



Chapter 4

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Chapter 4

Intercontinental Migration of Large Mammalian Carnivores: Earliest Occurrence of the Old World Beardog *Amphicyon* (Carnivora, Amphicyonidae) in North America

ROBERT M. HUNT, JR.¹

ABSTRACT

North American amphicyonid carnivorans are prominent members of the mid-Cenozoic terrestrial carnivore community during the late Eocene to late Miocene (Duchesnean to Clarendonian). Species range in size from <5 kg to >200 kg. Among the largest amphicyonids are Old and New World species of the genus *Amphicyon*: *A. giganteus* in Europe (18–~15? Ma) and Africa, *A. ingens* in North America (15.9–~14.2 Ma). *Amphicyon* first appears in the Oligocene of western Europe, surviving there until the late Miocene. Migration to Africa and North America takes place in the early Miocene. The genus occurs in the Arrisdrift fauna (Namibia) of southwest Africa, indicating migration south through the length of the African continent by the mid-Miocene. Its occurrence in Asia is problematical because of the tendency to place any moderately large Asian amphicyonid in the genus, and because of the fragmentary nature of many fossils.

Here I report the earliest North American occurrences of *Amphicyon* (18.8–~17.5 Ma), assigning these individuals to a new and previously undescribed species, *Amphicyon galushai*, from early Hemingfordian sediments of western Nebraska and north-central Colorado. In the New World, small early Hemingfordian *Amphicyon galushai* is probably ancestral to larger late Hemingfordian *A. frendens*, and to the terminal and largest species of the genus, early to mid-Barstovian *A. ingens*. Diagnostic basicranial and dental traits place these species in the Amphicyonidae, and demonstrate a close relationship of the North American lineage to the type species of the genus, *A. major*, from Sansan, France.

Amphicyon galushai is known from a complete adult skull, a partial juvenile skull, three mandibles, and the isolated teeth and postcranial elements of ~15 individuals, all from the early Miocene Runningwater Formation of western Nebraska. The species also is represented by a crushed rostrum from the Troublesome Formation, north-central Colorado.

Basicranial, dental, and postcranial anatomy distinguish *A. galushai* from its contemporary in the Runningwater Formation, the large digitigrade beardog *Daphoenodon*. The Runningwater Formation contains the last occurrence of *Daphoenodon* in North America and the first occurrence of *Amphicyon*; the overlap in stratigraphic ranges of these two carnivores provides a useful early Miocene biostratigraphic datum. The two amphicyonids occur together in the same quarries, associated with canid, mustelid, and rare procyonid carnivores, which are much smaller animals.

The North American species of *Amphicyon* (*A. galushai*, *A. frendens*, *A. ingens*) most likely adopted ecological roles similar to the large living felids (in particular, the lion *Panthera leo*). Their robust skeleton with powerful forelimbs, massive clawed feet, heavily muscled jaws with large canines, and a composite crushing/shearing dentition suggest a mobile predator that most likely stalked and ambushed prey from cover, overpowering its victims through sheer size and strength.

INTRODUCTION

Amphicyonid carnivores are a geographically widespread family of mid-Cenozoic arc-

toid carnivorans ranging in size from <5 kg to >200 kg. Although known from Eurasia, North America, and Africa, most fossils have come from Europe and the United States. The

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oldest North American amphicyonids from the late Eocene and early Oligocene were relatively small (<20 kg) carnivores, but by the early to mid-Miocene, several lineages exceeded 100 kg, and together with the large hemicyonine ursids, had become the dominant predators of the Holarctic continents (Ginsburg, 1961: 44–45, 178–179; Hunt and Tedford, 1993: 68; Hunt, 1998).

The earliest North American amphicyonids are Duchesnean (~37–40 Ma, late Eocene) fossils referable to *Daphoenus*, a small (2–4 kg) carnivore occurring from southern Canada to Texas (Hunt, 1996). *Daphoenus* ranges from the Duchesnean to the early Arikareean, and is the most common North American Paleogene amphicyonid. Following the appearance of *Daphoenus* in the early Duchesnean, *Daphoenictis* and *Brachyrhynchocyon* first occur in the late Duchesnean and early Chadronian, respectively, coexisting with *Daphoenus* throughout the Chadronian: all of these genera are small fox-sized carnivores (~4–10 kg). *Daphoenictis* and *Brachyrhynchocyon* become extinct at the end of the Chadronian, but *Daphoenus* (18–25 kg; Radinsky, 1980) persists into the Orellan (early Oligocene), and progressively increases in size during the Whitneyan. By the early Arikareean (late Oligocene), *Daphoenus* approaches the size (~20–30 kg) of a small wolf. These genera belong to the amphicyonid subfamily Daphoeninae, considered endemic to North America (Hunt, 1996).

