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A Miocene Rhinoceros Herd Buried in Volcanic Ash

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Grants 1706, 2059: To excavate the ash bed at Poison Ivy Quarry and to study its fossil contents.

In August 1977, personnel of the University of Nebraska State Museum (UNSM) opened a small test excavation at a promising fossil vertebrate locality in northeastern Nebraska. Several years earlier, while engaged in geological mapping, the writer had discovered a skull of a fossil rhinoceros weathering out of an outcrop of volcanic ash at the site. The skull proved to be articulated with an entire skeleton of a juvenile rhino and to be associated with numerous other complete skeletons. During the short 1977 field season 12 rhinoceros and 3 horse skeletons were collected from an area of only a few tens of square meters. Many other skeletons were noted, but time prevented their being collected.

The deposit is most remarkable. Mass occurrences of fossil mammals are sometimes found (e.g., at Agate Springs, Nebraska; see Matthew, 1923) but in almost all such cases articulated skeletons are rare or absent. The only comparable deposit presently known to the writer is at Höwenegg, Germany, where tuffaceous lacustrine sediments of Miocene age have yielded some 27 skeletons, mostly complete, of horses, antelopes, and rhinoceroses (Tobien and Jörg, 1959). Complete skeletons in volcanic ash have also been reported from Senèze in France (Schaub, 1944) but these are apparently isolated occurrences. The only mass assemblage of articulated skeletons of North American Tertiary mammals known to the writer is that of the Miocene "gazelle-camel" *Stenomylus* (Loomis, 1910) of which at least 40 skeletons, mostly in "death poses," were collected. These camels occur in a sandstone, not a volcanic ash.

Our preliminary work clearly indicated that the new site contained a wealth of information about the Miocene savannah mammalian community of the Great Plains not obtainable at any other known locality. Rapid burial in volcanic ash had apparently preserved details of skeletal anatomy not available in even the most complete Clarendonian rhino and horse skeletons previously known. The prospect of obtaining an untransported "death assemblage" perhaps representing entire herds of several kinds of hoofed mammals was very exciting. On June 1, 1978, a team from the UNSM began to excavate the site—now known as Poison Ivy Quarry (UNSM Paleontological Locality Ap 116). Four months were spent in the field. Laboratory preparation and analysis of the specimens began in September and is continuing.

Results so far have exceeded the most optimistic expectations. In addition to numerous rhinoceros and horse skeletons (the rhinoceros total is now 70), we also collected excellent specimens of camels and, surprisingly, birds—the latter complete with well-preserved tracheal cartilages and ossified tendons. Another unexpected discovery was exceedingly well-preserved fossil grass seeds inside the rhinoceros skeletons.

THE SITE

Poison Ivy Quarry lies at the center of the NE1/4, NE1/4, NW1/4, Section 8, Township 28 North, Range 7 West, Antelope County, Nebraska (Figure 1). The fossiliferous exposure is at the head of a ravine draining south into a small unnamed tributary of the south branch of Verdigre Creek. The site is approximately 225 km northeast of Omaha and 50 km south of the confluence of the Niobrara and Missouri Rivers.

TOPOGRAPHY

Verdigre Creek and its tributaries are dissecting an alluvial plain of low relief in northern Antelope County. Active headward erosion by the tributaries has produced numerous steep-sided ravines in the Verdigre Basin; many contain small bedrock exposures similar to that at the fossil quarry. The site is approximately midway between the northeastern border of the Sand Hills region of central Nebraska and the western border of the glaciated region of eastern Nebraska. About half of the land in the area is used for farming—primarily corn, soybeans, and small grain. The rest, including the quarry site and most other stretches of stream valley, is grazed by cattle.

GEOLOGY

The surficial geology of the Verdigre Basin has been discussed elsewhere (Voorhies, 1971, 1973, 1974). The local geologic column exhibits a sequence of flat-lying, predominantly fluvial clastic deposits, ranging from Miocene through Pleistocene in age, which unconformably overlie a Cretaceous marine shale. Approximately halfway through the "stack" of Cenozoic strata is the cap-rock member of the Ash Hollow Formation which contains the fossiliferous ash bed that has been the focus of the

