Fine structure in the occultation signatures of a given parallel ringlet should occur in the same order in ρ for all longitudes, if the orbits are all filled. The entwined model, however, would generally show differences and under particular conditions, even a radial reversal. A parallel model that is stabilized by self-gravity must have a greater radial width at apoapsis than at periapsis and a characteristic longitudinal reversal in the tilt of the local plane of the ringlet relative to its average orbital plane. Neither characteristic is known to be required for the entwined model, although both are structural possibilities (Fig. 2). Finally, the nodal precessions for the two models would be markedly different if they were stabilized in the ways suggested above.

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Miocene Burrows of Extinct Bear Dogs: Indication of Early Denning Behavior of Large Mammalian Carnivores

Abstract. *Partial skeletons of four species of extinct carnivores have been found in their dens excavated in the floodplain of an early Miocene ephemeral braided stream at Agate Fossil Beds National Monument, Nebraska. Bear dogs (Carnivora: Amphicyonidae) were the principal occupants; their den dimensions and body size are similar to those of living wolves and hyenas. Discovery of this predator community extends the record of denning behavior of large mammalian carnivores to the early Miocene, 20 million years ago.*

Relatively complete fossil skeletons of mammals preserved directly in their ancient environment provide insight into mammalian paleoecology. We report the discovery of a 20-million-year-old den complex (*1*) with partial skeletons of four species of extinct Miocene Carnivora. The remains, found in burrow fills over 30 m^2 in the floodplain of an early Miocene ephemeral stream, are an unusual occurrence in the fossil record (*2*).

The discovery extends the age of denning behavior of large terrestrial Carnivora to the early Miocene. It also indicates that amphicyonid carnivores (the dominant mid-Cenozoic land Carnivora) used dens and that denning was within the capability of many if not all amphicyonids, since species from two widely divergent lineages were found in separate dens (*3*). Furthermore, the skeletons in the den complex suggest that the dens were used in protection and care of the young and as shelter for adults; to our knowledge they provide the only evidence known in the Tertiary fossil record for the occupation of a den by a succession of carnivore species. The Agate den complex represents one of the oldest known burrow systems (*4*).

The history of this ancient predator community can be reconstructed from 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 sediment fill. The form and large size of the burrows, similar to burrows of living large canids and hyaenids, suggest their construction or remodeling by the largest terrestrial carnivores of the early Miocene, the amphicyonids or bear dogs. The bear dogs found in the dens resemble wolves in size and certain skeletal features, but are not closely related. The bear dog *Daphoenodon superbus* is represented by at least six or seven individuals, and a rare temnocyonine bear dog by one skeleton. A juvenile, a mature adult, and at least three old individuals of *Daphoenodon* can be identified from dental evidence. Skeletal features indicate that the remains of one or two other individuals, which are not represented by teeth, are adults. Although old individuals possibly died in the dens through normal attrition, the deaths of the juvenile and young adults in the burrows must have been premature and probably sudden. The partial disarticulation of all skeletons in the burrows and bite marks on some bones show that there was sufficient time for decomposition and scavenging of carcasses to take place before sediment burial.

In addition to bear dogs, the dens contained remains of small canid and mustelid carnivores. Because simultaneous occupation of a den by more than one species is uncommon among living Carnivora, the presence of more than one kind of fossil carnivore in these dens suggests they were used by a succession of species, that the smaller carnivores were occasional prey of the larger bear dogs, or both. However, the presence of only a few herbivore bone fragments within the burrows indicates that prey carcasses were infrequently taken into the dens, thus the small carnivores were probably den occupants.

The dens (Fig. 1) occur in an area 5 by 6 m in quarry 3 on Beardog Hill, Agate Fossil Beds National Monument, Nebraska. Carnivores burrowed into a stream channel fill of tuffaceous white fine-grained sandstone (Upper Harrison beds, Arikaree Group). Only 150 to 300 m north of the dens, this same sandstone contains the dense bone deposits of early Miocene rhinoceros, chalicothere, and entelodont, which were found at the national monument early in this century (*5, 6*). Thus the dens must postdate deposition of the principal Agate bone bed. The time that elapsed between formation of the great bone bed and the dens was probably brief in the perspective of geologic time, since fragments of the same carnivore species found in the dens have also been found in the bone bed (*6, 7*). These carnivores have short temporal ranges of at most a few million years. We suspect that the dens were emplaced only weeks to a few years after the Agate bone bed was deposited.