A second subfamily of amphicyonids, the Temnocyoninae, appears in North America in the earliest Arikareean (~29–30 Ma), and continues into the late Arikareean (Hunt, 1998). Temnocyonines are the first New World amphicyonids to attain large size following the extinction of creodonts (*Hyaenodon*) in North America in the early Arikareean. The oldest species is a small carnivore (~10–15 kg), dentally and postcranially similar to early Oligocene *Daphoenus*. During the Arikareean interval, the various temnocyonine lineages rapidly increase in size, culminating in late Arikareean species in several lineages that attained 80–90 kg, and were slightly larger than living wolves (*Canis lupus*).

Daphoenines and temnocyonines are not known outside of North America (Hunt, 1998). Nothing like them has been found in Asia, al-

though European haplocyonine amphicyonids from this same time interval evidently shared a common ancestry with temnocyonines, and the daphoenines are closely related to the European stem amphicyonid *Cynodictis* (Petter, 1966). The North American amphicyonids of Oligocene age are obviously different from Old World Oligocene species, yet were related, and were evolving in some cases in parallel (temnocyonines-haplocyonines).

In the late Arikareean and early Hemingfordian, in essence throughout the early Miocene, a number of large amphicyonids migrate from Eurasia into North America. These taxa belong to the Old World amphicyonid subfamily Amphicyoninae (Hunt, 1998). The earliest to appear is the large beardog *Ysengrinia* Ginsburg, followed by *Cynelos* Jourdan, and then by *Amphicyon* itself. This influx of amphicyonines, accompanied by other Old World ungulates and small mammals, indicates a prolonged interval (from 23 to ~16.5 Ma) of faunal exchange between Asia and North America in the early Miocene, using the trans-Beringian route.

INSTITUTIONAL ABBREVIATIONS:

AMNH	American Museum of Natural History, New York, NY
F:AM	Frick Collection, American Museum of Natural History, NY
MNHN	Muséum National d'Histoire Naturelle, Paris, France
UNSM	University of Nebraska State Museum, Lincoln, NE
USGS	U.S. Geological Survey, Federal Center, Denver, CO

ARRIVAL OF AMPHICYON IN NORTH AMERICA

North American early to mid-Miocene *Amphicyon* fossils are allocated here to three species: *A. galushai*, new species, *A. frendens* Matthew, and *A. ingens* Matthew. Although other large amphicyonids from the Miocene of North America have been placed in *Amphicyon*, many of these carnivores belong to other amphicyonid genera. The *Amphicyon* lineage in the New World is restricted here to these three species, ranging in time from the early Hemingfordian to the mid-Barstovian (18.8–~14.2 Ma). These species share the typical upper and lower dentition

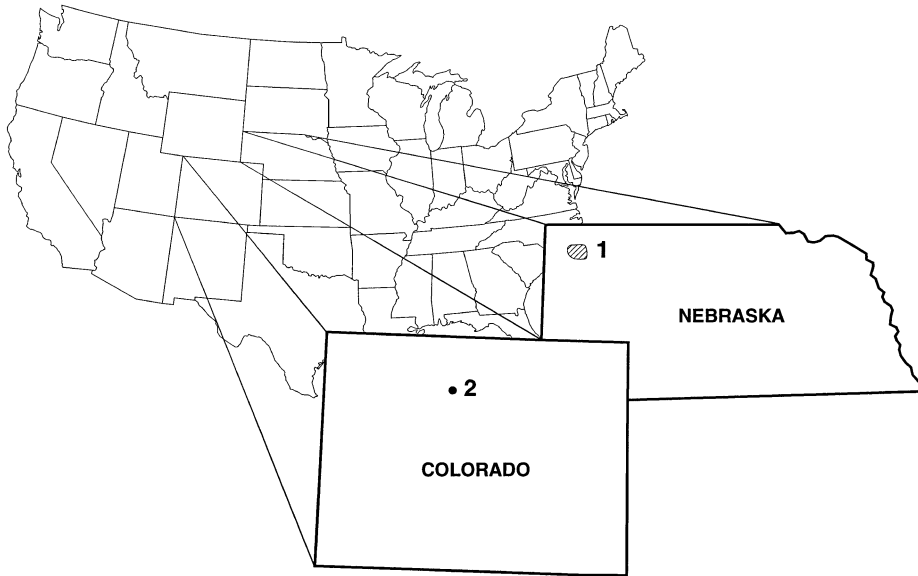


Fig. 4.1. Geographic distribution of *Amphicyon galushai* in North America: all fossils from early Miocene sediments of northwestern Nebraska (1, Runningwater Formation) and north-central Colorado (2, Troublesome Formation), and represent ~16 individuals.

and postcranial skeleton of the genus as evidenced in the holotype skull, mandibles, and postcranials of *Amphicyon major* from Sansan, France (Ginsburg, 1961).