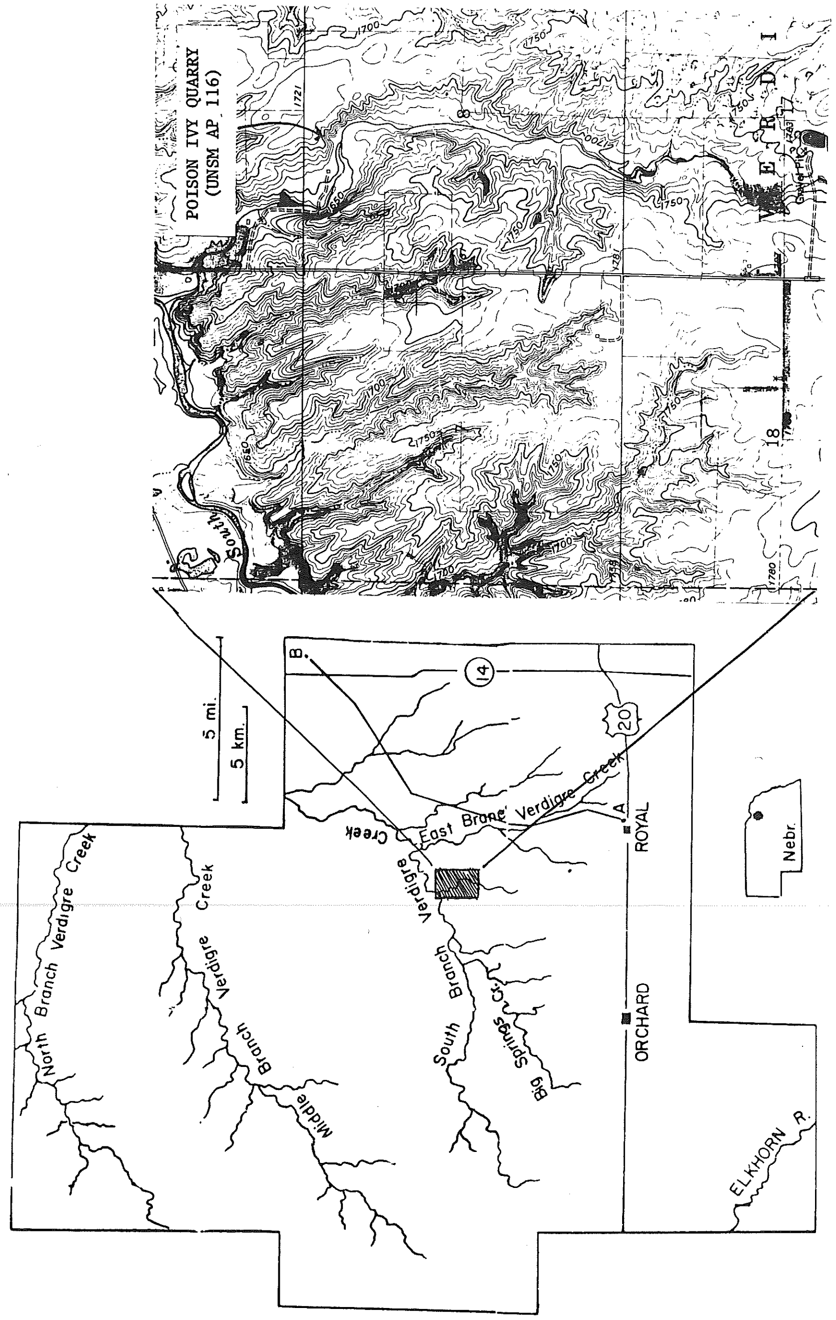

FIGURE 1. Location quarry (detailed map from the Orchard NW Quadrangle, USGS 7½ min. Topographic Series, 1963).

present study. The cap rock is a very widespread sheetlike sandstone deposit, which crops out extensively in the valley of the Niobrara River in northern Nebraska and southern South Dakota. Lenses of cemented sand in the cap rock tend to resist erosion and thus form prominent vertical cliffs and box canyons. This characteristic was noted by Skinner et al. (1968) at its type locality about 160 km west of Poison Ivy Quarry. The cap rock is a rather heterogeneous unit displaying abrupt lateral changes in lithology. Sandstone predominates but lenses of locally derived conglomerate, siltstone, claystone, diatomite, and volcanic ash are common. Volcanic glass, in addition to occurring in discrete beds, some 3 m thick, also occurs as disseminated shards among the sand- and silt-sized clasts in the bulk of the unit. Fossil vertebrates have been collected by the writer from several dozen exposures in the Verdigre Basin. The fossils are most commonly found in sandstone and tend to be broken and abraded.

The stratigraphy in the immediate vicinity of Ap 116 is shown in Figure 2. Note that the fossiliferous ash bed is more than 2.5 m thick at the fossil quarry but that it thins rapidly toward the north and west. The ash lies about a meter above the base of the cap-rock member. At the quarry it rests directly on a hard, calcareous-cemented sandstone containing rounded fragments of fossil bones and teeth. The lower contact is very sharp and well defined. The ash itself is unconsolidated except in the top few centimeters, which grade into a slightly consolidated silty clay. In addition, a layer of detrital sand and silt mixed with ash which occurs a few centimeters above the base of the ash bed is slightly consolidated. Except for the latter unit, the ash is remarkably pure and free of detrital material. The ash is laminated throughout its thickness except in the bottom few centimeters and (sometimes) adjacent to fossil skeletons where stratification tends to be obscure or absent. In plain view, many of the bedding planes in the ash show symmetrical ripple marks. In the immediate vicinity of the quarry the ash bed fills a depression that deepens toward the north and east. The top of the ash, in contrast with its base, is horizontal.

