EXTINCT CARNIVORES ENTOMBED IN 20 MILLION YEAR OLD DENS, AGATE FOSSIL BEDS NATIONAL MONUMENT, NEBRASKA

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Careful research of museum archives and early publications in the science of paleontology led to the discovery at Agate Fossil Beds National Monument, western Nebraska, of the oldest known record of denning behavior in large mammalian carnivores. In September 1981, paleontologists of the University of Nebraska State Museum found the 20 million year old dens by relocating an abandoned fossil site which in 1905 had produced unusual numbers of carnivore bones. The fossil remains of carnivores are usually rare at such sites because, in life, carnivores make up a much smaller percentage of the mammalian fauna than the plant-eating mammals. We do not expect to find many carnivore bones relative to the proportion of herbivore bones at a given site. But before we explain how this situation was resolved, let us first briefly mention the significance of the Agate Spring Quarries.

The Agate Spring Quarries have been known for eighty years as one of the greatest fossil mammal deposits in North America. Buried in stream-laid sandstone of Miocene age, the 20 million year old bone bed, exposed in two hills (Carnegie Hill, University Hill) overlooking the Niobrara River valley of northwest Nebraska, has produced thousands of bones of extinct herbivores to paleontologists excavating for North American museums and universities. So abundant are the fossil bones of mammals that a man could walk on a pavement of bones without touching the sediment in some areas in these quarries.

The bones are found in a stratum or bed about 0.5 meter thick at the base of an ancient Miocene stream channel (the Miocene is an epoch of geologic time that extends from about 5 m.y. to 24 m.y. ago). Fine sand is closley packed around the bones, most of which are no longer connected in the framework of a skeleton, but have come apart (the technical term is disarticulated), so that the bone bed is a logjam of individual bones. Partial skeletons, or fully articulated skeletons, are not common but do occur. By examining the enclosing sediment under the microscope, we find that the sand grains are either the minerals quartz and feldspar or fragments of volcanic glass, each making up about one-third of the sandstone. Many sharpsided unworn sand grains made of quartz and feldspar can be seen, some with small pieces of volcanic glass still fused to their surfaces. The absence of wear indicates these angular sand grains have not been transported great distances and/or for long periods of time by streams. Probably more than 50% of the sediment in the ancient stream channel was originally brought into the region by wind from distant volcanic centers to the west.

The presence of both stream-deposited and wind-worked sediment in the Agate stream channel (and other channel fills of similar age elsewhere in the region) lead us to believe these are ephemeral streams, flowing only in times of abundant rainfall, probably in short bursts of considerable volume, interspersed with long periods of inactivity when the dry sandy bedload of the stream is worked by wind.

Bone at the bottom of the channel is often fragmented and the individual pieces well-rounded. Much of this type of bone is unidentifiable in terms of the kind of animal it represents. Earlier collectors frequently reported that the floors of these quarries were often rich in these worn bones and bone fragments, the edges smoothed by abrasion over some unknown time interval. These pieces of worn bone have been abraded by periodic floods. They represnet the end product of a process of disassociation and breakdown of the original skeleton by biotic agencies such as scavengers, carnivores, the trampling of ungulates; by stream processes; and by seasonal climatic fluctuations.

Associated with the fragmented bones are vast numbers of whole bones, unattached to any other bones, but complete and relatively unabraded. Surprisingly, these whole bones generally belong to only three kinds of mammals.

By far the most common mammal in the quarries is a small lightly-built rhinoceros (*Menoceras*) about the size of a pony. We judge it to be a good open-country runner from its skeletal anatomy. Males carried a paired horn on the tip of the nose, but females were hornless. Because both sexes among the living Old World rhinos have horns, paleontologists first believed they had discovered two distinct species, but soon the absence of horns in the female *Menoceras* became apparent as a large sample accumulated.