The earliest occurrences in North America are rare fossils from the lower part of the Runningwater Formation in Sioux County, Nebraska, and from the lower part of the Troublesome Formation, Colorado (fig. 4.1). Each of these occurrences is represented by a single specimen: a partial maxilla with M2 from the Runningwater Formation (UNSM 26393, Foster Ranch), and a crushed rostrum with fractured teeth (P3–M2) from the Troublesome Formation (USGS D645 [65-G-6], U.S. Highway 40 roadcut; Izett, 1968: 42–45). The remaining specimens of *A. galushai*, including all known postcranial remains, come from stratigraphically higher levels of the Runningwater Formation in Box Butte and Dawes Counties, Nebraska.

These two first occurrences of *Amphicyon* in North America are dated by radiometric calibration of paleomagnetic data supplemented by independent biostratigraphic evidence. Paleomagnetic sampling of the lower part of the Runningwater Formation northeast of Agate, Sioux County, northwestern

Nebraska (Skavdahl Dam section of MacFadden and Hunt, 1998: 160), indicated that this part of the formation corresponds to Chron C5En, the upper part of C5Er, and the lower part of C5Dr of the Global Polarity Time Scale (GPTS; Berggren et al., 1995). This interval of the GPTS is dated to ~18.2–18.8 Ma. Calibration of the paleomagnetic zones of the lower Runningwater Formation was based on a zircon fission track date of 19.2 ± 0.5 Ma on the Eagle Crag Ash (Hunt et al., 1983) ~30 km north of the Skavdahl Dam section. The maxilla of *Amphicyon* from the Foster Ranch (UNSM 26393) was found ~20 km southeast of the paleomagnetically zoned Skavdahl Dam section in fine sandstone associated with typical cross-stratified sands and granitic gravel of the lower Runningwater Formation in Sioux County. The Foster Ranch site and Skavdahl Dam section are both in the lower part of the formation; however, the Foster site is within the axial Runningwater paleovalley whereas the Skavdahl Dam section is ~8 km north of the paleovalley axis.

Biostratigraphic evidence for the existence of *Amphicyon* in the ~18.2–18.8 Ma interval comes from the joint occurrence of *A. galu-*

shai and the temporally restricted oreodont *Merycochoerus* in the lower part of the Troublesome Formation in north-central Colorado. Skulls of several individuals of the large early Hemingfordian oreodont *Merycochoerus magnus* were collected from the same outcrop that produced the palate of *A. galushai* (USGS D645; Izett, 1968). This oreodont, restricted to the lower Runningwater Formation in Nebraska, is found exclusively in exposures of the formation northeast of Agate that include the Skavdahl Dam paleomagnetic section of MacFadden and Hunt (1998). *Merycochoerus magnus* is succeeded in the upper Runningwater Formation by its more advanced descendant *Merycochoerus proprius*. The Skavdahl Dam paleomagnetic section and contiguous outcrops of the lower Runningwater Formation in Sioux County are tentatively correlated with lower Runningwater exposures of the paleovalley axis that produced the Foster Ranch *Amphicyon* maxilla 20 km to the southeast.

Teeth and postcranial bones of *Amphicyon galushai* also have been found in UNSM Hemingford Quarries 7B, 12B, and 12D in the upper part of the Runningwater Formation. Thus, on current stratigraphic evidence, *A. galushai* ranges throughout the vertical extent of the Runningwater Formation. The mammal faunas from these upper Runningwater quarries include species of ungulates slightly more evolved than their progenitors in the lower part of the formation, and are among the most advanced Runningwater faunas known. Current age estimates for a volcanic ash in the upper Runningwater Formation in stratigraphic proximity to the terminal paleosol ("Platy Bench" of Galusha, 1975) capping the formation are ~17–17.5 Ma, suggesting that deposition of Runningwater sediments occurred over an interval of 1–1.5 million years.

The Box Butte Formation disconformably overlies the Runningwater beds in northwest Nebraska, resting directly on the terminal Runningwater paleosol at a number of localities. A maxilla of an amphicyonid (F:AM 95276) was reported from Foley Quarry in the Box Butte Formation in association with fossil equids and other mammals (Galusha, 1975: 57). Although Galusha suggested that the maxilla belonged to *Amphicyon*, his concept of the genus included fossils today at-

TABLE 4.1
Minimum Number of Individuals (MNI) of
Amphicyon galushai (North America) from the
Runningwater Formation, Northwestern Nebraska