The overall geometry of the ash bed, its well-preserved continuous, horizontal stratification and the presence of ripple marks all suggest that the ash accumulated in a body of standing water—a pond or lake. (The size of the presumed body of water cannot yet be determined as only part of the southwest "shoreline" is exposed for study.) Deposition of the ash bed appears to have been essentially continuous and very rapid. The only lithologic evidence of significant interruption of sedimentation detected so far is the "clastic wedge" of silty sand mixed with ash which occurs near the base of the ash bed. This unit appears to represent clastic material washed into the pond or depression from the pre–ash-fall land surface shortly after the initial ash fall. Paleontological evidence discussed below suggests that the washing in of locally derived debris along with ash from the initial fall probably represents a hiatus of no more than a few weeks. After this interruption, the depression appears to have filled to the brim very rapidly; no further non-ash contaminants reached the depression.

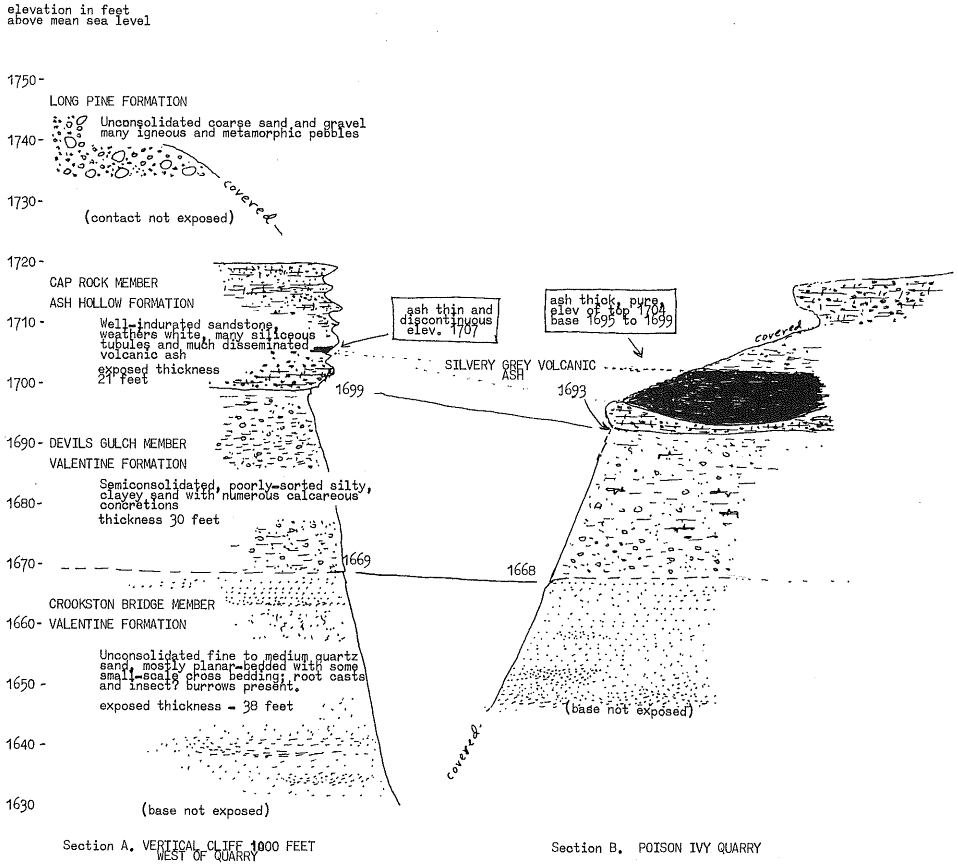

FIGURE 2. Geologic sections in the vicinity of Poison Ivy Quarry.

THE 1978 EXCAVATIONS

Test excavations in 1977 indicated that a concentration of skeletons probably lay buried beneath a grass-covered hillside between two ravines about 30 m apart. The fossiliferous horizon lay just under the sod at the downslope (southwestern) edge of the target area, but was covered by as much as 5 m of apparently unfossiliferous overburden at the upslope (northeastern) margin. Because of the great volume of overburden, and the considerable hardness of some of it, we decided to have it removed by bulldozer. At the beginning of the field season, in early June, further test pits were hand-dug to verify the previous conclusion that skeletons were present only at the base of the ash bed. Finding no evidence to the contrary, we arranged for a bulldozer to clear away the overburden to approximately 0.7 m above the level of the highest known bone in the ash bed. Members of the excavation team watched for fossils as the bulldozing proceeded; but none was observed except a fragment of tortoise carapace, which occurred about a meter above the bulldozed floor. It was not clear whether the tortoise had originally been buried high in the ash bed or had been brought to that level by the burrowing activity of a modern animal. The latter is judged more probable. Definite rodent burrows are common, especially at the southeastern edge of the excavation.

Within three hours the bulldozer had prepared a level surface roughly 30 × 15 m. This area was surveyed and laid off into a grid of 3-m squares (Figure 3). Vertical control was established with a pin surveyed into the northeastern wall of the excavation. Several squares were excavated simultaneously; unexcavated walls were left between squares as a record of the stratigraphy. Paleontological, lithologic, and bulk sediment samples were located by grid square number (assigned at the northwestern corner). Position within a square and stratigraphic position were plotted and sketched on planimetric maps of the excavation. Major features were photographed. Approximately half of the bulldozed area, or 30 squares, was excavated in 1978.