Next in abundance in the quarries is a bizarre claw-footed browsing chalicothere (*Moropus*), with large curved terminal toe bones. These toe bones or phalanges originally were mistaken for the claws of giant ground sloths. The bones of *Moropus* have tended to be concentrated in particular areas within the quarries. As with the small rhinocerous, young, middle-aged and old individuals are present.

Last, occasional remains of the giant entelodonts (*Dinohyus*) occur scattered throughout these quarries, usually as isolated bones, often worn and fragmented. However, two nearly complete skeletons of entelodonts have been found, one in each of the two major hills at Agate.

Other mammals are represented in the quarries only by rare remains such as isolated teeth, jaw fragments, and occasional limb and foot bones. Small horses and camels, oreodonts, birds, protoceratid antelope, moschid deer, and a few carnivores are known. Interestingly, the known number of carnivore bones from the quarries of the two main hills (Carnegie Hill, University Hill) totals less than 30, whereas the bones of herbivores (*Menoceras, Moropus, Dinohyus*) number in the thousands.

As I studied the records of the early excavations, it became evident that one quarry, called Carnegie Quarry 3 (Fig. 1), located on a small hill (Beardog Hill) about 180 to 275 meters southeast of the main quarries was atypical in producing only rare fragmentary bones of herbivores. Yet for some reason, numerous carnivore bones had been found in this quarry. I became curious about this reversal of the usual carnivore/herbivore ratio. The site had been reported by its discoverer, Olaf Peterson of the Carnegie Museum, to be in the same Miocene stream channel deposit as the quarries in the main hills.

Specifically, Peterson in 1905 had found the first fossil remains of a rare amphicyonid carnivore or 'beardog' at Quarry 3, which he named *Dephoenodon superbus* (Fig. 2), More than one beardog was discovered at the site. In addition, he also found a small true dog or canid (*Phlaocyon annectens*) about the size of a small fox, and a mustelid carnivore (*Paroligobunis simplicidens*) about the size of a living wolverine. Two of the beardog skeletons were nearly complete, and partially articulated in the sediment. What was the explanation for this unusual aggregation of extinct carnivores?

In 1977, I mapped the geology of the Agate National Monument for the National Park Service, and confirmed at that time that the uppermost 6 to 7 meters of Beardog Hill were originally part of the same Miocene stream channel

