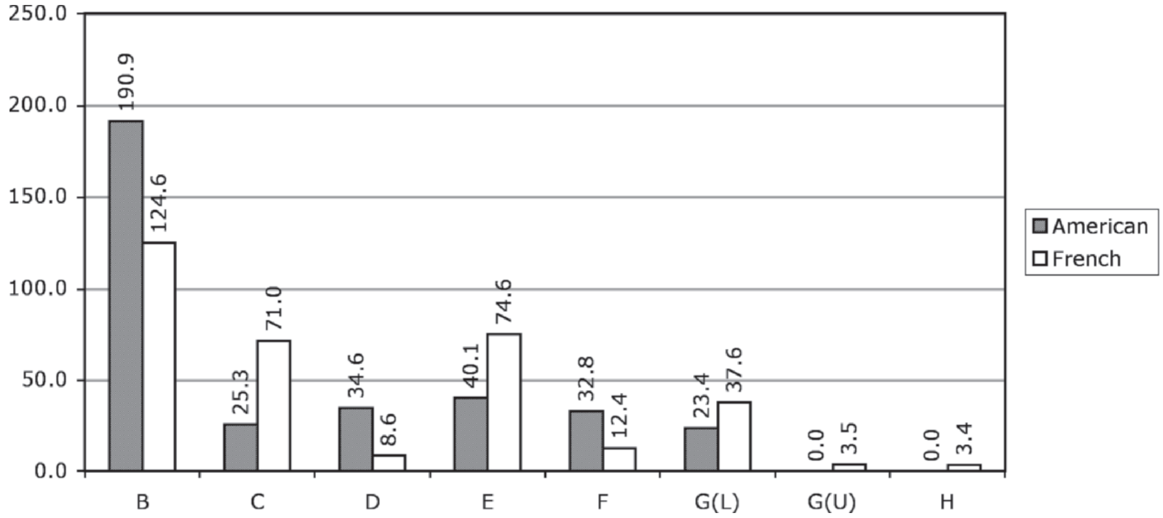


Figure 15. Densities of elephant dental specimens.

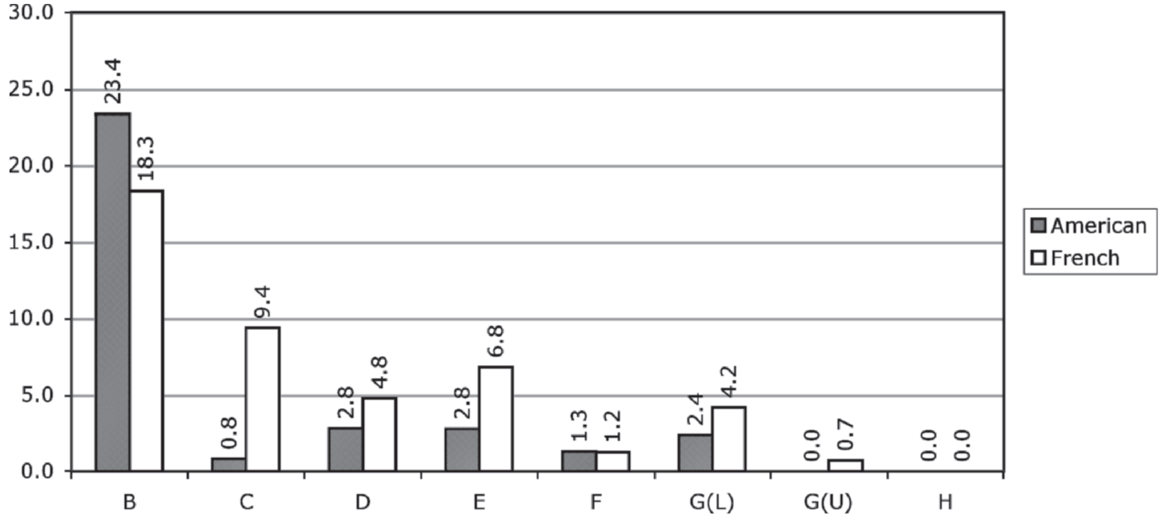


Figure 16. Densities of elephant crania and jaw fragments.

And clearly elephant postcrania were almost entirely a French affair, being important for evolutionary studies, but much less so for dating (Figure 17).

The American bias against postcrania is clearly apparent in the elephant densities. Even astragali did not fare well; only one was collected by the Americans, whereas the French recovered 13.

HIPPOPOTAMIDAE

Hippos are very common elements in the Shungura fauna and may have suffered because of their ubiquity. In addition, as mentioned above, their worn teeth tended to fragment at high rates. The French were clearly more dedicated to the recovery of hippo specimens in general (Figure 18).

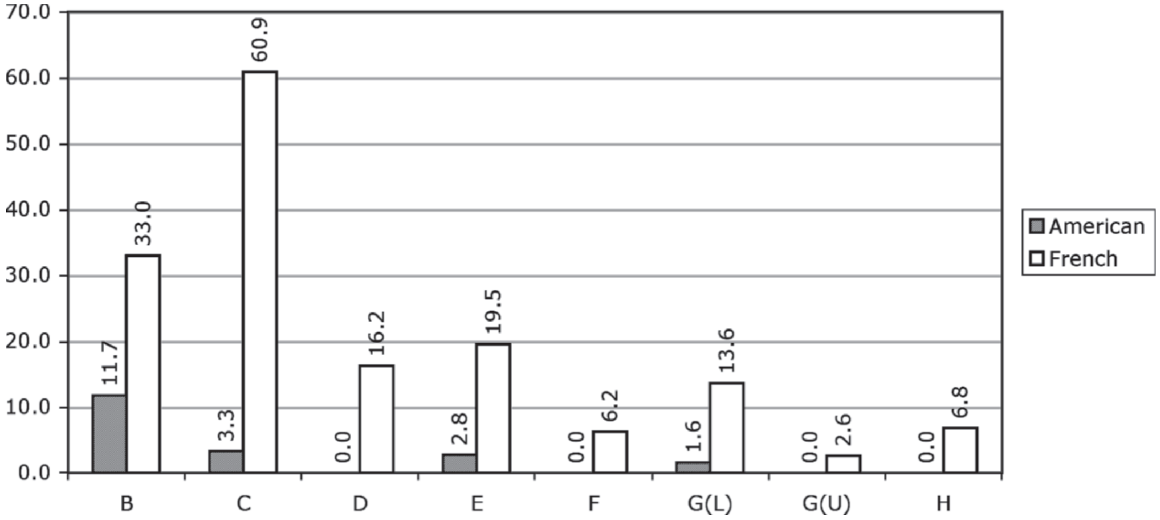


Figure 17. Densities of elephant postcrania.

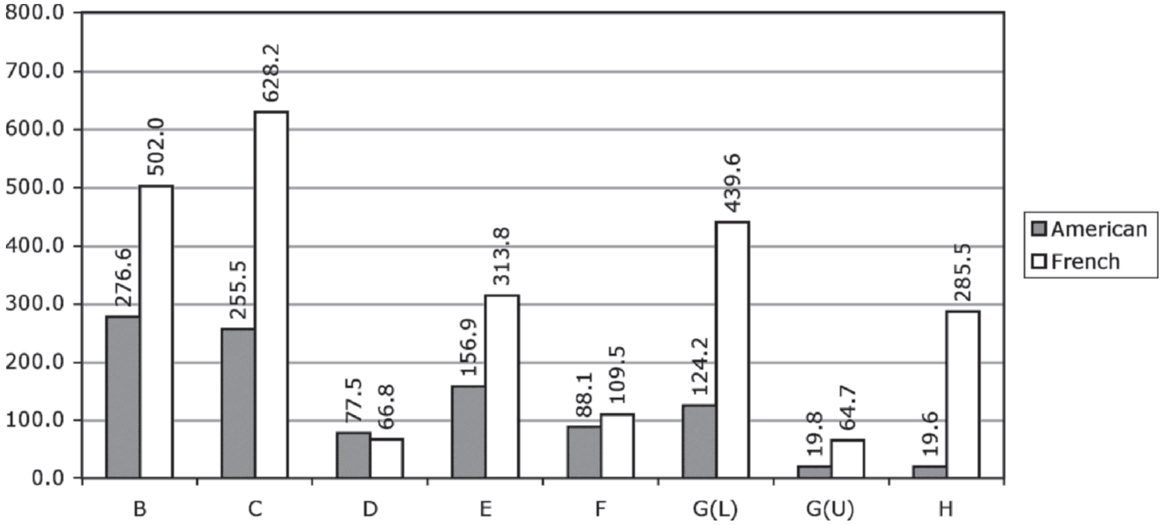


Figure 18. Densities of hippo specimens.

Elements that were part of the American collection protocol, crania, jaw fragments, and complete premolars and molars, however, were apparently collected with equal effort (Figure 19).

As in the case of the elephants, the French more consistently collected a wider array of hippo postcrania than did the Americans (Figure 20), because most of these were not part of the American collection protocol. The French collected more than twice the number of hippo specimens as the Americans (1685 and 4116, respectively), with much of the difference in numbers accounted for by tooth fragments and postcranial elements.

In contrast, hippo astragali, part of the American collection protocol, were consistently collected. In their case, densities alternate except for Member D, suggesting similarity in collection effort (Figure 21).