Quarry or Locality	MNI
Dunlap Camel Quarry	3
Cottonwood Creek Quarry	1
Marsland Quarry	1
Hovorka's Quarry	1
Hemingford Quarry 7B	2
Hemingford Quarry 11B	1
Hemingford Quarry 12B	1
Hemingford Quarry 12D	3
Foster Ranch	1
Sect. 23, T.30N, R.49W	1
Total MNI	15

tributed to both *Amphicyon* and *Cynelos*. The maxilla contains deciduous teeth and also the adult P4 and M1. These teeth are most similar to those of *Cynelos idoneus* from the Sheep Creek Formation, which is a smaller carnivore relative to contemporaneous *Amphicyon*. Only one additional amphicyonid has been found in the Box Butte Formation in over half a century of collecting, a nearly complete skeleton (UNSM 48413) lacking the skull and mandibles, found by Dr. Loren Toohey in 1996 in the same drainage as Foley Quarry. This amphicyonid skeleton appears to be too small to belong to *Amphicyon*, and may represent the same species of *Cynelos* as the maxilla. Unfortunately the lack of associated teeth prevents confirmation of this assignment.

Particularly rich samples of the large North American species of *Amphicyon* have been found in the Sheep Creek Formation (*A. frendens*) and Olcott Formation (*A. ingens*) of central Sioux County, northwest Nebraska. These fossils occur in sufficient quantity to demonstrate dimorphism in skeletons and teeth of both species, presumably representing large males and much smaller females (Hunt, 1998).

HISTORY OF COLLECTION

The North American early Hemingfordian hypodigm of *Amphicyon* (fig. 4.1) includes the remains of ~15 individuals from 10 localities in northwest Nebraska (table 4.1) and the single individual from north-central Col-

orado. The UNSM sample of *A. galushai* was collected from 1934 to 1941 (and a skull in 1959) by field parties of the Division of Vertebrate Paleontology, working in fossil-rich early Miocene outcrops designated the "upper Marsland Formation" by UNSM paleontologists. In 1965, Harold Cook, in a posthumous publication, recognized that these fluvial sediments filled an early Miocene paleovalley that extended across northwest Nebraska from west to east for more than 150 km (Cook, 1965; Skinner et al., 1977). These sediments represented a discrete lithostratigraphic unit that Cook named the Runningwater Formation; the rock unit included granitic gravels derived from the Rocky Mountains to the west, and contained abundant early Hemingfordian mammals.

The efforts of UNSM paleontologists resulted in the discovery of large numbers of ungulates (primarily camels, the dromomerycid *Aletomeryx*, several species of equids, and the oreodonts *Merychys* and *Merycochoerus*) from the Hemingford Quarries of the University of Nebraska. Canids were the most frequently encountered carnivores; mustelids, ursids, and amphicyonids were much less common. Over time a small sample of *Amphicyon* was brought together; many of these fossils initially went unrecognized, simply labeled as "large carnivore."

Similarly, the field collectors of the Frick Laboratory, American Museum of Natural History, New York, also working in the Runningwater Formation of northwest Nebraska from 1937 to 1965, discovered specimens of *A. galushai* in quarries north of the Niobrara River. This sample included the most complete and best preserved cranial material of the species, the holotype mandible and paratype cranium of *A. galushai*, which was collected by Ted Galusha from Dunlap Camel Quarry in 1939.

SYSTEMATICS

ORDER CARNIVORA BOWDICH, 1821

DIVISION ARCTOIDEA FLOWER, 1869

FAMILY AMPHICYONIDAE TROUESSART, 1885

Amphicyon Lartet, 1836

TYPE SPECIES: *Amphicyon major* (Blainville, 1841).

INCLUDED SPECIES: *Amphicyon major* (Blainville), *Amphicyon giganteus* (Schinz), *Amphicyon laugnacensis* Ginsburg, *Amphicyon ingens* Matthew, *Amphicyon frendens* Matthew, *Amphicyon galushai*, new species.

DISTRIBUTION: *Amphicyon galushai-frendens-ingens* group: early Hemingfordian to early Barstovian of northwestern Nebraska; early Hemingfordian of north-central Colorado; early to mid-Barstovian of northeastern Colorado; early Barstovian, Barstow Syncline, California, and Española Basin, New Mexico.

Reported temporal range of Old World *Amphicyon* (*s.s.*): Europe, MN zone 1 to MN zone 11 (Ginsburg, 1999), 23.8–~9 Ma (Steininger et al., 1996), early Miocene to early late Miocene; early mid-Miocene of southern Africa (Hendey, 1978: 12, fig. 4; Morales et al., 1998); early Miocene of northern Vietnam (Ginsburg et al., 1992).