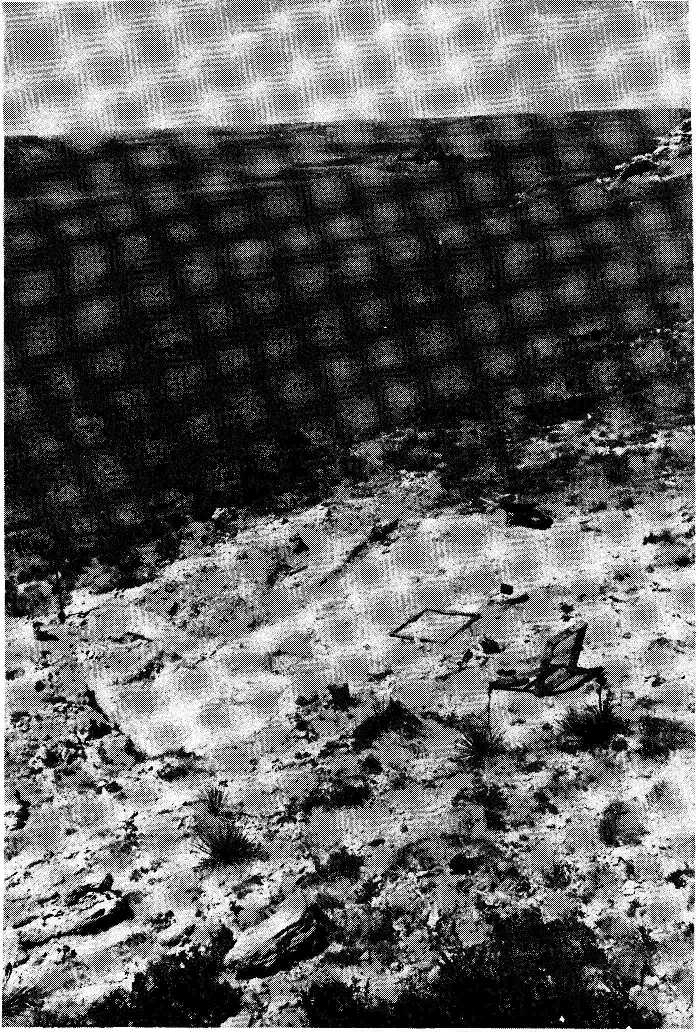

Figure 1. Carnegie Quarry 3 in foreground at Beardog Hill, Agate Fossil Beds National Monument, Sioux Co., Nebraska. Carnegie Hill with its mammal bone bed appears at extreme upper right.

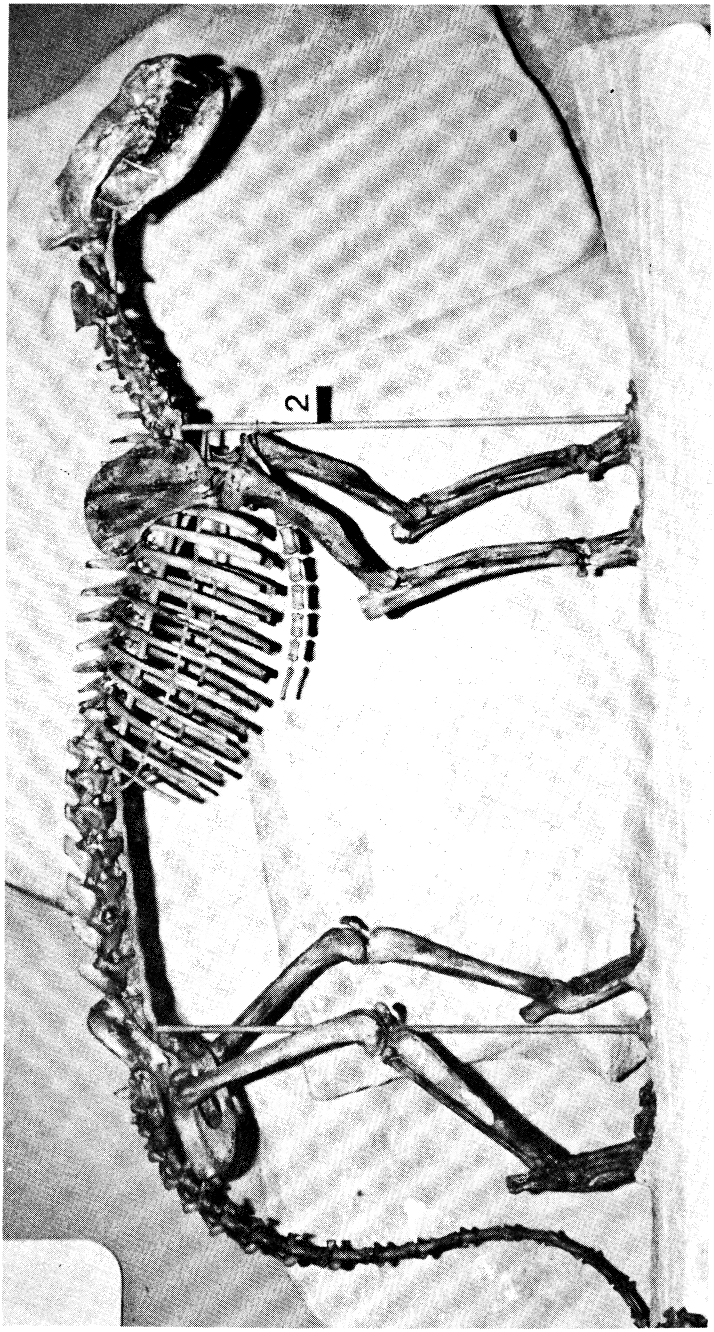

Figure 2. The female beardog *Daphoenodon* found by Olaf Peterson at Quarry 3 in 1905, presumably in Den 1. Skeleton mounted at Carnegie Museum, Pittsburgh.