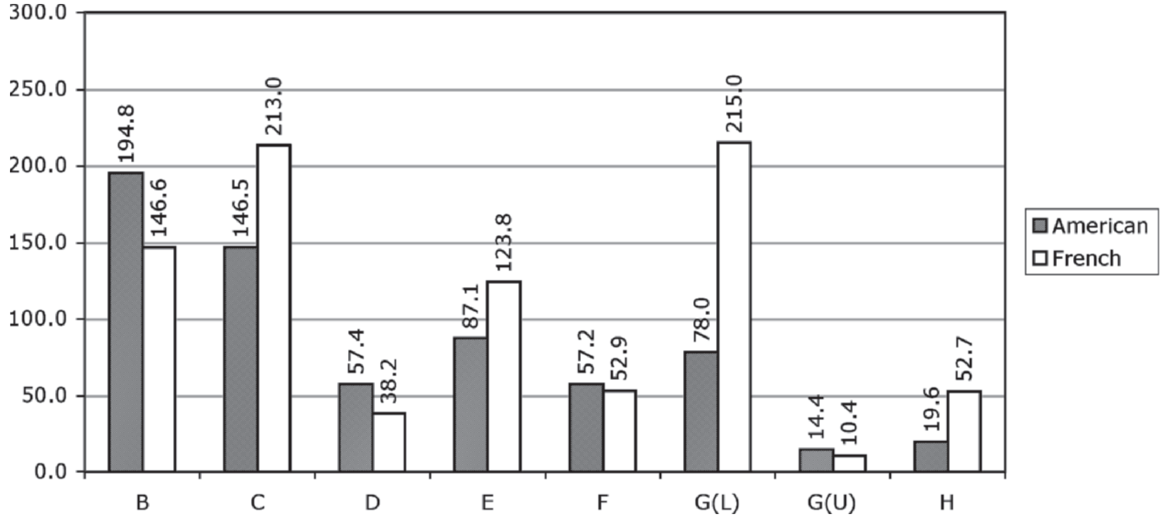


Figure 19. Densities of hippo crania, jaw fragments, and complete Ps and Ms.

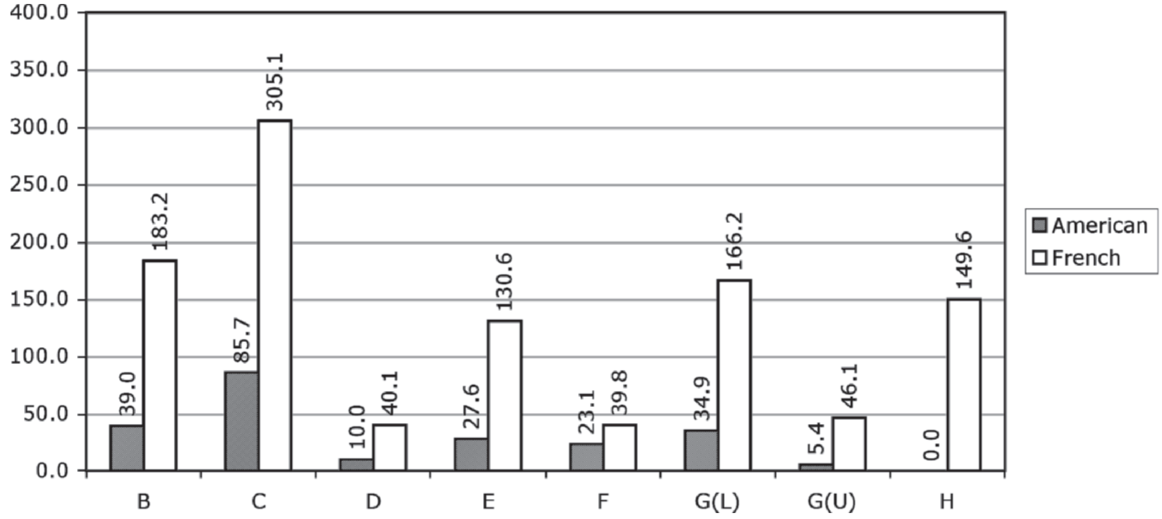


Figure 20. Densities of hippo postcrania.

SUIDAE

The densities of pig specimens alternate through the members, although weakly so in Members F and G(U), suggesting that both contingents sought them with about equal effort (Figure 22). This pattern for all pig specimens masks, however, interesting collection biases in certain elements.

For example, H. B. S. Cooke had suggested to me that even fragmentary third molars, typically the talons and talonids, might be important in questions of dating. Thus, in an exception to the standard collection protocol, I collected all pig third molars, including fragments consisting of the posterior part of these teeth. The practice led to a clear collection bias in pig third molars except in Members G(U) and H, where American exposures were very small (Figure 23).

In contrast, the densities of complete premolars and molars alternate, except in Members F and G(U), suggesting if anything a slight French bias in collecting (Figure 24).

A similar pattern, with a slight French bias, is seen in the densities of crania and jaw

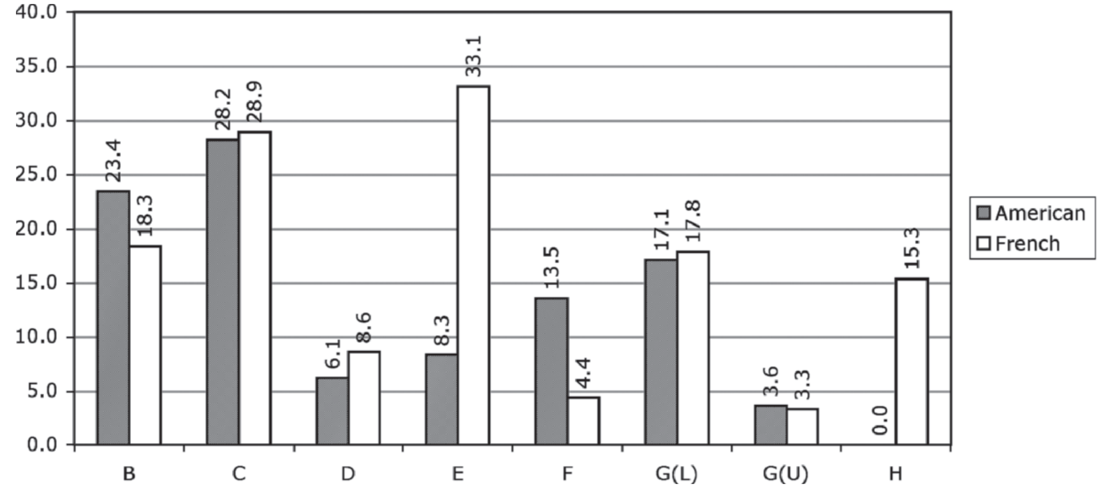


Figure 21. Densities of hippo astragali.

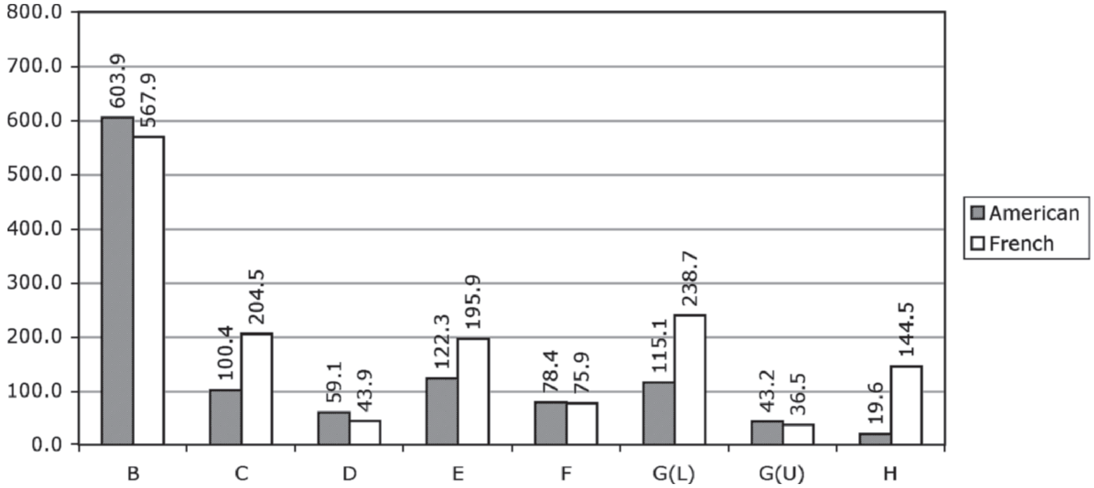


Figure 22. Densities of suid specimens.

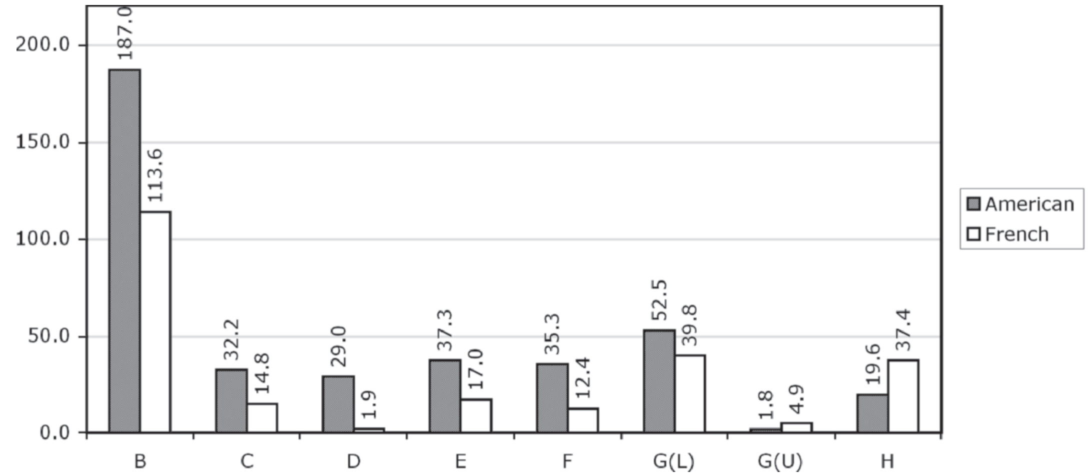


Figure 23. Densities of complete and fragmentary suid third molars.

fragments, but here only Member D breaks the alternating pattern (Figure 25).