Most of the vertebrate fossils were collected by conventional plaster-jacketing techniques after having first been treated with a polyvinyl acetate preservative. Usually, only enough matrix was removed from each specimen to determine its identity, limits, and orientation before applying the cast. We did, however, expose several skeletons rather completely so that informative photographs could be taken. In most cases, we found that less damage to the specimens resulted when field cleaning was kept to a minimum.

The fact that most of the specimens were partly or entirely articulated created special problems in collection. An adult rhinoceros skeleton enclosed in plaster would weigh at least a ton and would be very difficult to handle. Therefore, we generally removed the skeletons in smaller, more manageable sections. Each hind limb (femur to foot) of an adult rhino, for example, was usually collected as a unit. The pelvis, sacrum, and caudals usually came out together. Ribs were usually removed individually but in some cases bundles of ribs or entire rib cages were collected as units. It

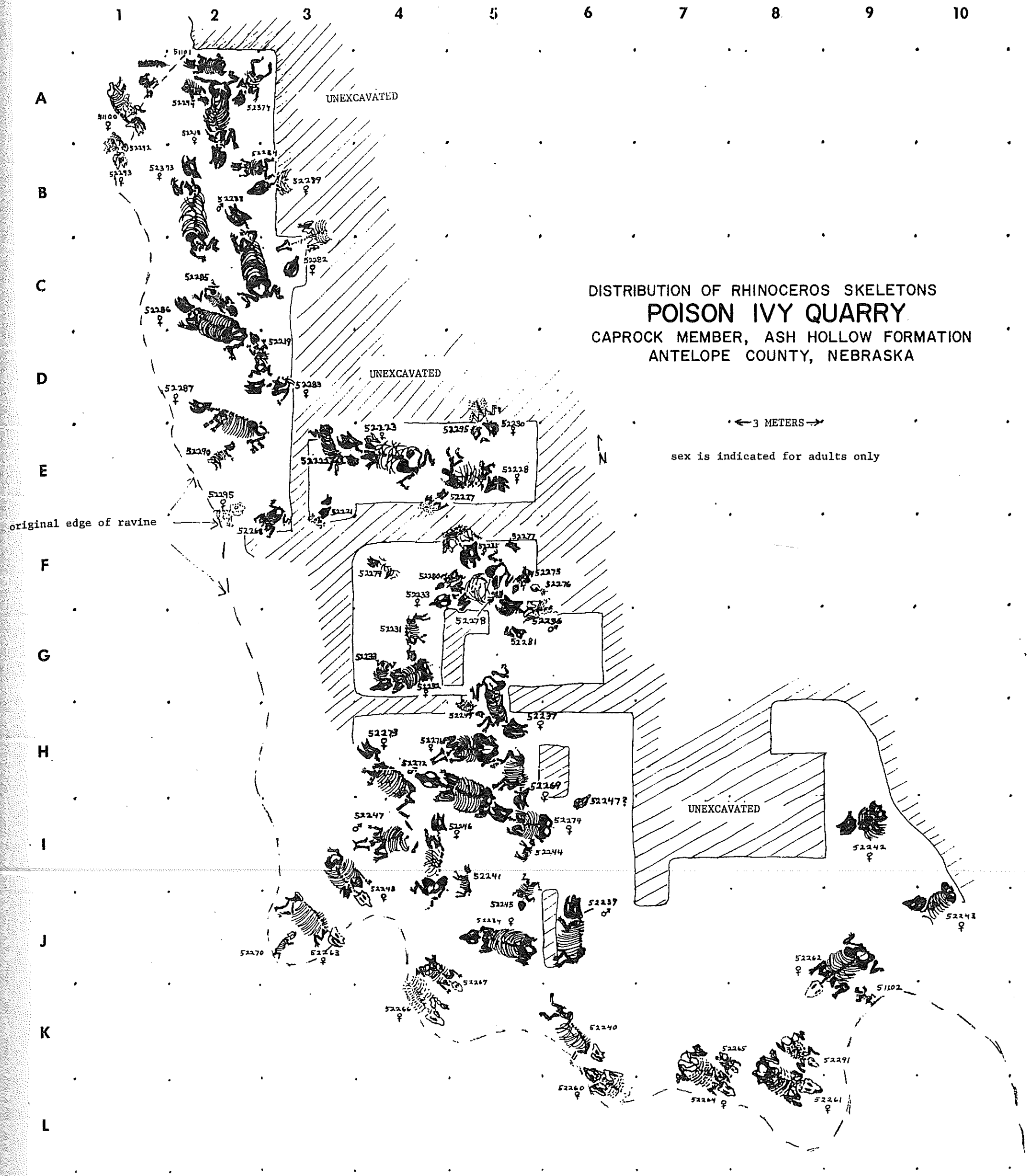

FIGURE 3. Distribution of rhinoceros skeletons in Poison Ivy Quarry, Cap Rock Member, Ash Hollow Formation, Antelope County, Nebraska. Sex is indicated for adults only.

was often possible to collect entire skeletons of smaller animals (horses, juvenile rhinos) in one or two casts.

Skeletons were often intertwined and overlapped making excavation exceedingly tedious and slow. It was not always clear, in the field, which limbs belonged with which skulls. Fortunately, our field records are sufficiently clear to match bones of individual skeletons once the specimens have been prepared in the laboratory.