fill as the bone-packed channels in the main hills. Peterson had been right. It was clear that the quarry must be somewhere in the channel deposit making up the upper part of the hill. Mistakenly, I assumed that the Quarry 3 carnivores were buried within normal stream sediments deposited in a channel. Unfortunately, Peterson left no pictorial or written record on Quarry 3's location, other than a photograph published in 1910 indicating that it was somewhere on Beardog Hill. The best approach would be to carefully search the perimeter of the hill for evidence of a previous excavation.

In 1981, the Park Service granted permission for a preliminary excavation at Beardog Hill. A renewed search for records at the Carnegie Museum in Pittsburgh produced no conclusive result, so a test excavation at the hill became the logical next step. However, it now seemed to me that there was little proability of ever locating the exact site. There were a number of places around the periphery of the hill where the quarry could have been located. Adoption of a routine procedure in field paleontology, however, proved me wrong, and led to the discovery of the site.

When a fossil skeleton occurs in bedrock near the surface of the ground, fragments of the skeleton often graudally work into the soil that develops on the bedrock. Routinely, paleontologists pass the surface soil through screens to recover these bone fragments, which may include important parts of the skeleton that otherwise would be lost. Often such fragments in the soil are the first clues that a skeleton is present in the bedrock below the soil. Since the bone bed in the quarries of the main hills lay at the very base of the channel bed, we placed trenches at Beardog Hill so that they would intersect the base of this same bed. Two such trenches produced nothing of interest: no bone or bone fragments, no sign of earlier digging was found. For our third attempt, we moved about 8 meters north from our original trenches. Upon sieving the soil, carnivore bone fragments appeared on the screens: part of the shin bone or tibia. These were recognized as beardog bones, in fact the same species found by Peterson, and the work continued in some excitement. The probability that we had located the quarry was high, for since carnivore bones are scarce in most field settings, beardog bones of the kind found by Peterson in Quarry 3 were an improbable and thus a strongly confirming find. However, unknown to us at the time, the unequivocal evidence proving that this was Quarry 3 was not to be discovered until some months later.

When we sieved the surface dirt and recovered the fragmentary beardog bones, we had no thoughts that one of these pieces would match one of the Carnegie bone fragments found in 1905. One of the most exciting moments of the work on the Agate fossils was Carl Swisher's match of the partial tibia (UNSM 10-81) with one of the Carnegie fragments (CM 1589D), proving that they were once part of the same bone. The attempt to achieve such a match began in my office laboratory in Lincoln one afternoon in late April 1982. Josh Kaufman, Carl Swisher, and I had been trying to match the bone fragments sieved from the soil at Beardog Hill with fragments collected by Peterson in 1905. After working at this for more than an hour, Swisher returned to a box of fragments tried earlier, and on the second attempt, fitted a small fragment from 1905 to our partial tibia. The two pieces were collected 76 years apart!

Despite the lack of conclusive proof that we had relocated Quarry 3 in September 1981, the presence of *Daphoenodon* bones in the soil was reason enough to begin a thorough study of the locality. There was little doubt in our minds that we had found the place. Rather than cut into the bedrock, we began by removing all the soil over an area of about 9 square meters (Fig. 3). Removal of the soil exposed a west-sloping bedrock surface that merged at the south end of the quarry with a 1-2 meter-high vertical wall of Miocene sandstone. This sandstone wall contained a paleosol or ancient soil within the channel sediments, indicating that the land surface had stabilized for a time before renewed stream deposition. The paleosol occurs from 0.7 to 1.5 m above the base of the channel bed at about the same stratigraphic level as a paleosol in the main hills above the Agate bone bed. (Possibly these two paleosol horizons represent the same ancient soil.)