As is to be expected there is a strong bias in the favor of the French with regard to densities of suid postcrania (Figure 26). The pattern is even stronger if one removes multiple specimens that constitute single individuals from Member G(U) of the American collections. The corrected value of the density then becomes 7.2 specimens per km^2.

The alternating pattern of densities is seen again with regard to suid astragali (Figure 27).

Although over all suid densities suggest essentially equal effort in search and recovery of these specimens, two clear biases are hidden in these numbers, the American bias towards collection of fragmentary third molars and the French bias towards postcrania.

GIRAFFIDAE

Giraffid specimens also have alternating densities, except in Members G(U) and H where American numbers are very small,

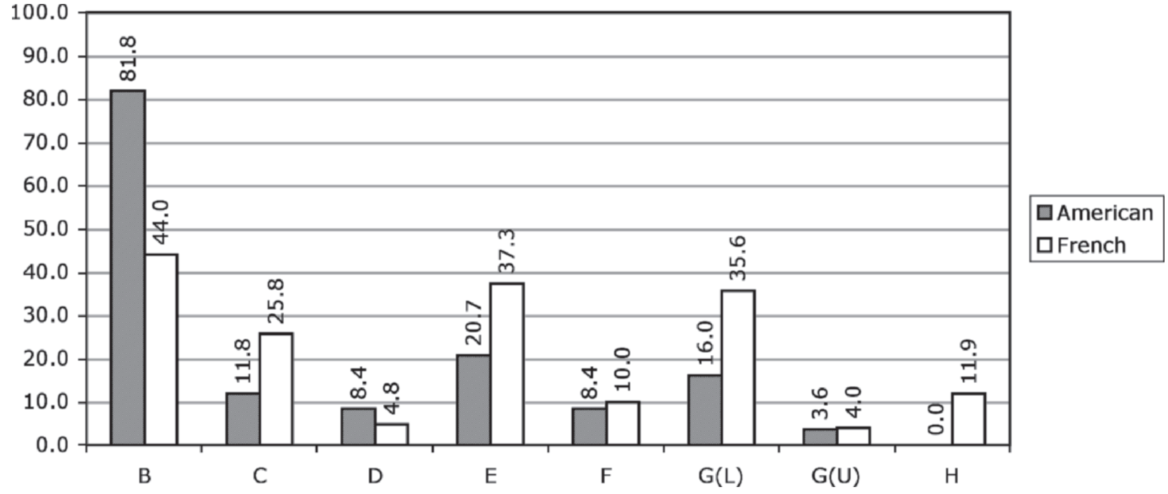


Figure 24. Densities of complete premolars and molars.

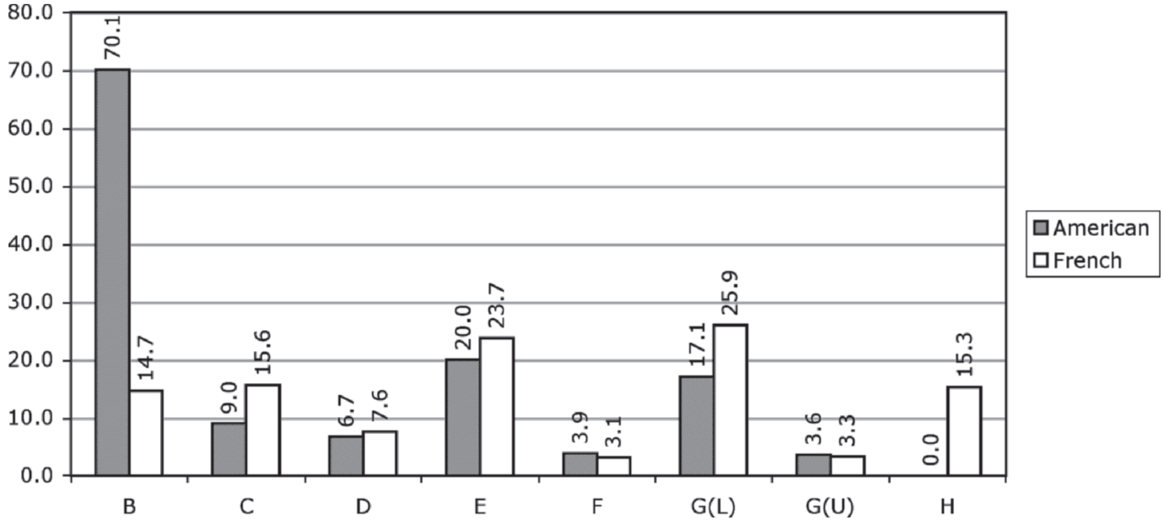


Figure 25. Densities of suid crania and jaw fragments.

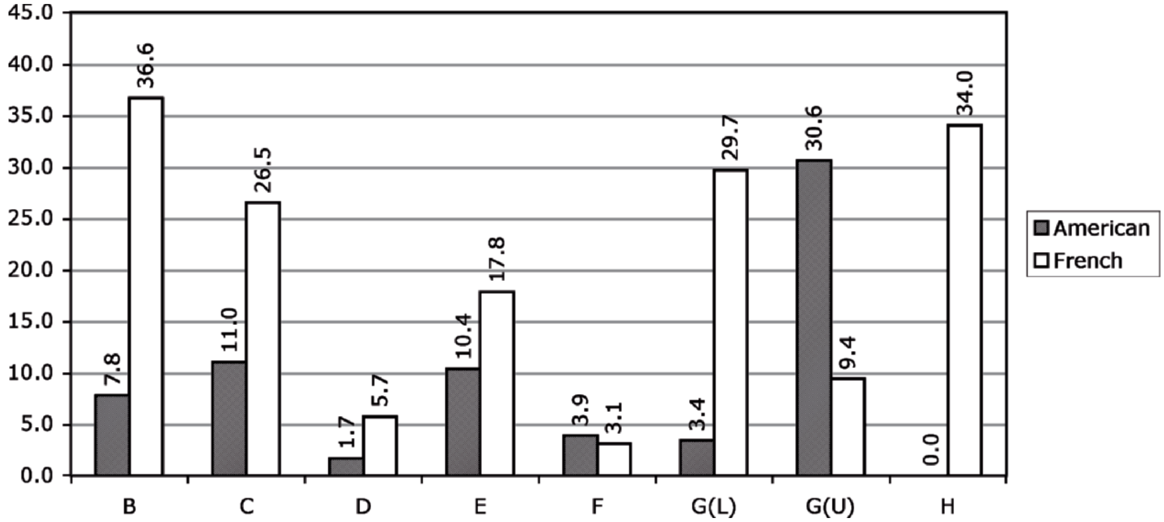


Figure 26. Densities of suid postcrania.

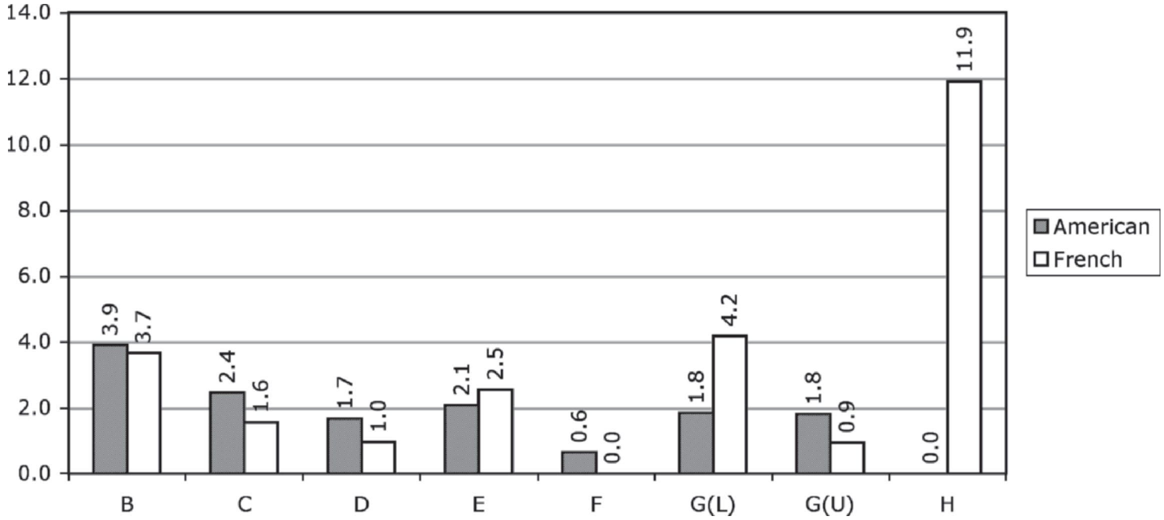


Figure 27. Densities of suid astragali.

suggesting similar search and recovery effort (Figure 28).