Den dimensions approximate those of wolves, coyotes, and hyenas today (*8*). Den 1 (Fig. 1) contained two nearly complete skeletons of the bear dog *Daphoenodon superbus*, an adult female and juvenile male (*9*). The den has slightly inclined (burrow A) and nearly vertical (burrow B) entrance tunnels about 70 cm apart that lead down about 1 m to a pit that probably once contained the main den chamber (*10*). The entrance tunnels are preserved in vertical section (Fig. 2); slope erosion had removed part of these and the other burrows at the site, revealing burrow walls and internal sandy fill. As preserved, internal diameters of burrow A range from 15 to 46 cm, and from 30 to 66 cm for burrow B. Burrow B ascends into a 70-cm thick paleosol, but no surface opening has been identified.

Den 2, slightly more than a meter from den 1, contained the partial skeleton of a temnocyonine bear dog that was scattered through a laminated fine sand which fills the northeast end of the den. The bones, mostly disarticulated, occur through a vertical distance of 45 cm. Leading southwest from the skeleton is a passageway (burrow C) 2 m long that appears to have been continuous with the burrow housing the carnivore. The passageway, which is exposed in a nearly horizontal section by slope erosion, has a maximum diameter of 80 to 90 cm at the northeast end, narrowing to 40 cm, and ending in a terminal lobe about 50 cm wide, much like lobes seen in coyote burrows (*8*). The burrow floor is gently inclined to the southwest about 15 cm/m.

Den 3, less than a meter from den 2, is the least defined of the burrow systems; it includes a partial skeleton of an aged *Daphoenodon superbus* that is scattered at one level in 0.5 m^2 of burrow fill, and a passageway (burrow D) 30 to 55 cm in diameter exposed in horizontal section and apparently pointing toward the *Daphoenodon* skeleton. Whether the laminated fine-grained sandy fill surrounding the aged bear dog was in continuity with the fill of burrow D is not certain, since the intervening area has been recently eroded.

The sedimentary infill of all burrows is primarily a soft uncemented gray tuffaceous silty sand, frequently thinly laminated in layers about 1 mm thick that conform to the contours of the burrow. The gray burrow fill contrasts in tone with the white stream channel sandstone that forms the burrow walls. In burrows A and C, the thin laminae are grouped in sets; the direction of inclination of these sets indicates that the den filled progressively by sediment influx through the burrow mouth. In burrow B, 10- to 20-cm-thick layers of homogeneous fine sand are separated by a 25-cm-thick rubble of poorly sorted sand and subangular sand pebbles, suggesting rapid filling, with breakdown and incorporation of part of the burrow wall. Although we are not able to determine the exact amount of time required for infilling, the nature of syngenetic sedimentary structures shows that the process was episod-