Extending downward about a meter from this paleosol into the sandstone wall at the south end of the quarry were two large burrows (burrows A and B, Fig. 4), found on the third day of the 1981 excavation (September 11, 1981). Each burrow was filled with sediment, primarily a fine gray ash-rich sand. The gray sandy fill contrasted sharply in tone with the white sandstone bedrock intruded by the burrows. In one of the burrows (burrow A, Fig. 4), the sand was distinctly stratified in thin layers about 1 mm thick, demonstrating that the sand had been progressively introduced into the burrow, filling it in over an indeterminate amount of time. Sets of this layered sediments were separated from each other in the burrow by erosion surfaces; thus some time was involved, time enough to deposit thinly layered sediment, then erode some part of it, and then deposit at least two similar sets of layers at a later time. A second burrow (burrow B, Fig. 4) contained 10 and 20 cm-thick layers of homogeneous fine gray sand separated by a 25 cm-thick rubble of poorly sorted sand and sand pebbles, suggesting breakdown and incorporation of part of the burrow wall. This same burrow also preserved a vertical steeply cut margin between two masses of sediment fill that could indicate reexcavation of the burrow after it had become partially filled. We traced the two burrows upward, but could find no openings on the present ground surface.

Next we examined the bedrock below the burrows. We had carefully removed the soil without disturbing the buried bedrock surface. To our surprise, there appeared a shallow hemispherical depression in the bedrock about a meter in diameter and 20 cm maximum depth. It was similar in shape to pits left by professional paleontologists upon the removal of a large block of sediment containing fossils. Immediately we remembered that Peterson had removed the two nearly complete skeletons of *Daphoenodon* in a single large block of sandstone (Peterson, 1910, p. 206). If this was the place from which the sandstone block had been collected, the two nearby burrows could explain why the two skeletons had been found together, one an adult female, the other a juvenile male about 6 months to 1 year old (Fig. 5, Den 1). Proof was lacking, but the circumstantial evidence seemed compelling.

The discovery of the burrows provided us with our first hypothesis as to the reason Quarry 3 had produced so many carnivores. Possibly Quarry 3 had breached an ancient den complex. But it seemed unlikely we could confirm this. We could see no bone in the fill of the two burrows that we had uncovered, and apparently Peterson had left no photograph of his removal of the two beardogs in the sandstone block. Furthermore, we thought that Peterson and his party would have extended the excavation to its limits, taking all fossils available, as was customary at such sites at the time.

More as a matter of professional thoroughness than with any real belief in finding more fossils, we extended the excavation to the north, meter by meter. To

Figure 3. Josh Kaufman (left) and Bob Hunt re-open Quarry 3 for the Nebraska State Museum in September 1981 by removing soil at the site. Photo courtesy of M. Swanson, Harrison, Nebraska.