DIAGNOSIS (NEW WORLD SPECIES): Mid-sized to very large (~40–>200 kg) North American amphicyonid carnivorans with skull lengths of 27–31 cm (early Hemingfordian), 37–39 cm (late Hemingfordian), and about 42–52 cm (early to mid-Barstovian). Lower carnassial (m1) lengths: *Amphicyon galushai* (early Hemingfordian, Nebraska), 30.2–32.2 mm ($N = 3$); *A. frendens* (late Hemingfordian, Nebraska), ~33.5–39.8 mm ($N = 11$); *A. ingens* (early to mid-Barstovian, Nebraska, Colorado, New Mexico, and California), 36.0–44.9 mm ($N = 20$). Rudimentary flask-shaped auditory bulla formed by a slightly inflated ossified ectotympanic that fully encloses the middle ear; participation of entotympanics in the auditory bulla uncertain. Hypotympanic sinus of the middle ear invades the floor of the bony external auditory meatus even in the oldest North American (early Hemingfordian) crania. Dental formula 3-1-4-3/3-1-4-3: reduction of premolar (p1–3, P1–3) size and height (relative to *Daphoenodon*) but without loss of premolars. There is no premolar crowding as seen in *Pliocyon*. There is marked hypertrophy of posterior molars (m2–3, M2–3), producing the largest such teeth evolved within the family. M1–3 length commonly greater than twice the length of P4 as a result of molar expansion, in contrast to *Daphoenodon*, *Ysengrinia*, and temnocyonines, which

all lack this degree of molar expansion (in *A. galushai*, M1–3 length is approximately twice the length of P4). Enlarged M2 somewhat wider transversely than M1; M2 subtriangular in early species, rapidly becoming subrectangular in later larger forms, and projecting lingually farther than the inner edge of M1. M2 protocone connected to paraconule, but metaconule isolated as in European *Amphicyon*. P4 short, wide, robust with small parastylar cusp and weak to moderate development of the protocone. The m1 has a swollen inflated appearance, always retains a metaconid (lost or vestigial in *Ysengrinia*), and has a wide talonid with prominent, somewhat laterally placed, ridgelike hypoconid. The m2 is rectangular, with trigonid elevated above talonid, protoconid much larger than metaconid, and a small vestigial paraconid (the arcuate crest at the anterior end of the m2 trigonid in *Cynelos* is absent). A laterally placed, low hypoconid dominates the m2 talonid. M3/m3 are flat, massive teeth with subdued occlusal topography.

Sexual dimorphism is present, particularly evident in the teeth and limb bones of the latest and largest species. Postcranial skeletal traits can be combined with dental characters to identify the genus: the limb skeleton is massive and robust, and the radius, ulna, and tibia are short relative to the upper limb bones, as in large living ursids. Metapodials are short, not elongate, and the digits spread more widely than in living canids. Specializations for cursoriality such as lengthened lower limb segments and elongate, appressed metapodials (as in living canids) are absent. The feet, however, are paraxonic (principal weight-bearing axis passing between metapodials 3 and 4), unlike those of living ursids, and are more similar to those of large living felids such as *Panthera*.

Amphicyon galushai, new species

TYPE SPECIMEN: F:AM 25406, complete left mandible with p2–m2, with single alveoli for the canine, p1, and m3; the holotype and paratype were both collected in 1939.

PARATYPE: F:AM 25400, nearly complete cranium (lacking the nasals and parts of the zygomatic arches) with left and right P4–M1, and alveoli for all other teeth (d.f. 3-1-4-3).

TYPE LOCALITY AND HORIZON: Dunlap Camel Quarry, Runningwater Formation, Dawes Co., NE. The holotype and paratype were collected in the same quarry, and are similar in size but represent different individuals, based on toothwear.

ETYMOLOGY: The species is named for the late Ted Galusha, Frick Curator Emeritus, field geologist and paleontologist for the Frick Laboratory (AMNH), whose dedicated efforts resulted in important collections of Miocene mammals from western Nebraska.

REFERRED SPECIMENS: (A) From the Runningwater Formation, Hemingford Group, northwest Nebraska (year of collection at end of each entry):