Laboratory preparation of the fossils has been very time-consuming but rewarding. Many of the specimens are preserved in exquisite detail. The bones are only slightly mineralized, however, and frequently still have spaces unfilled by sediment. They are consequently exceedingly fragile, which considerably increases the time needed for preparation. Our laboratory procedure has been to open the field jackets and prepare one side as completely as possible without disturbing the original arrangement of the bones. This maximizes our ability to reconstruct accurately the preburial postures of the skeletons, which in turn offers one of the most important clues to the origin of the deposit. Before fossils are removed from their field jackets and completely cleaned, sketches and/or photographs are made to document their original orientations.

During the 1978 field season, an estimated 18 tons of field-packaged vertebrate fossils were shipped from Poison Ivy Quarry to the University of Nebraska State Museum for preparation and study. This material consisted of 1508 individually numbered items whose original horizontal and vertical position in the quarry can be determined by reference to the field records.

When microvertebrate remains were observed during excavation, bulk sediment samples were collected for screen washing. Our success in obtaining small vertebrates was very disappointing. Although we screened several tons of sediment, only a few incomplete microvertebrates were found.

As the fossils are prepared, they receive the number of the field jacket that contained them. This "field number" remains with the specimen as a guide to its provenience within the quarry. Ultimately, each bone also receives a "permanent" UNSM number. In cases where there is little or no doubt about the association of elements of an individual skeleton, a single UNSM number is applied to all bones of that individual. Isolated bones of unknown or doubtful affinity each receive a separate UNSM number.

By the end of February 1979, about 300 field casts, approximately a fifth of the 1978 collection, have been opened and at least partly prepared. Included are all of the rhinoceros skulls and jaws, about two-thirds of the horse and camel skulls and jaws, and a sampling of the birds, turtles, and smaller mammals.

COMPOSITION AND AGE OF THE FAUNA

Although rhinoceros skeletons make up the great bulk of the materials collected from the ash bed, the 1978 excavations uncovered a considerable variety of smaller animals as well. Currently identified vertebrates from Poison Ivy Quarry are listed in Table 1. Detailed identification of the nonmammalian remains has not yet been attempted. It is clear, however, that at least two kinds of turtles are present: a large land tortoise and a small aquatic turtle. Likewise at least two kinds of birds are represented: a long-legged (wading?) bird and a raptorial bird the size of a hawk.

The mammals belong to species already recognized in late Clarendonian faunas in the northern plains: for example, the Minnechaduza (Webb, 1969) of Nebraska and the Mission (Macdonald, 1960) and Big Spring Canyon (Gregory, 1942) local faunas in South Dakota. The horses *Pseudhipparion gratum, Cormohipparion occidentale,* and *Pliohippus supremus,* the rhinoceros *Teleoceras major,* the camel *Procamelus grandis,* and the oreodont *Ustatochoerus* cf. *skineri* occur jointly in all of these faunas (sometimes under other names) and their presence together in the ash bed strongly indicates a close correlation with these sites. The horse, oreodont, and rhino species are distinctly more advanced than their counter-

TABLE 1. Inventory of Fossil Vertebrates Collected from Poison Ivy Quarry (University of Nebraska State Museum Locality Ap 116) by the End of the 1978 Field Season

KINDS OF ANIMALS	MINIMUM NUMBER OF INDIVIDUALS
Rhinoceroses *(Teleoceras major)*	70
Horses (in order of abundance: *Pseudhipparion gratum, Cormohipparion occidentale, Pliohippus supremus, Calippus* sp., cf. *Astrohippus)*	>20
Camels *(Procamelus grandis, Aepycamelus* sp.)	6
Small "deer" (cf. *Longirostromeryx)*	5
Carnivores (cf. *Cynarctus,* cf. *Leptocyon)*	2
Rodents (heteromyid indet.)	1
Birds	>10
Turtles	>10

parts in the early Clarendonian Burge fauna (Webb, 1969). A late Clarendonian age for the Poison Ivy Quarry assemblage is thus assigned with considerable confidence.

RHINOS

The short limbs, nasal horns, large premaxillary bone and upper incisors, and hypsodont cheek teeth leave no doubt that the rhinoceros remains from Poison Ivy Quarry represent the genus *Teleoceras* Hatcher. A single, quite variable species appears to be represented by all the material studied so far (70 individuals, mostly skulls and teeth). Most previous authors have referred the characteristic late Clarendonian medium-sized *Teleoceras* to Cope's species *T. fossiger*. Skinner et al. (1968) however, have shown that the type specimen of *T. major* Hatcher, the genotypic species, was collected from rocks equivalent in age to the Cap Rock Member of the Ash Hollow Formation and is specifically distinct from the later, larger species *T. fossiger*, characteristic of Hemphillian age sediments. Tanner (1975) has also referred Cap Rock teleocerine material to *T. major* and has figured a maxilla from a prolific Cap Rock site, the Quinn Rhino Quarry (UNSM Bw-101) as evidence that *T. major* has smaller, simpler cheek teeth than *T. fossiger* from stratigraphically higher sites. On the basis of skulls collected in 1977 from Poison Ivy Quarry, Voorhies and Stover (1978) found that the type of *T. major* falls within the size and morphological range of the ash-bed rhino and concluded that the latter can be referred with confidence to *T. major*.