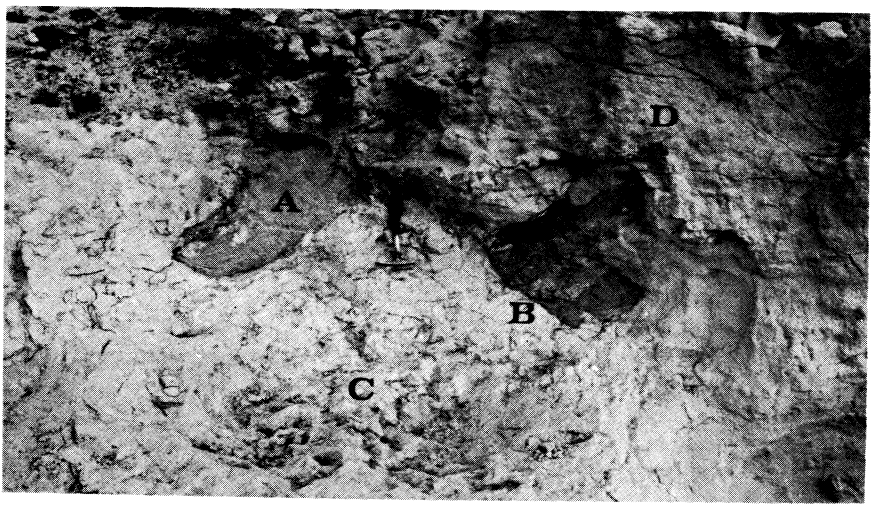

Figure 4. Burrows A and B of Den I exposed in wall of Miocene sandstone. (A) burrow A; (B) burrow B; (C) presumed location of Peterson's Den I chamber; (D) early Miocene paleosol. Hammer length, 28 cm.

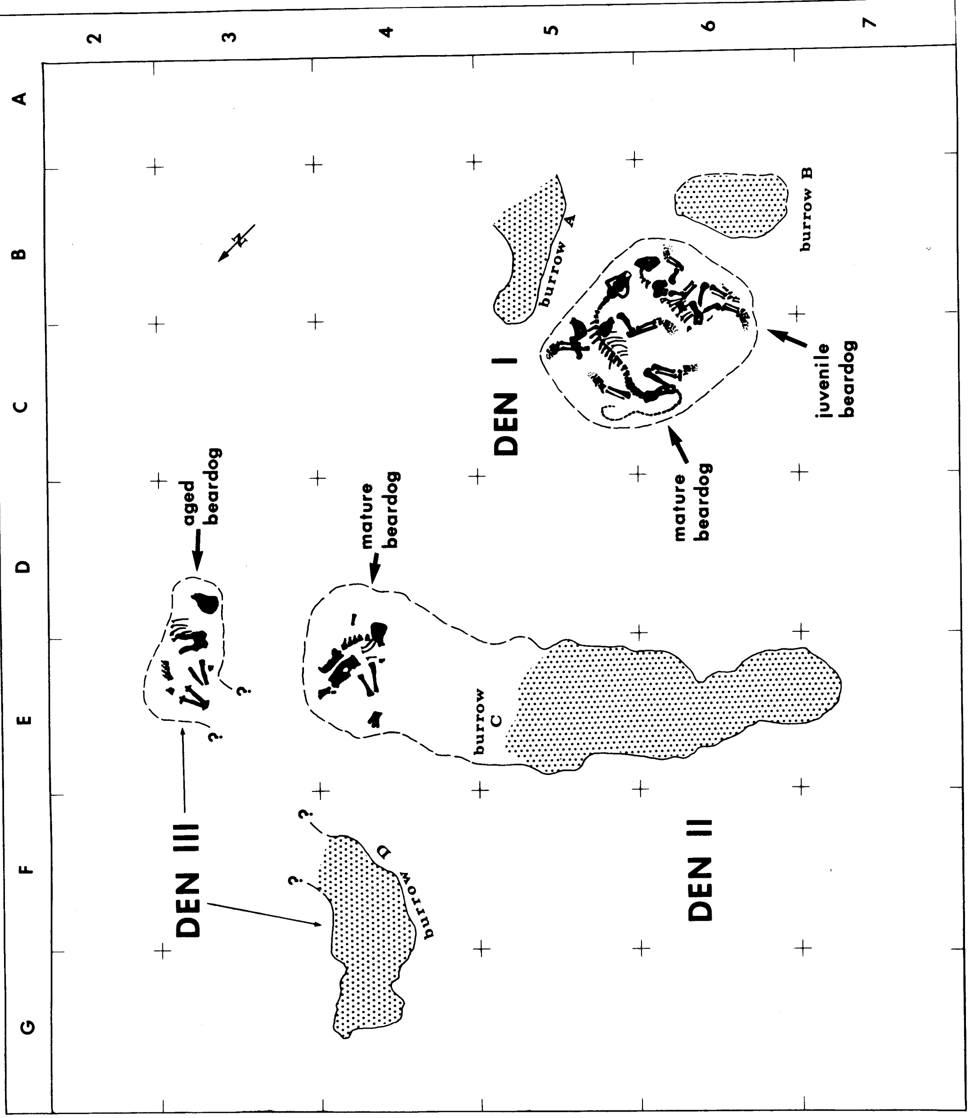

Figure 5. Plan map of early Miocene carnivore dens, Quarry 3, Agate Fossil Beds National Monument. Stipple pattern indicates Miocene burrow fill that also surrounds beardog skeletons. Dens I and III contained the beardog *Daphoenodon*; Den II produced a rare temnocyonine beardog. Excavation grid is in square meters.