Densities of various cranial and dental elements (crania, jaw fragments, and complete premolars and molars) also have alternating frequencies (Figure 29).

The densities of giraffid postcrania have a slight French bias, as one might expect (Figure 30), while the densities of astragali have a slight American bias (Figure 31). These are both expectations one might have, given the American collection protocol.

EQUIDAE

Equid numbers and densities have a consistent French bias, in that, except for Member B, French densities are usually higher no matter the element under consideration (Figure 32).

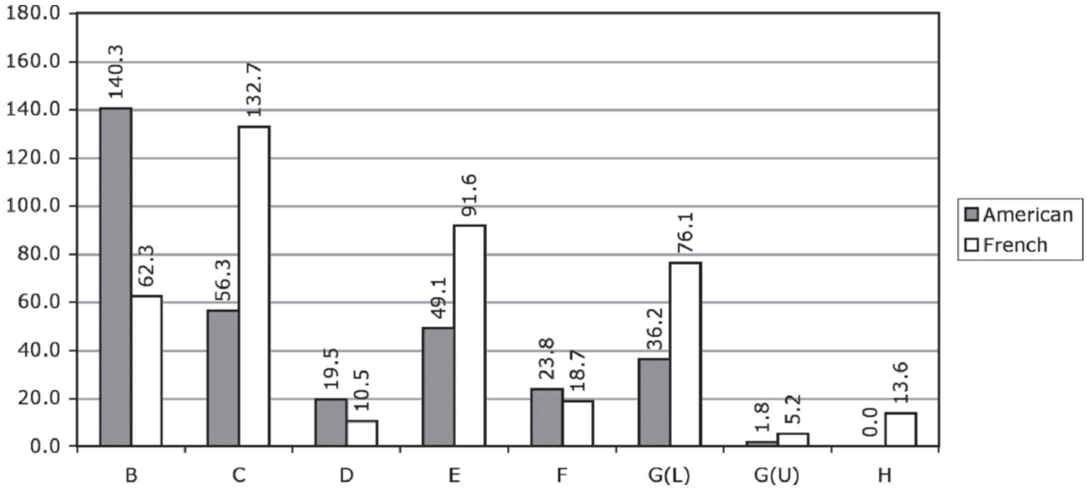


Figure 28. Densities of giraffid specimens.

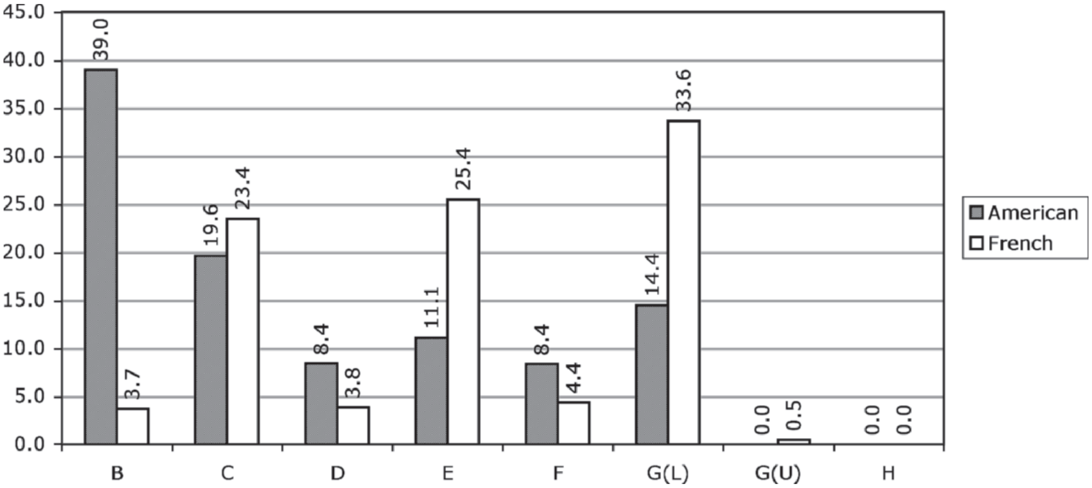


Figure 29. Densities of giraffid crania, jaw fragments, and complete Ps and Ms.

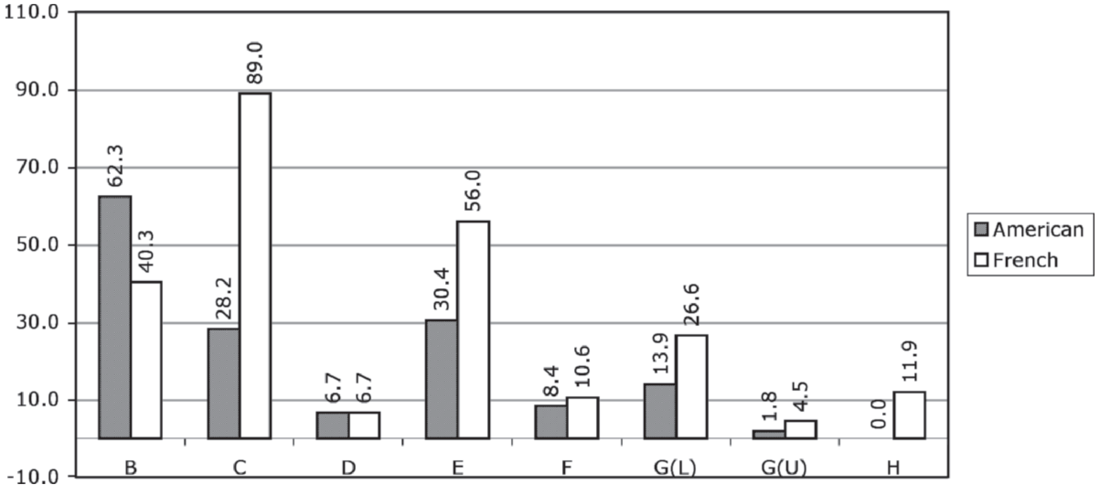


Figure 30. Densities of giraffid postcrania.

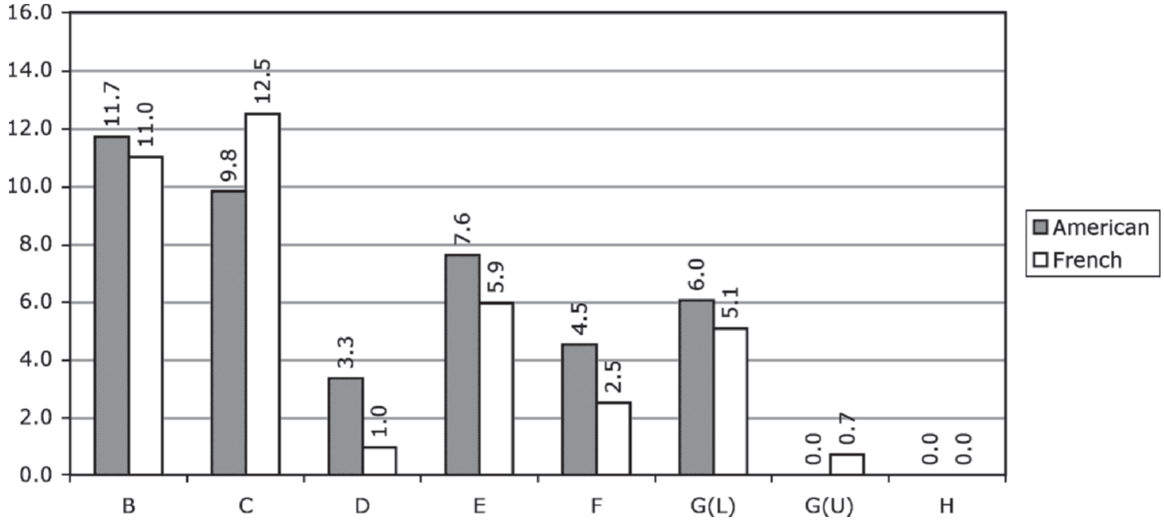


Figure 31. Densities of giraffid astragali.

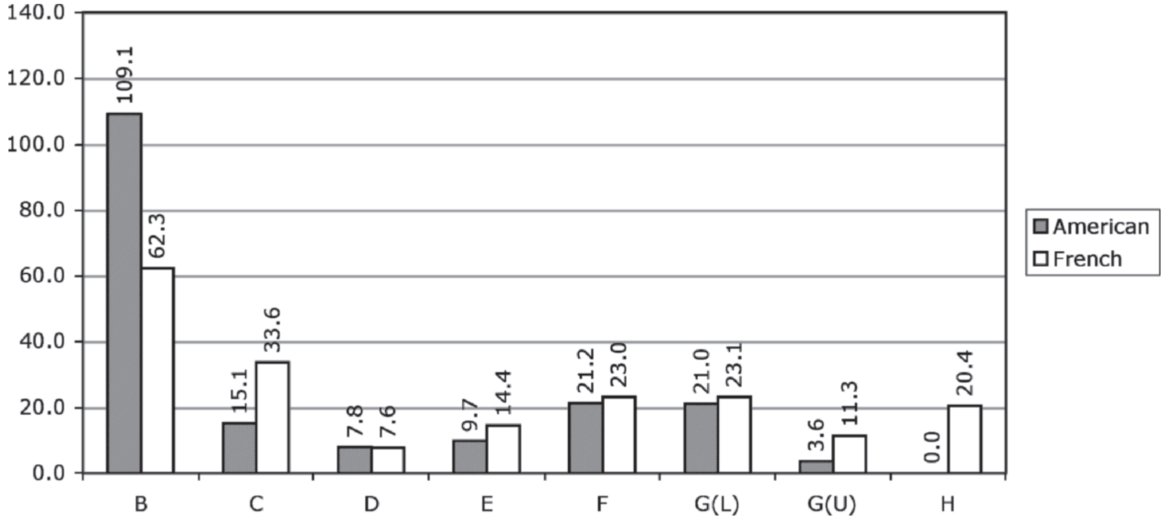


Figure 32. Densities of equid specimens.