HORSES

Five of the eight known genera of Clarendonian horses occur in Poison Ivy Quarry. All five are grazers, subfamily Equinae; neither *Hypohippus* nor *Megahippus*, the Clarendonian browsing horses, subfamily Anchitheriinae, has yet been encountered in the ash bed. The three most abundant horses, each represented by skulls, jaws, and skeletons of adults and juveniles, are *Pseudhipparion gratum*, *Cormohipparion occidentale*, and *Pliohippus supremus*. In the material so far prepared, *Calippus* is represented only by a skull and mandible and *Astrohippus* by a skull. When fully prepared these specimens will allow a detailed anatomical comparison to be made among these horses in an effort to understand how so many closely related animals could occupy the same area at the same time without competitively excluding each other.

CAMELS

The commonest camelid at Ap 116 is *Procamelus grandis;* five individuals, four of them less than a year old, have been identified so far. The limbs of a giant camel, probably *Aepycamelus* were collected in 1978; the remainder of the skeleton appears to be present and will be collected in 1979.

OTHER MAMMALS

Several badly trampled skeletons of the small cervoid *Longirostromeryx* were collected and constitute the first definitely associated postcranial material of this animal. Jaws and associated postcranials of the omnivorous canid *Cynarctus* and teeth of the fox-sized canid *Leptocyon* are the only record of carnivores in the fauna except for several large coprolites and the presence of bite impressions on a few of the horse bones. A single tooth of a pocket mouse comparable to *Perognathus* is the only record of a rodent in the fauna.

ORIGIN OF THE DEPOSIT

I interpret the sequence of events leading to the death and burial of the animals at Poison Ivy Quarry as follows:

- The site was originally a shallow depression, possibly a pond formed as an oxbow, on the floodplain of a low-gradient stream.

Evidence: The ash bed is lenticular in shape; its thin, continuous laminations and ripple-marked bedding planes indicate accumulation in standing water with little or no current action. The sandstone beneath the ash bed in contrast is poorly sorted and laterally discontinuous with numerous fossil root casts and some cross bedding.

- The site was a water hole for local populations of large mammals.

Evidence: Numerous fragmentary bones and teeth (mostly rhinos, horses, camels, mastodonts, and turtles) occur in the silty sand just below the ash bed. These remains are broken, abraded, and scattered, possibly by trampling. Fish remains at this level indicate the presence of permanent water.

- A volcanic ash fall buried the local landscape—probably to a depth of 0.1 to 0.2 m.

Evidence: This is the thickness of the lowermost portion of the ash bed at Poison Ivy Quarry; it is uncontaminated with sand and silt and therefore almost certainly represents direct air-fall ash. Volcanic ash varying in thickness from a few centimeters up to 4 m crops out discontinuously at the same stratigraphic level (a few meters above the base of the cap rock) over an area of several hundred square kilometers in the Verdigre Valley in the vicinity of the quarry.

- Herds of three-toed horses, camels, and small deer died catastrophically during the late phases of the initial ash fall (large numbers of pond turtles and wading birds perished at the same time).

Evidence: Skeletons of these animals occur *above* the basal ash considered to be original air-fall material. Evidence of simultaneous death is twofold: study of individual age at death of the animals and intermingling of the skeletons at the same stratigraphic level (sandy ash) in similar states of preservation.

- Some carcasses decomposed slightly and were subjected to scattering; trampling, scavenging, and water currents probably all played a part in this.

Evidence: The skeletons of the smaller animals are somewhat disarticulated and scattered through the layer of sandy ash that occurs above the pure, basal ash and represents an influx of locally derived material into the pond. The sandy ash contains some small-scale cross bedding indicating weak currents. A rainstorm triggered by the ash fall may have supplied the necessary water. At least one horse skull shows two punctures almost certainly caused by the canine teeth of a scavenger. Many of the skeletons exhibit differential smashing (some parts well preserved, adjacent portions flattened and broken) in a manner highly suggestive of trampling by animals.

- Herds of rhinos and a few late-coming horses and camels arrived at the water hole and died, again very rapidly, perhaps a week or so after the principal die-off of smaller animals.

Evidence: The rhinoceros skeletons almost all are lying on, not in, the sandy ash—in contrast with the horses, camels, and birds; they frequently directly overlie smaller skeletons and are better articulated and less scattered than the smaller skeletons. Rapid death of the rhinos is indicated by the studies of individual age reported below.

- The rhino skeletons were rapidly buried by ash, probably in a few weeks or less.

Evidence: The three-dimensional preservation of most of the rhinoceros skeletons, many of them in crouched positions with the legs directly beneath the body, indicates that the carcasses were still largely intact when buried.

- The depression completely filled with ash, sealing in the skeletons. This was probably accomplished within a few weeks or less by wind blowing in ash from the surrouding ash-blanketed countryside.