my amazement, we came upon fragments of the skull of a temnocyonine beardog, a very rare carnivore belonging to a different lineage than *Daphoenodon,* about 3 meters north of the first burrows we had discovered (Fig. 5, Den II). Initially, we did not realize this animal was in a burrow, but this soon became evident when the skeleton was removed in a block of sandstone, and the contrast between burrow fill and burrow wall was plainly evident at the place where the block had been taken up.

Discovery of this animal in situ in a burrow brought home to us the significance of the find: here was proof that at least one carnivore had been entombed in a burrow, and here was support for the hypothesis that Peterson's carnivores could have been found within burrows as well.

The site was closed for the season after this discovery. We returned to the university to work over the data we had gathered, and to reexamine Peterson's carnivore sample of 1905 which the Carnegie Museum's paleontologists had kindly loaned us. I began to try to work out the position of the newly discovered beardog in the sandstone block that we had collected, using radiographs taken at a local hospital. Kaufman and I also began to learn as much as we could about denning behavior in living carnivores, helped by advice from Blaire Van Valkenburgh, a studnet of carnivore ecology at Johns Hopkins University. We learned that dens used by large carnivores are not always dug by them; rather, they often enlarge a preexisting hole made by another mammal. The beardogs found by us and by Peterson are the largest land carnivores of their time--only one other species is larger than the ones found in Quarry 3, and it is also an amphicynoid. Clearly if these beardogs had not excavated these burrows, they probably enlarged them to an acceptable and inhabitable size, since there were no other burrowing mammals of their bulk to accomplish this for them.

Furthermore, radiographs of the temnocyonine showed there was less than a complete skeleton present; bones were scattered through the block of sandstone indicating that the skeleton had been disarticulated prior to final burial. I could recognize the skull and even individual teeth in the radiographs, and a number of their bones of the skeleton, but discovered that the x-rays were not penetrating through the full thickness of the block. We would have to prepare the block manually to determine the extent of the skeleton.

In July 1982, the site was reopened. Almost immediately we found that a 2 to 3 meter-long burrow was associated with the temnocyonine beardog found the previous fall (burrow, C, Fig. 5). We had been walking over this burrow during the previous field season and had not even recognized it. Once exposed to view, it too contained the gray layered sandy fill present in the first burrows found. In this case, however, we were seeing the burrow cut in horizontal section, whereas the first two burrows (burrows A, B, Fig. 4) had been exposed in a vertical wall. Dimensions of these burrows are very similar to burrows of living wolves and hyenas, whose body size is also like that of the beardogs (gray wolves range in weight from about 27 to 80 kg; the spotted hyena ranges from 59 to 82 kg; striped and brown hyenas have weights from 27 to 54 kg, according to Walker, 1968).

Again removing only the soil, we extended the lateral dimensions of the excavation, and soon encountered a second beardog skeleton (Fig. 5, Den III) in the first day of work (July 12, 1982). It was also preserved in gray sandy burrow infill. The jaws of the beardog were the first part of the skeleton discovered. Heavy wear on the teeth showed it to be an aged individual of *Daphoenodon superbus,* the same species that Peterson had found. With our discovery of this second carnivore in burrow fill, the possibility that we had found a Miocene den complex changed in our minds to a strong probability. In addition, we now had evidence of a broad age spectrum of *Daphoenodon superbus;* young, mature, and aged individuals were all represented (Fig. 5).