This is true whether one is concerned with cranial and dental specimens (Figure 33) or with postcrania (Figure 34), a pattern that is not seen in any other family and one for which I have no ready explanation.

RHINOCEROTIDAE

Rhinos are rare in the Shungura Formation as large mammals go (see Table 2) and seemingly suffer from high rates of dental fragmentation as discussed above. Thus, contrary to standard collection protocol, the Americans collected all dental fragments, as apparently did the French. Perhaps as a consequence, rhino densities, in contrast to those of equids, show neither an American or French bias (Figure 35). Unusually, the Americans collected more rhino postcranial specimens (nine) than did the French (six) from Sectors 1 through 27, but all of these were collected in 1968 before the standard collection protocol was instituted.

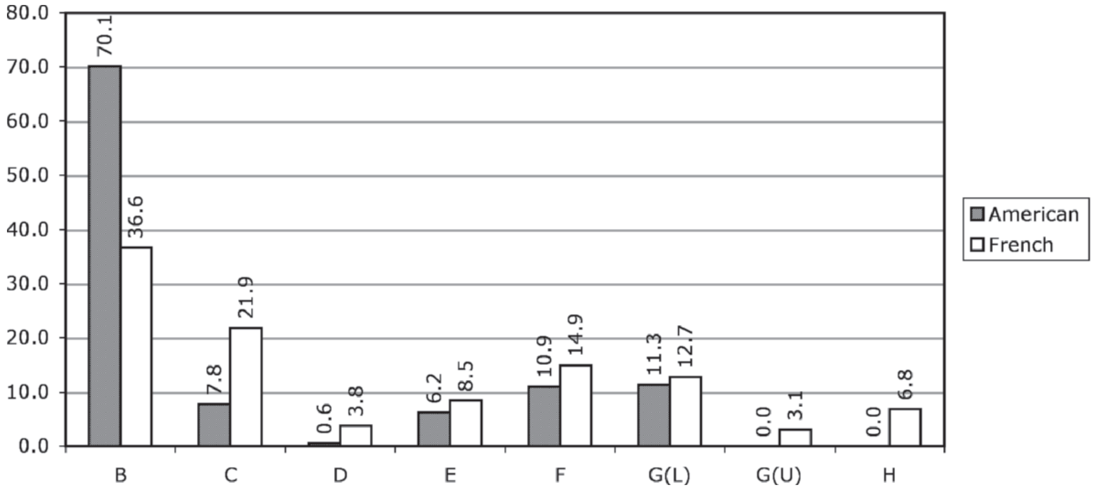


Figure 33. Densities of equid crania, jaw fragments, and complete premolars and molars.

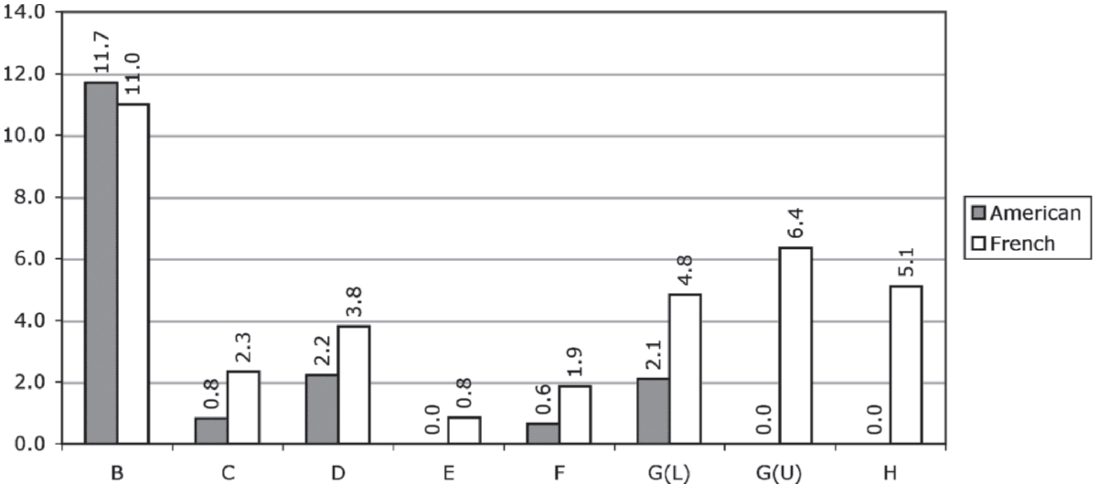


Figure 34. Densities of equid postcranial specimens.

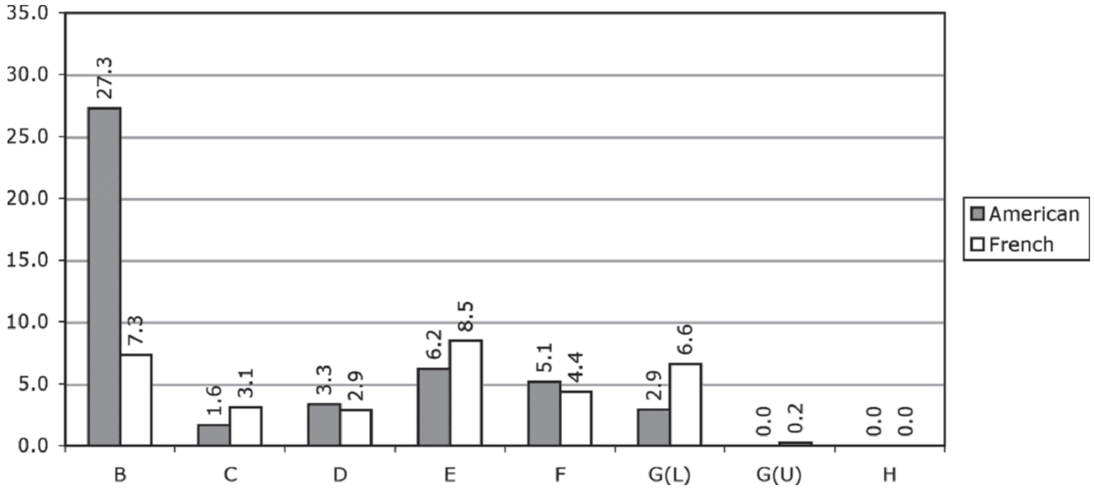


Figure 35. Densities of rhino specimens.

DEINOTHERIIDAE

Deinothere specimens too are uncommon in the Shungura Formation and, because their teeth contain vast volumes of dentine with a very thick covering of enamel, they are typically found as enamel fragments. Because of the rarity of complete teeth, the Americans decided to pick up even single dental fragments if they seemed to represent single individuals. This appears to have produced a bias towards the American collection with regard to deinothere cranial and dental fragments (Figure 36). In contrast, the bias is clearly towards the French with regard to postcranial elements, for they collected 34 specimens, while the Americans collected none. The American bias for cranial and dental and the French for postcrania clearly play out even in this uncommon taxon.

BOVIDAE

And finally I come to the Bovidae, by far the most numerous of the macromammalian families, constituting nearly half of all the specimens found (Table 2). When all body elements are considered together, the American and French teams seem to have collected specimens with similar strategy and effort, for densities of specimens alternate through the members, except for Member G(U) (Figure 37).

A similar but somewhat weaker alternating pattern is seen in the densities of complete teeth and jaw fragments, in that, Member F has equal densities and the French higher densities in Member G(U) suggesting a slight French bias (Figure 38).

The collections of bovid postcranial elements also have a slight French bias. Members D and G(U) have higher French densities, whereas both have higher American densities in the alternating pattern (Figure 39).

As might be expected given the American collection protocol, the French bias in astragali densities is weaker than for postcrania taken as a whole, for only Member G(U) breaks the alternating pattern (Figure 40).

Given that the American and French densities of bovid teeth, jaw fragments, and postcrania suggest similar collection strategies and intensities, with, at most, a slight bias towards higher French densities, it comes as some surprise that the collections show a consistent American bias in the densities of crania with horn cores (rare), frontlets (conjoined horn cores), and horn cores with bases (Figure 41) (also noted by Geraads and Coppens, 1995). Only in Member H are

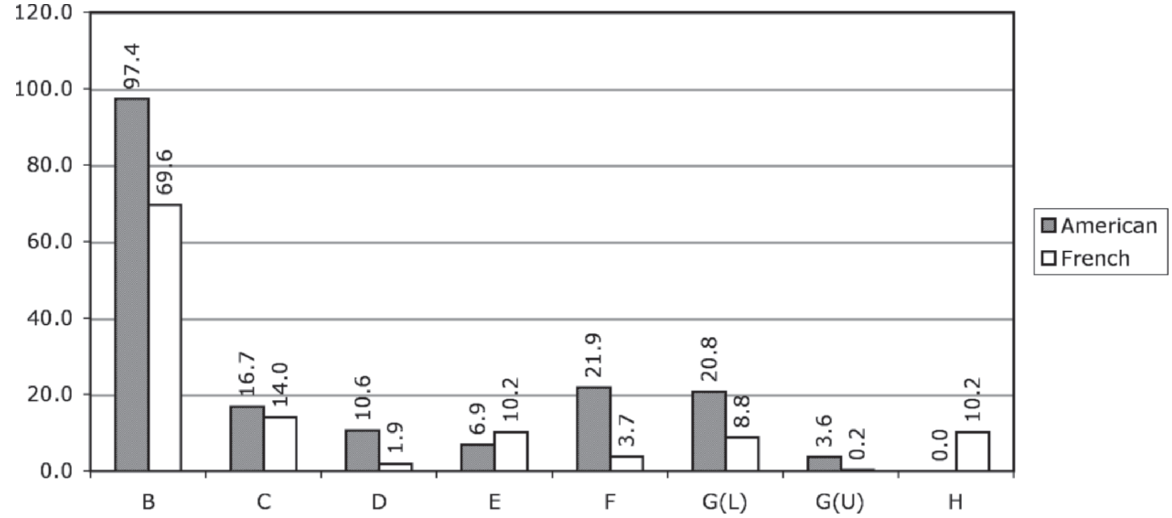


Figure 36. Densities of deinothere cranial and dental specimens.