Dental: (1) F:AM 25407, right mandible with p2–m2, Dunlap Camel Quarry, Dawes Co., NE, 1937; (2) F:AM 95013, left m2 (worn), Dunlap Camel Quarry, Dawes Co., NE, 1939; (3) F:AM 25401, left P4, Dunlap Camel Quarry, Dawes Co., NE, ?1937; (4) F:AM 25436, right mandible with p2–m2, Cottonwood Creek Quarry, Dawes Co., NE, 1965; (5) F:AM 25437, left M2, Cottonwood Creek Quarry, Dawes Co., NE, 1965; (6) UNSM 25687, right maxilla with P3–M1, Marsland Quarry (UNSM Loc. Bx-22), Box Butte Co., NE, 1934; (7) UNSM 25579, left M1, Hemingford Quarry 7B (UNSM Loc. Bx-7), Box Butte Co., NE, 1938; (8) UNSM 25575, left P4, Hemingford Quarry 7B (UNSM Loc. Bx-7), Box Butte Co., NE, 1939; (9) UNSM 25762, right M3, Hemingford Quarry 7B (UNSM Loc. Bx-7), Box Butte Co., NE, 1938; (10) UNSM 25929, left P4, Hemingford Quarry 12B (UNSM Loc. Bx-28), Box Butte Co., NE, 1938; (11) UNSM 26392, left p4, Hemingford Quarry 12D (UNSM Loc. Bx-12), Box Butte Co., NE, 1938; (12) UNSM 25578, left M2 (large), Hemingford Quarry 12D (UNSM Loc. Bx-12), Box Butte Co., NE, 1937; (13) UNSM 26393 (a cast), right partial maxilla with M2, broken alveoli for M1, alveoli for M3, Foster Ranch, sect. 5, T.27N., R.53W., Sioux Co., NE (from a fine sandstone above Fe-stained crossbedded sandstone and granitic gravel), collected 1985; (14) UNSM 1570–59, cranium, slightly crushed, lacking posterior braincase, with right P2–M2, left broken canine, partial M1, M2, Hovorka's Quarry (UNSM Loc. Bx-21), Box Butte Co., NE, 1959.

Postcranial: From Hemingford Quarry 12D, UNSM Loc. Bx-12: (1) UNSM 25561, partial left scapula, 1937; (2) UNSM 26383, left humerus, 1941; (3) UNSM 25559, left ulna, 1937; (4) UNSM 25557, right radius, 1938; (5) UNSM 26384, left calcaneum, 1941; (6) UNSM 26385, right calcaneum, 1941; (7) UNSM 26386, left calcaneum, 1941; (8) UNSM 25581, right calcaneum, 1939; (9) UNSM 26387, right astragalus, 1937; (10) UNSM 26388, right astragalus, 1941; (11) UNSM 26389, right astragalus, 1937; (12) UNSM 26390, right cuboid, 1937; (13) UNSM 25582, right metatarsal 1, 1939; (14) UNSM 26391, left metatarsal 2, 1938; (15) UNSM 25565, left metatarsal 4, 1938; (16) UNSM 25568, right metacarpal 2, 1938; (17) UNSM 25573, left metacarpal 3, 1939; (18) UNSM 25560, right femur, 1941; (19) UNSM 26394, right cuboid, 1939.

From Hemingford Quarry 7B, UNSM Loc. Bx-7: (20) UNSM 26376, proximal right ulna, 1939; (21) UNSM 26377, right metatarsal 2, 1939; (22) UNSM 26378, left metatarsal 3, 1937; (23) UNSM 26379, left metatarsal 3, 1937; (24) UNSM 25569, left metacarpal 2, 1939; (25) UNSM 26380, right metacarpal 5, 1939.

From Hemingford Quarry 12B (UNSM Loc. Bx-28): (26) UNSM 26375, left distal humerus, large, 1938.

From Hemingford Quarry 11B (UNSM Loc. Bx-26): (27) UNSM 26381, right distal humerus, heavily water-worn, 1940.

From SE 1/4, NE 1/4, sect. 23, T.30N., R.49W., Dawes Co., NE: (28) UNSM 26382, left calcaneum, 1940.

From Cottonwood Creek Quarry, Dawes Co., NE: (29) F:AM 25458, astragalus; (30) F:AM 25447, metacarpal 1; (31) F:AM 25448, metacarpal 2; (32) F:AM 25452, metacarpal 4; (33) F:AM 25438, metatarsal 3; (34) F:AM 25446, metatarsal 4, all collected in 1965.

(B): From the Troublesome Formation, NW4, SW4, sect. 9, T.1N, R.79W, base of U.S. Highway 40 roadcut, Grand County, north-central Colorado, USGS D645 (65-G-6), crushed rostrum including left maxilla with P3–M2, broken canine and P1, alveoli for M3, collected by G. A. Izett, July 1962.

DIAGNOSIS: Smallest North American species of *Amphicyon*, basilar length of skull 27–