Evidence: Rapid infilling is indicated by the lack of major hiatuses in the laminated ash above the level of the skeletons. Wind rather than water transport is suggested by the lack of sand and silt in the upper portions of the ash. Any significant erosion by water would surely have cut through the thin loose mantle of ash on the hillsides and washed sandy debris into the pond. This did not happen, suggesting that filling was complete before the next major rainstorm.

In summary, I suggest that the fossils represent populations of animals that died catastrophically around a shallow water hole during or shortly after a major ash fall that blanketed the surrounding countryside with volcanic ash. Smaller animals (horses, camels, birds) died first and began to decompose, but were buried in a mixture of sand and ash washed into the water hole, possibly during a rainstorm. Before disarticulation of the smaller animals was well advanced, but after deposition of the sandy ash, a large number of rhinoceroses entered the water hole, trampling many of the smaller skeletons; the rhinoceroses then died and were quickly covered by volcanic ash, which probably sifted into the water hole as the ash blanket on the landscape was reworked by wind.

DID *TELEOCERAS* FORM HERDS?

The mere presence of a large number of individuals at one location does not prove gregariousness in fossil (or living) animals. For example, otherwise solitary animals might congregate around a shrinking water hole in times of drought and might die and be buried together; such an aggregation could then be mistakenly taken as evidence for herd-forming behavior. Likewise if a few animals died and were fossilized at the same place each year over a long period of years, the large fossil "population" that accumulated could be misinterpreted as a herd.

Keeping such caveats in mind, I believe that the Poison Ivy rhinos represent a herd, a genuine social group. The evidence suggesting this derives from several sources. The stratigraphy of the site and condition of the skeletons clearly indicate that the animals died together, very rapidly; the carcasses did not accumulate over a period of many years. Secondly, as discussed more extensively below, the biological composition of the fossil rhino "population" has several features, especially a highly unbalanced adult sex ratio, which are difficult to account for on the assumption that the quarry sample represents a random sample of nongregarious animals from a large area. If *Teleoceras* individuals lived solitary lives, as do modern rhinos, and normally were widely dispersed then their congregation, death around a water hole should result in a sample consisting of roughly half males and half females. As shown below, this is not the case; the fossil rhino population is structurally more similar to that of modern gregarious hoofed animals than to that of solitary forms.

POPULATION DYNAMICS

The geological/taphonomic evidence discussed above suggests that the skeletons in the ash bed provide us with a "snapshot" of living herds as they existed at a remote moment in time. The mechanisms of death and burial appear to have been sufficiently nonselective that the ratios of young to old and male to female animals were preserved intact, without the usual distorting factors (e.g., sorting, abrasion). The sample from Ap 116 is, therefore, almost ideal for study using the techniques of population dynamics (Deevey, 1947).

Few studies of this type have been attempted with fossils. Kurtén (1953) pioneered the approach; more recently Voorhies (1969) and Saunders (1978) have analyzed fossil "populations" and tried to extract meaningful information about birth, death, and reproductive rates from them. In almost all studies of population dynamics in extinct animals it has been necessary to estimate the proportion of very young individuals. Probably because of their susceptibility to destruction (e.g., by weathering, scavenging), remains of juveniles tend to be underrepresented in fossil collections. In contrast, the Poison Ivy Quarry sample studied so far contains a large number of juveniles. Young rhinos, horses, and camels appear to be present in the high numbers expected in healthy herds. Only the rhino sample has been studied in any detail, however. Preliminary results are given below.

AGE AND SEX DISTRIBUTION

The age at death of each of the 70 individual rhinoceroses collected so far has been determined on the basis of tooth eruption and wear (Kurtén, 1953; Voorhies, 1969). Table 2 shows the age distribution of this sample.

The skulls of the youngest animals—those retaining the full deciduous (milk) dentition—fall readily into three distinct age groups with no intermediates. These are interpreted as three successive year-classes of calves. The tight clustering of the rhino calves into age groups allows three important inferences to be drawn:

- Births were seasonal in *Teleoceras* as in modern hoofed mammals of the Great Plains (bison, prongbucks) rather than occurring at all seasons as in modern African rhinos (Goddard, 1966).
- The animals must have died over a very short period of time—surely less than a month—otherwise much more "blurring" of the age groupings would be expected.
- The deaths must have occurred shortly before the calving season (spring?) because members of the youngest age group already have considerable wear on their teeth. (Additional support to this interpretation is provided by the presence of probable near-term fetuses in the pelvic cavities of several adult females.)

The adult rhinos cannot yet be assigned accurate ages in years although when a somewhat larger sample becomes available (perhaps 150 or so) this may be possible. If the crown heights of adult teeth are measured and the values plotted, distinct, more-or-less evenly spaced clusters can be interpreted as year classes. In the writer's experience, a sample size roughly equal to three or four times the maximum longevity (in years) of a hypsodont ungulate is necessary to ensure the success of this method. A second method of precise age determination—the interpretation of growth lines in the cementum or dentine in teeth—is now being attempted on a small scale in our laboratory and shows some promise of success. The method has the disadvantage of involving some unavoidable destruction of specimens in the extraction and sectioning of teeth.