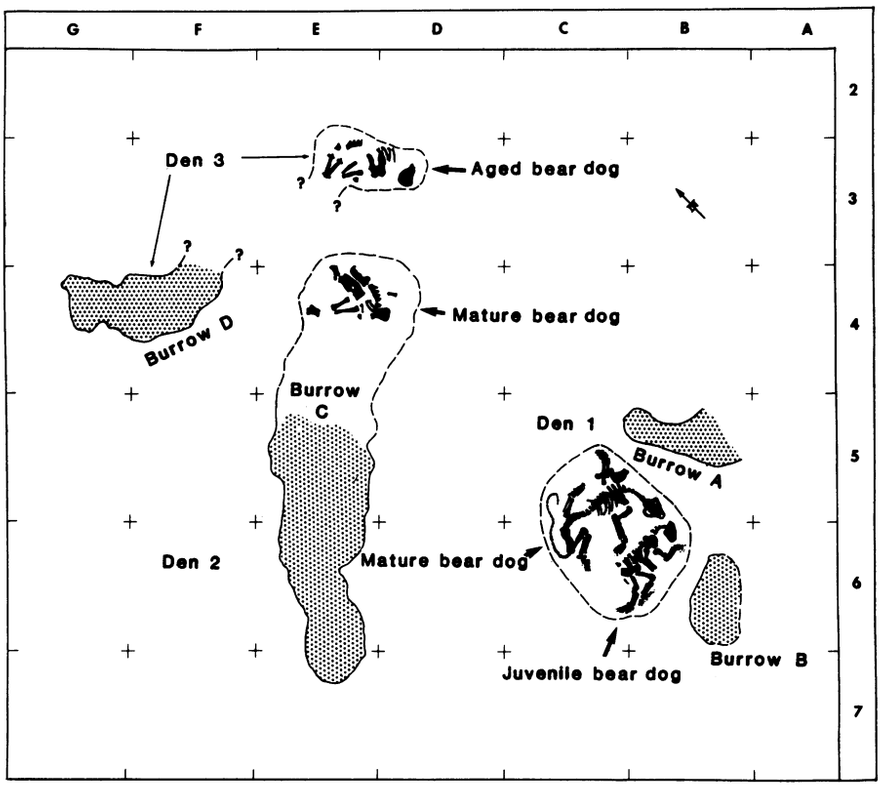

Fig. 1. Plan map of early Miocene carnivore dens, quarry 3, Agate Fossil Beds National Monument, Nebraska. Stipple pattern indicates Miocene burrow fill of fine-grained sand that also surrounds bear dog skeletons. Dashed lines indicate den boundaries as of July 1982 (dens 2 and 3) or where a boundary is uncertain (Peterson's den 1). Excavation grid is in square meters.

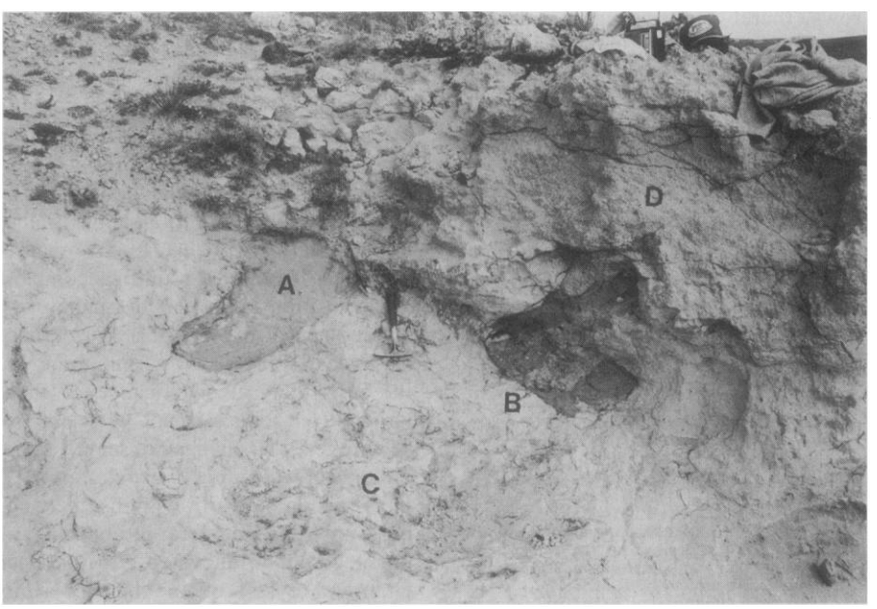

Fig. 2. Den 1 burrows (Fig. 1) of extinct bear dog *Daphoenodon* exposed in vertical Miocene sandstone cliff. (A) Burrow A; (B) burrow B; (C) presumed location of Peterson's den chamber; and (D) early Miocene paleosol. Hammer length, 28 cm.

continuous; yet the general homogeneity of the infill suggests that we are not dealing with much time, perhaps weeks to a few years.

Four species of carnivores, represented by about 11 individuals, have been found in the three dens: the bear dog *Daphoenodon superbus*, the unnamed temnocyonine bear dog, a small canid *Phlaocyon annectens*, and the mustelid *Paroligobunis simplicidens*. Two species of bear dogs were found by us in place in the burrows: the aged *Daphoenodon* in den 3 and the adult temnocyonine in den 2. Because of the proximity of these dens to an early Miocene braided stream (*11*), flooding of the burrows is the most likely cause of death of younger animals.

In summary, this unusual site appears to represent a den complex of early Miocene amphicyonid, canid, and mustelid carnivores that was developed during an unknown time interval in the channel floodplain of a wide, shallow, ephemeral stream which was subject to intense periodic floods, probably seasonal in nature. *Daphoenodon* was the principal occupant of the dens, but other bear dogs, canids, and mustelids used them for shelter, and *Daphoenodon* females probably used the dens to care for their young. Before the den complex was buried by stream sediments, floodwaters may have drowned juvenile and young adult bear dogs (including a mother-cub pair) in their dens. The carcasses decomposed in the burrows and were disturbed by scavengers and additional floods. As shifting episodic streamflow resulted in channel migration over the dens, ash-rich sediment gradually filled the burrows, thereby preserving a remarkable association of young, mature, and aged extinct Carnivora.