31 cm; basicranium of amphicyonid type (Hunt, 1998), auditory bulla formed primarily if not entirely by the ectotympanic, with an accessory hypotympanic sinus invading the osseous floor of the external auditory meatus. Dental formula 3/3–1/1–4/4–3/3; I1–2 small, I3 enlarged, based on size of incisor alveoli (incisors and canines not preserved in jaws); lower incisors probably not enlarged but size difficult to determine from poorly preserved i1–3 alveoli; P1–3/p1–3 reduced, short, without posterior accessory cusps (p4 with posterior accessory cusp, occasionally present on p3), with strong cingula, and separated by short diastemata. P4 more or less in the form of an isosceles triangle in occlusal view (somewhat *longer* than M1, table 4.2), with reduced protocone, in contrast to *Daphoenodon*, in which the P4 protocone is prominent. A relatively low m1 trigonid (in contrast to tall m1 trigonid of North American late Arikarean *Ysengrinia*), paraconid shortened and positioned almost directly anterior to protoconid, entoconid present but weak (no entoconid in *Daphoenodon* and *Ysengrinia*), posterior part of m1 trigonid and anterior talonid slightly swollen. M1 triangular in occlusal view, anterior border convex, posterior border convex or straight, but not concave; lingual cingulum developed almost entirely posterior to protocone, and separated from it by a short curvilinear groove; M1 paraconule indistinct, but small, distinct metaconule present, as in European species; protocone close to the anterior border. M2/m2 enlarged relative to M1/m1. The m1/m2 length ratio is 1.5–1.6. M2 subrectangular and slightly smaller than M1 (the marked enlargement of M2 in *A. frendens* and *A. ingens* is not evident); M2 projects lingual somewhat farther than M1, anterior border of M2 slightly convex, posterior border somewhat concave; M2 lingual cingulum wide, thick, rounded, separated from protocone by wide groove; protocone only slightly displaced toward anterior border of tooth. More or less rectangular m2; talonid shorter than trigonid. The m3 single-rooted or with fused double-roots.

Postcranial skeleton reflecting ambulatory life mode (a walking gait interspersed with short bursts of speed): upper limb bones robust, massive; lower limb bones robust, not elongated; retained primitive ability to supi-

TABLE 4.2
Dental Measurements (in millimeters) of *Amphicyon galushai* (North America)

Mus. no.	P1	P2	P3	P4	M1	M2	M3	P1-M2
Runningwater Formation, Nebraska								
UNSM 1570-59	—	10.5×6.2	13.1 × 7.8	24.8 × —	23.5 × 27.3	15.7 × 24.9	—	96.6
F:AM 25400	—	(11.8) ^a	(15.4)	25.6 × 15.7	23.4 × 29.3	17.1 × 26.7	×(12.2)	108.3
UNSM 25687	—	—	14.1 × 8.8	28.1 × 17.9	24.8 × 32.9	—	—	—
UNSM 25575	—	—	—	27.3 × 16.3	—	—	—	—
UNSM 25929	—	—	—	31.4 × (18.6)	—	—	—	—
F:AM 25401	—	—	—	26.1 × 14.9	—	—	—	—
UNSM 25579	—	—	—	—	20.4 × 28.0	—	—	—
UNSM 25578	—	—	—	—	—	18.8 × 28.9	—	—
F:AM H394-2791K	—	—	—	—	—	17.6 × 26.5	—	—
Meade Collection (Agate, Nebraska)	—	—	—	—	—	19.6 × 27.4	—	—
Troublesome Formation, Colorado								
USGS D645	—	—	(16.3)	(30 × 16.1)	(21.7)	17.6 × 25.8	×(12.5)	114.9
Mus no.	p1	p2	p3	p4	m1	m2	m3	p2-m2
Runningwater Formation, Nebraska								
F:AM 25406	(9.1 × 6)	10.6 × 6.7	12.4 × 6.7	17.5 × 9.6	30.2 × 16.1	20.6 × 15.4	(10.8 × 7.3)	103.0
F:AM 25407	(12.1 × 7.3)	10.9 × 6.8	13.8 × 7.7	18.5 × 10.0	31.1 × 16.5	19.7 × 15.9	—	105.6
F:AM H409-3044	(9.8 × 7.7)	11.3 × 6.9	14.3 × 7.8	19.7 × 10.0	32.2 × 15.7	18.5 × 13.8 ^b	(12.6 × 7.3)	105.1
UNSM 25-11-11-38	—	—	—	18.2 × 10.4	—	—	—	—
F:AM 95013	—	—	—	—	—	19.4 × 13.3	—	—

^a () Indicates estimated measurement.

^b Worn tooth.

nate/pronate the manus on the lower forelimb; metapodials relatively short when compared to elongated metapodials of contemporary *Daphoenodon*; astragalus short, with distal condyle not shifted underneath the proximal trochlea (in contemporary *Daphoenodon* the astragalus is elongate, with distal condyle shifted underneath the proximal trochlea); calcaneum ursid-like, distally broad, robust, generally wider and not as deeply grooved on the posterior surface of the sustentaculum for the flexor tendons of the hindfoot, in contrast to *Daphoenodon* in the same quarries in which the groove on the sustentaculum is pronounced and the calcaneum is taller and narrower.