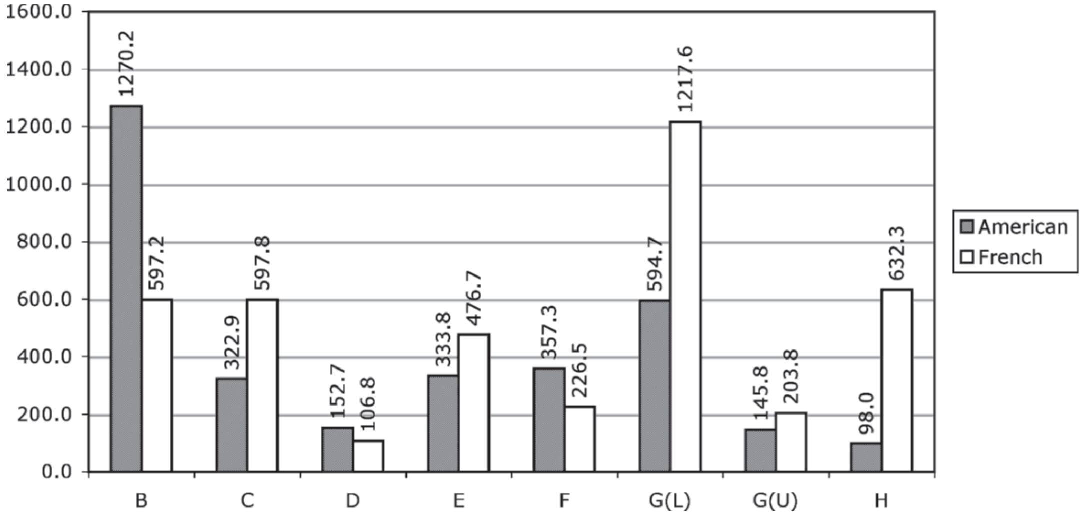


Figure 37. Densities of bovid specimens.

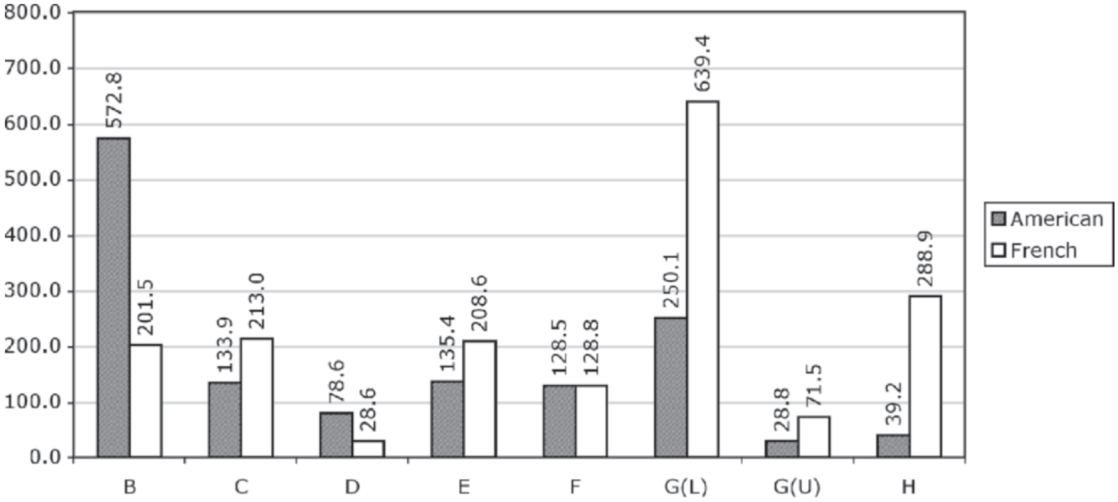


Figure 38. Densities of complete bovid teeth and jaw fragments.

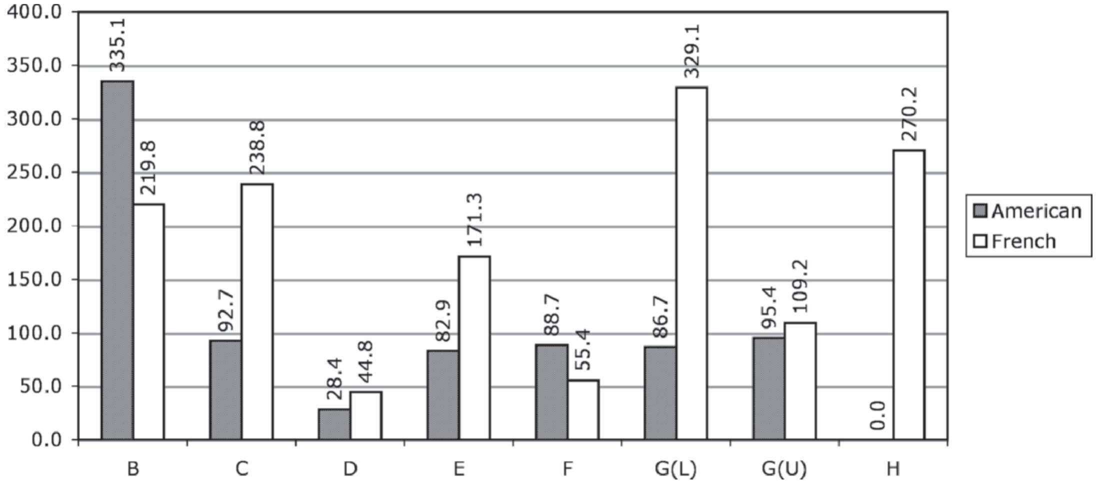


Figure 39. Densities of bovid postcrania.

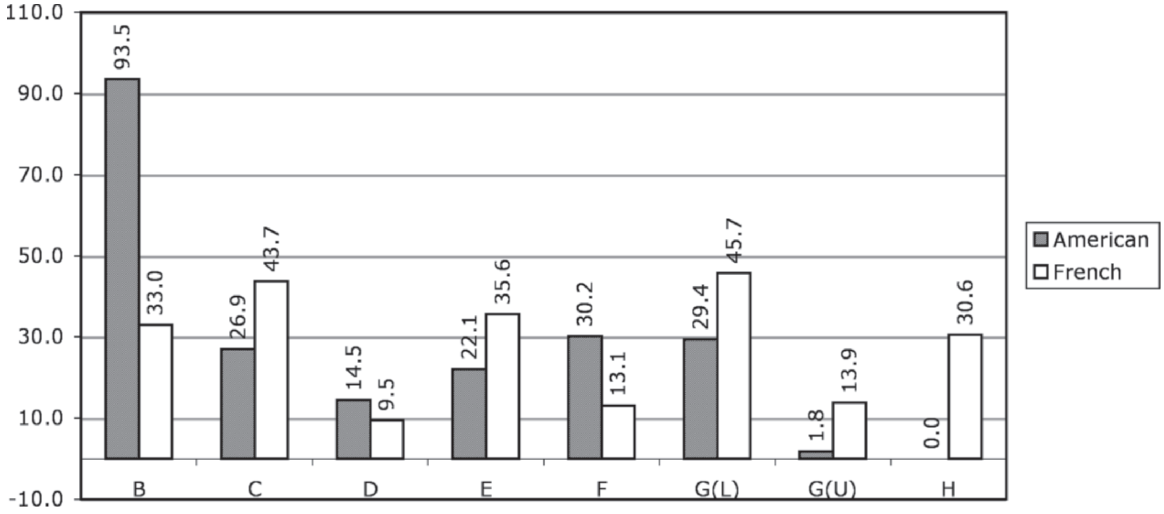


Figure 40. Densities of bovid astragali.