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2. E. Riggs [*Fieldiana Geol.* **8**, 59 (1942); *ibid.* **9**, 69 (1945)] reported finding partial skeletons of two small carnivores, each found separately in the burrows of fossorial rodents, early Miocene, Harrison Formation, Sioux County, Nebraska, in 1906. They were not in burrows of their own making. R. J. Emry (personal communication) has discovered bones of two individuals of the small early Oligocene canid *Hesperocyon*, as well as bones of many smaller mammals, probably prey of the canid, in an early Oligocene burrow in Wyoming. He believes that the burrow was occupied by, but probably not excavated by, *Hesperocyon*.
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10. The adult and juvenile *Daphoenodon* were found in 1905 by O. Peterson [(*7*); *Ann. Carnegie Mus.* **4**, 51 (1907)], who discovered and named quarry 3 and reported from it three or four other individuals of *Daphoenodon*, a small canid, and mustelid. Despite the number of carnivores and the absence of herbivores, Peterson did not identify the site as a den complex. To determine why only carnivores were found, we relocated Peterson's original site. By screening topsoil at the most probable locality at Beardog Hill in September 1981, we found a proximal *Daphoenodon* tibia that fit a bone fragment collected by Peterson in 1905. In Fig. 1, quarry 3 could have been limited to meter squares B–D 5–6, an area of 6 m^2, where the bone fragment was found.
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Intracellular *p*H Regulates Transitions Between Dormancy and Development of Brine Shrimp (*Artemia salina*) Embryos

Abstract. *The intracellular* pH (pH_i) *of encysted gastrula-stage embryos of the brine shrip,* Artemia, *as previously shown by in vivo phosphorus-31 nuclear magnetic resonance spectroscopy, increases by more than 1 unit during arousal from cryptobiotic dormancy and decreases by the same amount during reinduction of dormancy. These changes in* pH_i *are now shown to be a fundamental regulator of the transitions between dormancy and metabolism: acidification of activated embryo* pH_i *by more than 1 unit with carbon dioxide induced a state comparable to natural dormancy, while alkalinization of dormant embryo* pH_i *with the weak base ammonia terminated natural dormancy. This demonstration of* pH_i*-mediated regulation of cryptobiotic dormancy extends the known scope for* pH_i *as a regulator of development to include multicellular stages of the metazoan life cycle.*

Cellular dormancy, a spectrum of hypometabolic states involving inhibition of both catabolic and anabolic processes, is common to some stage of the life cycles of most organisms. Arousal from the comparatively modest dormancy of the sea urchin egg is regulated in part by a moderate (~ 0.4 unit) alkalinization of intracellular *p*H (*p*H_i) (*1, 2*). Even larger increases in *p*H_i (~ 1 unit) accompany the transitions between dormancy and metabolism of bacterial (*3*) and perhaps also yeast spore (*4, 5*) germination, but the physiological significance of these larger *p*H_i changes is not yet clear (*6*). The largest *p*H_i changes observed under biologically meaningful conditions (> 1 unit) accompany transitions between profound dormancy (cryptobiosis) and development in encysted gastrula-stage embryos (cysts) of the brine shrimp, *Artemia salina* (*7*). While the extreme degree of dormancy of *Artemia* cysts is unusual among metazoans, its true reversibility, enabling study of both initiation and termination of dormancy, offers opportunities to further test the role of *p*H_i in metabolic regulation.

The *Artemia* cyst displays two distinguishable but related forms of dormancy (*8*). Newly released from the ovisac, the cyst remains developmentally arrested for extended periods. Under natural conditions, such aerobic dormant cysts, which are so called because the embryos remain dormant even in the presence of oxygen, are activated to resume metabolism and development by desiccation and subsequent aerobic rehydration. When rehydrated in the absence of oxygen, however, they remain dormant, or reenter dormancy if oxygen is withdrawn after aerobic rehydration; we term these "anaerobic dormant" cysts because they normally remain dormant only under anoxic conditions. Aerobic dormancy, anaerobic dormancy, and aerobic development thus represent three alter-