TABLE 2. Age Distribution of Fossil Rhinoceroses (*Teleoceras major*) from Poison Ivy Quarry

	NUMBER OF INDIVIDUALS	INFERRED AGE IN YEARS
Group I (young calves)	14	¾
Group II (middle calves)	10	1¾
Group III (old calves)	8	2¾
Group IV (subadults)	5	3¾-6
Group V (young adults)	21	6-11
Group VI (middle-aged adults)	11	11-20
Group VII (old adults)	none	20-40

Age assigned to groups on basis of tooth eruption and wear.

Possibly a combination of techniques—a primary age grouping based on tooth wear with supplementary detailed growth ring studies of selected individuals spanning the age spectrum from juveniles through older adults—will provide us with an accurate picture of the age distribution within the *Teleoceras major* sample at Poison Ivy Quarry.

SEX DIFFERENTIATION

Skulls of adult rhinos from Ap 116 show marked sexual dimorphism. As long ago as 1898, H. F. Osborn studied a number of skulls and jaws of *Teleoceras fossiger* from various localities in Kansas and Nebraska and stated that individuals with large lower tusks were males while small-tusked individuals were females.

This evidence was strongly suggestive but not wholly convincing because it was based on specimens from over a large area, not demonstrably the same age. Osborn's hypothesis, however, is strikingly confirmed by our discovery of fetal bones within the pelvic cavity of an adult skeleton (UNSM 52373) with small tusks (20.1 × 22.5 mm in cross section). The difference in tusk width between males and females was very significant. Other possibly sex-related features such as overall size and horn size appear to differ much less than do tusk diameters.

SEX DISTRIBUTION

Using tusk size as a criterion for sexing the adult rhinos, we arrive at a rather surprising sex distribution: Only 5 adult males are present compared with 32 females. The unbalanced sex ratio is particularly evident in the young adults among which females outnumber males 25 to 1.

In view of the large sample size, the scarcity of males is unlikely to be due to chance. Likewise it seems unlikely that males somehow preferentially escaped death—the high percentage of "prime" adults in the death assemblage strongly argues that the agent of mortality was nonselective: All animals present, regardless of "vigor," were killed.

My present interpretation, then, is that adult males, especially young ones, were greatly outnumbered at the water hole (at least the part excavated so far) at the time the ash accumulation occurred. This suggests that the social behavior of *Teleoceras* was much different from that of modern African rhinoceroses, which are generally solitary except for mother-young associations and brief encounters during breeding (Leuthold, 1977). A social grouping more like that in some modern gregarious ungulates is suggested. For example, plains and mountain zebras (Leuthold, 1977) form stable breeding herds of females accompanied by single adult stallions. Young subdominant males are actively excluded by the "harem master" and form "bachelor herds" of their own. (Several skeletons exhibit healed broken ribs suggesting that active butting contests occurred.)

GRASS SEEDS AS CLUE TO DIET

Tiny silicified plant fossils were first noticed when the hyoid apparatus—tongue bones—of an adult female rhinoceros was being cleaned. In view of the possibility that these might represent food residues, we began to examine the matrix removed from the fossil mammal skeletons even more carefully to determine whether plant fragments were undigested food or had been introduced into the skeletons along with the ash particles. After carefully subjecting cubic meters of ash outside the skeletons to fine screening and flotation without finding any "seeds," we are now confident that the rather numerous plant fossils found inside several of the skeletons represent food ingested by the animals shortly before death.

The seeds (technically floral bracts) have been identified by Joseph R. Thomasson, an authority on fossil grasses, as belonging to three extinct species: *Berriochloa primaeva, B. nova,* and *B. communis.* The specimens are amazingly well preserved with details of the epidermal cell patterns readily observable in scanning electron photomicrographs. The new evidence conclusively shows that this animal was a grazer.

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Michael R. Voorhies

Social Behavior and Communication of Neotropical Frogs

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In addition to the grant from the National Geographic Society, the project received support from the University of Connecticut Research Foundation. From June through August, 1978, my graduate assistant Beverly J. Greer and I studied the vocal behavior of several species of hylid frogs at one location in Panama and the reproductive and territorial behavior of a centrolenid frog in another.

VOCAL BEHAVIOR OF HYLID FROGS

Anuran vocalizations traditionally have been considered highly stereotyped signals, but males of many species alter their calls in response to conspecifics calling nearby (Wells, 1977). For example, Rand (n.d.) found that male *Physalaemus pustulosus* (Leptodactylidae) have advertisement calls consisting of a tone-like "whine" note and 1 to 3 click-like notes. Males calling in relative isolation usually give only the whine notes, whereas those in choruses give both whines and clicks. Rand hypothesized that the click notes were more easily located by females in a noisy chorus, and he demonstrated that females preferentially move toward calls with the larger number of clicks in two-choice playback experiments.

Other species in several families around the world apparently exhibit similar changes in calling behavior in response to competing males, but none has been studied experimentally (Wells, 1977). Good candidates for such studies include several Neotropical hylid frogs that have complex multipart calls consisting of buzz-like introductory notes followed by several click-like secondary notes (Fouquette, 1960; Duellman, 1970, 1978). Although Fouquette studied vocal isolating mechanisms in three of these species, there has been no attempt to study relationships between vocal-