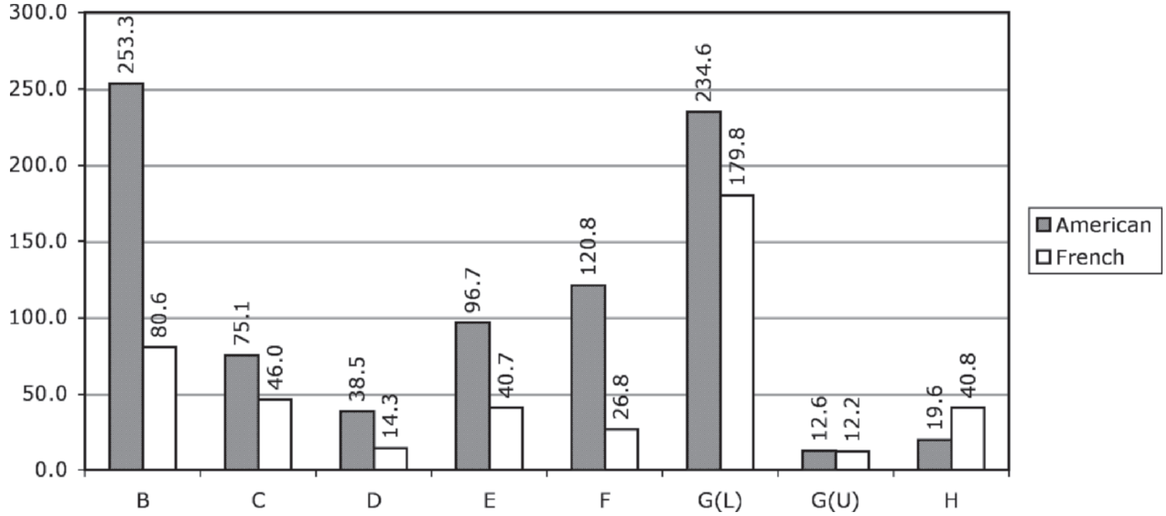


Figure 41. Densities of bovid crania, frontlets, and horn cores.

American densities lower than the French and, as will be remembered, the American area of Member H is very small.

The higher American densities are most puzzling in Member G(L), because in nearly every other taxon and skeletal element discussed above, French densities are highest in this member. Clearly something curious is going on with regard to the densities of bovid horn cores. I suspect that the higher American densities result from collection bias in which the French less consistently collected horn cores, especially fragmentary ones, than did the Americans, a collection bias similar to those documented on both sides in the numerous cases discussed above. If this is the case, then it is possible that the counts of French horn-core specimens and their relative taxonomic abundances are not representative of the numbers actually on the ground, leading to differences in taxonomic abundance between the American and French collection that are apparent, but not real. If my suspicion is correct, then it presents a significant problem given the potency of the Bovidae and their horn cores in the reconstruction of paleoenvironments. In contrast, Alemseged et al. (2006) think that the differences in counts and relative abundances of horn cores result from paleoenvironmental differences between the American and French collection areas. Resolution of this argument will likely result only from recollection of both the American and French areas, especially in Member G(L), using methods specifically designed to recover representative samples.

Faunal "Hot Spots"

The large differences in densities between the members that are seen in the above analyses were not expected when I began this analysis. Upon further reflection, however, they may result because of fossiliferous "hot spots" that are unevenly distributed between the American and French areas. Members B, C, E, and G(L) show especially large density differences between the areas in Table 4 and Figure 6. Inspection of the distribution of surface specimens across these members suggests that the "hot spot" concept might be the answer.

Two localities in the American area of Member B produced most of the surface specimens from this member, Locality 1 produced 448 and Locality 2 produced 332, totaling 780. The Americans recovered 992 macromammalian surface specimens from the surface of Member B, thus these two localities produced 78.6% of the total. Locality 1 is one of the larger American localities, covering 50,384 m^2 on de Heinzelin's map. Locality 2 is much smaller covering 5,012 m^2. The total exposures of Member B in the American area cover 256,655 m^2. Localities 1 and 2, thus, make up 21.6% of the total area. This analysis is complicated by the fact the French began to collect in what became American Locality 1 in 1967, calling it their Locality Omo 28. When the Americans moved south to the Type Area in 1968, it was agreed that the French could continue to collect in Locality Omo 28 in later years, which they did, especially in 1968. If I add the French specimens from Locality Omo 28 to American Locality 1, its total goes to 1,287 and the total for Member B goes to 1,831. Now the specimens from Localities 1 and 2 comprise 88.4% of the total number from the American area of Member B—good illustrations of what I mean by hot spots. In contrast, in the French area of Member B, the locality with the highest count, Locality Omo 3, produced only 217 specimens, whereas, all the others, some at least half the size of American Locality 1, produced far fewer (see Figure 42).

In contrast, French densities are usually highest in Member C, again probably resulting from a differential distribution of hot spots. French Locality Omo 18 produced 1,243 macromammalian surface specimens from an area of 102,572 m^2. Locality Omo 40 produced 358 specimens from an area of 88,004 m^2. The two localities thus produced 50.6% of the specimens collected in the French area of Member C, from only 14.9% of its area. The American area of Member C also contains a hot spot, Locality 32, which produced 396 macromammalian surface specimens from an area of 28,176 m^2, 12.6% of the specimens from American Member C in only 1.1% of its area. The larger number of specimens from Omo 18 and 40 outweigh, however, the higher density of Locality 32, producing the overall higher densities in the French area.

The French area of Member E typically produces the highest densities of macromammalian surface specimens and contains a single hot spot in this member, Locality Omo 57. This locality produced 39.3% of the total specimens from Member E (685 out of 1,743) in 2.8% of the area (32,492 m^2 of 1,179,028 m^2). The locality with the highest count in the American area of Member E is Locality 146 with 215 specimens.

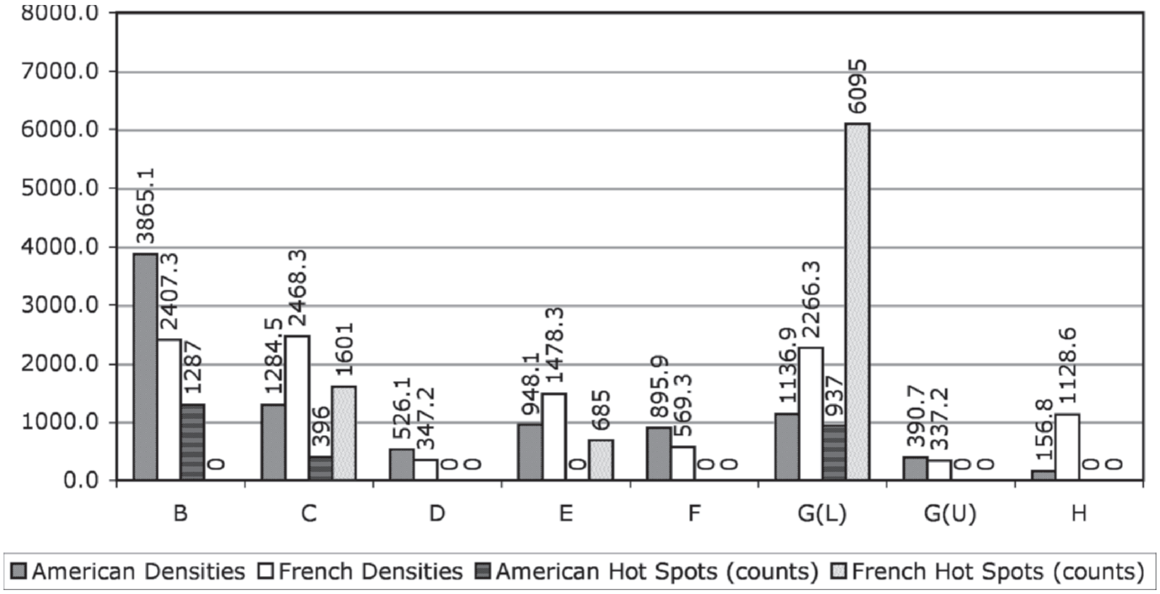


Figure 42. American and French densities and hot spot counts.

The French area also most often produced the highest densities of specimens from Member G(L). Four hot spots warrant discussion. Locality Omo 75 is a huge area (hardly a spot) whose boundaries are only partly marked on de Heinzelin's map. Locality Omo 75 includes three other localities that were established at a later time—Localities Omo 138, 139, and 140. Its area, including the areas of the three newer localities, is estimated to be 374,583 m^2. The four localities together produced 2,274 macromammalian surface specimens out of the 10,310 specimens recovered from Member G(L) or 22.1%. Locality Omo 75 covers 8.2% of the total area (4,549,295 m^2) of the member. Locality Omo 29 is also a very large (208,838 m^2) and poorly bounded locality, including four localities that were established at a later time—Localities Omo 222, 223, 231, and 234. Together, the five localities produced 1,156 macromammalian surface specimens or 11.1% of the specimens in 4.6% of the surface area of Member G(L). In contrast, Locality Omo 47 is well defined on de Heinzelin's map and small, covering only 24,315 m^2. It includes an earlier defined locality, Locality Omo Sh 2–3. The two localities produced 1,753 macromammalian surface specimens, 17.0% of the total from Member G(L), in 0.5% of it area. Locality Omo 47 is an exemplary hot spot. These three localities—Omo 29, 47, and 75 (and their included localities) produced 50.1% of the specimens from Member G(L) in 13.4% of its area. Locality Omo 323 produced 912 macromammalian surface specimens, so it too probably qualifies as a hot spot, but it was defined and collected in 1976, after de Heinzelin had completed his work in the Shungura Formation, and not included in his maps. I therefore do not know nor can I measure its areal extent.

The American area of Member G(L) contains two hot spots of macromammalian surface specimens, Localities 7 and 627. Locality 7 produced 462 (10.7%) and Locality 627 produced 475 (11.0%) of the 4,328 specimens recovered from the surface of Member G(L). Locality 7 covers 41,170 m^2 (1.1%) and Locality 627 covers 9,567 m^2 (0.3%) of the 3,807,007 m^2 of exposures of the member. Again, although the densities of these two localities are very high, the numbers of specimens they produced are overwhelmed by those of the French hot spots.