Our second excavation at Quarry 3 ended on July 30, 1982, following very hot weather. We returned in the coolder weather of October and continued work (October 16 to 21, 1982), before early snowfall ended our efforts. We extended the site to the north and west, carefully removing the soil, and cleaning and examining the bedrock surface. Again, a new and relatively large den was discovered, terminating in what appeared to be three tunnels branching from a main den chamber. A beardog vertebra and mustelid food bone (*Paroligobunis*) were found in the fill of the burrow system at the surface. We did not excavate the fill, but decided to work it later in the 1984 seasons.

Here, however, the floor in each of the three terminal lobes of the den was nearly level with the bedrock surface. The upper parts of these burrow lobes and their fill had been stripped away, either by slope erosion, or possibly by the Carnegie excavators. This latter alternative is a resonable possibiltiy, especially since 3-4 additional individuals of *Daphoenodon* were discovered in Quarry 3 by Peterson. Although the dens found by us in 1981-82 show no tool marks (excavation picks used by paleontologists often leave narrow linear grooves in bedrock that persist for many years in the arid climate of the central Great Plains), we probably will never be certain how much of the area that we have uncovered was in fact first excavated by the Carnegie party of 1905 (some additional excavation was done by the Carnegie group in 1908 which resulted in the discovery of a superb *Daphoenodon* skull, lower jaw, and some associated skeletal material, CM 2774, but again no detailed record of the location of the find in Quarry 3 was kept).

The significance of the den complex is not only in the extinct Carnivora that were found there. It lies as well in what we have learned about the way of life of these animals. The discovery tells us for the first time that amphicynoid carnivores used burrows; amphicynoids are the lárgest and therefore presumably the dominant mid-Cenozoic terrestrial carnivores (the Cenozoic Era of geologic time extends from about 65 million years ago to the present). Prior to this find, we had known little about their ecology. Because member species of two diverse lineages have been found in the burrows, there is a good possibility that many amphicynoids could burrow and use dens, at least on occasion. Secondly, the great age (about 20 million years) of the den complex, based on its stratigraphic relation to two dated volcanic ash beds, places it as the oldest evidence of denning behavior of large mammalian carnivores.

A historical scenario summarizing what we presently know about these dens can be based on the size and form of the burrows, the ages of the carnivores (established by the degree of eruption and wear on teeth), the condition of the skeletons, and the nature of the sediment fill.

The number of tunnels and their considerable size suggest a major denning area, used by a number of animals. The presence of young, mature, and aged beardogs in the burrows tells us that whereas older animals could have died normally at the end of their customary lifespan, the young animals must have expired prematurely. After death, bite marks and the scattering of some bones show decomposition and scavenging of carcasses took place. Last, careful study of the sediment infill indicates that the dens filled episodically over a period of time, not continuously in one event. As noted earlier, there is evidence that some dens were partially filled, then reexcavated. Probably the dens were used by a succession of animals over time, as has been documented for some modern burrow systems.

Eventually the den complex filled completely with sediment, and a migrating Miocene stream entirely buried the burrows under at least 5 meters of later channel deposits. Nearly 20 million years would pass before this remarkable association of carnivores and their shelters would again see the light of day.

We plan to continue the work at Quarry 3 over the next years. The probability that more dens will come to light is high. If enough burrows can be found, then it will become feasible to work out the fill of several and thus come to an understanding of their content and manner of filling. To date, we have not disturbed the laminated sedimentary fill of the burrows since we do not know how rare such discoveries will be in the future. Perhaps prey carcasses will occur in some dens, or other associations of females with juveniles will be discovered. The possibilities are exciting, and made more so by the relationship of the den site to the great bone bed in the main Agate hills. Through such research efforts, the hard won understanding of the fossils at Agate, built over time by many dedicated paleontologists and their assistants, is gradually expanded and refined, added to and improved, until we are able to comprehend something of the prehistory of this site on the plains, which is a part of the large picture of the evolution of life on Earth.

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