Members D, F, G(U), and H appear not to contain hot spots, although the methods I use may not be able to detect them in these members, given their small counts and/or areas.

The occurrence of differentially distributed hot spots in the American and French areas may explain the differences in densities of macromammalian surface specimens from the various members. Why they alternate in density is not known, but may result purely from chance, remembering that the boundary between them, the watering road, was chosen because it was well marked and known to everyone, not because it had any paleontological consequence.

Lessons to be Learned from This Analysis

Given that the American and French collection areas were contiguous, of roughly the same size, with their centers lying only 9 km apart and that the sediments in the two areas were laid down by the same river at the same time, one might expect that the two collections would be very similar. That this is not the case is clear from the discussion above. It should also be apparent that the causes for the differences from this expectation are varied and complex.

Some of the differences result from well-documented variation in areas of exposure available to the contingents or to differences in effort. For example, the larger French collection, at least in part, results from two more years of field expeditions to the Shungura Formation and to larger areas of exposures. The larger number of excavated specimens and micromammals in the American collection result from more excavation effort over a longer period of time. The common pattern of larger numbers of postcranial elements in the French collection is explained by the fact that the Americans decided not to collect them for most taxa, while the French did. Other differences are less easily explained, however, principally because collecting methods and records were not formulated or not kept.

One of the more important of these concerns the large differences in apparent specimen density in the areas of the two contingents. Although differences in effort might have produced these differences, I think it unlikely for a number of reasons. First, the pattern of densities of primate taxa, especially hominids but also monkeys, both highly valued, is generally similar to that of the fauna as a whole. One might expect that if effort determined the densities, then those of the most highly valued taxa would differ from those of more general concern. Second, it is nearly universally the case, whatever taxon one considers, that American densities are highest in Member B, for example, while those of the French are highest in Member G(L). I think that systematic differences in effort are unlikely to have produced these differences in densities, given the very different interests that the members of the expeditions held and given that much of the collecting occurred before the stratigraphic structure of the formation was well understood or mapped. I think, therefore, that the alternating pattern of densities results from similar effort being applied to exposures of sediments of inherently different fossil richness. The American and French areas differ in density, in all likelihood, because of the differential distribution of specimen "hot spots." Why they alternate in density may result purely from chance.

How all of this affects taphonomic and taxonomic analyses, especially those based on specimen frequencies, is of some interest. I suggest, for example, that those body elements whose densities show the alternating density pattern, indicating similar collection strategy and effort, are more likely to be representative samples of the exposed sediments than those whose density patterns are biased towards one contingent or the other. These elements then might be best used in comparisons of the collections aimed at determining the primary cause of the density differences (e.g., paleoecological). Similarly, the collections of these specimens might be combined to provide larger samples for use in comparing the faunae from different members to discover faunal differences in time. In contrast, body elements whose density patterns suggest biases principally produced by differences in strategy or effort might be avoided for these types of analyses.

And finally, although I developed implicit rules concerning the collection of specimens, as describe above, and these rules were generally followed by other members of the expedition after they were formulated, the rules were never made part of an explicit research strategy nor was their rationale discussed. In hindsight, I now think that the implicitness of the rules lead to some of the biases in the American collection discussed above; even I did not always follow them. If undocumented biases are not to creep into fossil collections, collection strategies should be explicit, their rationale generally agreed upon, and strict adherence to them rewarded.

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Appendix

Counts of macromammals specimens from the surface of Sectors 1 to 27 (Type Area) of the Shungura Formation

	American Collection											
	Ba	A	B	C	D	E	F	G(L)	G(U)	H	J	Total
Hominidae	0	0	5	22	16	11	17	18	1	0	0	90
Jaw fragments	0	0	0	1	0	0	1	3	1	0	0	6
Cercopithecidae	0	0	236	1109	259	294	385	603	55	1	0	2942
Complete and fragmentary isolated teeth	0	0	221	738	198	198	279	485	7	1	0	2127
Complete isolated teeth	0	0	129	371	78	93	91	193	6	1	0	962
Complete teeth and skull fragments	0	0	138	441	89	108	107	221	7	1	0	1112
Postcrania	0	0	29	271	42	74	62	74	45	0	0	597
Carnivora	0	0	7	39	4	5	11	21	4	0	0	91
Elephantidae												
Dental specimens	0	0	49	62	62	58	51	89	0	0	0	371
Crania and jaw fragments	0	0	6	2	5	4	2	9	0	0	0	28
Postcrania	0	0	3	8	0	4	0	6	0	0	0	21
Hippopotamidae	0	0	71	626	139	227	137	473	11	1	0	1685
Crania, jaw fragments, complete Ps and Ms	0	0	50	359	103	126	89	297	8	1	0	1033
Postcrania	0	0	10	210	18	40	36	133	3	0	0	450
Astragali	0	0	6	69	11	12	21	65	2	0	0	186
Suidae	0	3	155	246	106	177	122	438	24	1	0	1272
Complete and fragmentary M3s	0	0	48	79	52	54	55	200	1	1	0	490
Complete Ps, M1s and M2s	0	1	21	29	15	30	13	61	2	0	0	172
Crania and jaw fragments	0	0	18	22	12	29	6	65	2	0	0	154
Postcrania	0	0	2	27	3	15	6	13	17	0	0	83
Astragali	0	0	1	6	3	3	1	7	1	0	0	22
Giraffidae	0	1	36	138	35	71	37	138	1	0	0	457
Crania, jaw fragments, complete Ps and Ms	0	1	10	48	15	16	13	55	0	0	0	158
Postcrania	0	0	16	69	12	44	13	53	1	0	0	208
Deinotheriidae	0	0	25	41	19	10	34	79	2	0	0	210

(*Continued*)

Counts of macromammals specimens from the surface of Sectors 1 to 27 (Type Area) of the Shungura Formation—cont'd.

	American Collection											
	Ba	A	B	C	D	E	F	G(L)	G(U)	H	J	Total
Bovidae	0	0	326	791	274	483	556	2264	81	5	0	4780
Jaw fragments and complete teeth	0	0	147	328	141	196	200	952	16	2	0	1982
Postcrania	0	0	86	227	51	120	138	330	53	0	0	1005
Astragali	0	0	24	66	26	32	47	112	1	0	0	308
Crania, frontlets, and horn cores	0	0	65	184	69	140	188	893	7	1	0	1547

	French Collection											
	Ba	A	B	C	D	E	F	G(L)	G(U)	H	J	Total
Hominidae	0	1	2	18	1	17	6	40	0	1	0	86
Jaw fragments	0	0	0	1	0	2	0	6	0	0	0	9
Cercopithecidae	1	19	86	841	71	267	124	736	25	5	0	2175
Complete and fragmentary isolated teeth	1	18	81	715	54	220	96	480	19	3	0	1687
Complete isolated teeth	1	13	45	378	25	107	40	281	9	3	0	902
Complete teeth and skull fragments	1	13	46	441	32	132	51	390	10	4	0	1120
Postcrania	0	1	4	58	10	19	16	136	5	1	0	250
Carnivora	0	2	1	14	1	11	3	51	7	0	0	90
Elephantidae												
Dental specimens	4	8	34	91	9	88	20	171	15	2	2	444
Crania and jaw fragments	0	1	5	12	5	8	2	19	3	0	0	55
Postcrania	2	20	9	78	17	23	10	62	11	4	0	236
Hippopotamidae	9	100	137	805	70	370	176	2000	275	168	6	4116
Crania, jaw fragments, complete Ps and Ms	0	19	40	273	40	146	85	978	44	31	2	1658
Postcrania	9	37	50	391	42	154	64	756	196	88	4	1791
Astragali	0	3	5	37	9	39	7	81	14	9	1	205
Suidae	0	139	155	262	46	231	122	1086	155	85	3	2284
Complete and fragmentary M3s	0	10	31	19	2	20	20	181	21	22	1	327
Complete Ps, M1s and M2s	0	29	12	33	5	44	16	162	17	7	1	326
Crania and jaw fragments	0	1	4	20	8	28	5	118	14	9	0	207
Postcrania	0	6	10	34	6	21	5	135	40	20	0	277
Astragali	0	2	1	2	1	3	0	19	4	7	0	39

Giraffidae	0	8	17	170	11	108	30	346	22	8	1	721
Crania, jaw fragments, complete Ps and Ms	0	0	1	30	4	30	7	153	2	0	0	227
Postcrania	0	2	11	114	7	66	17	121	19	7	1	365
Astragali	0	2	3	16	1	7	4	23	3	0	0	59
Equidae	1	7	17	43	8	17	37	105	48	12	2	297
Crania, jaw fragments, complete Ps and Ms	1	4	10	28	4	10	24	58	13	4	2	158
Postcrania	0	3	3	3	4	1	3	22	27	3	0	69
Rhinocerotidae	1	3	2	4	3	10	7	30	1	0	5	66
Deinotheriidae	2	14	19	18	2	12	6	40	1	6	0	120
Bovidae	10	41	163	766	112	562	364	5539	866	372	101	8896
Jaw fragments and complete teeth	0	15	55	273	30	246	207	2909	304	170	20	4229
Postcrania	3	13	60	306	47	202	89	1497	464	159	65	2905
Astragali	0	3	9	56	10	42	21	208	59	18	3	429
Crania, frontlets, and horn cores	6	4	22	59	15	48	43	818	52	24	6	1097