DESCRIPTION

CRANIUM AND MANDIBLES: Two skulls and three mandibles from separate localities (Dunlap Camel Quarry, Cottonwood Creek

Quarry, Hovorka's Quarry) within the Runningwater Formation indicate a mid-sized amphicyonid about the size of *Ursus arctos*. The holotype mandible (fig. 4.2) is similar to a mandible initially referred to *Amphicyon major* by Roman and Viret (1934, pl. 1, fig. 1) from the late Burdigalian of La Romieu, southern France. The La Romieu *Amphicyon* was later referred to *A. giganteus* by Ginsburg and Telles-Antunes (1968).

The paratype skull (F:AM 25400, basilar length, 31 cm) is an adult from Dunlap Camel Quarry (fig. 4.2). The size of the canines suggests it is a female. It is uncrushed, allowing its proportions to be accurately compared with those of other contemporary amphicyonids. The form and proportions of the skull are similar to the only known European skull of the genus (*A. major*, Sansan, basilar length, ~33.6 cm; Bergounioux and Cruzel, 1973). Although the Sansan skull is crushed,

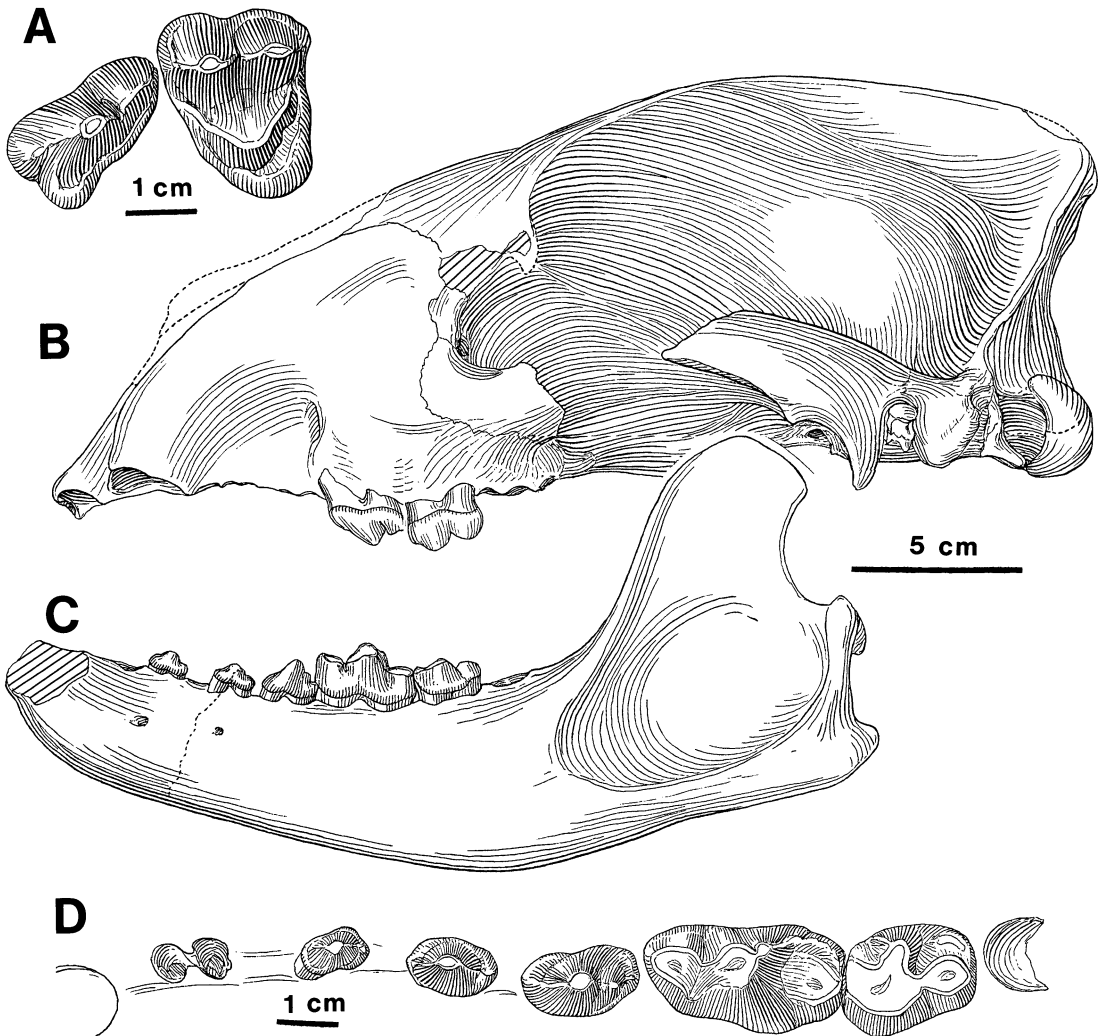


Fig. 4.2. *Amphicyon galushai*, new species: (A) P4–M1, paratype (F:AM 25400), occlusal view; (B) paratype cranium with P4–M1 (F:AM 25400), lateral view; (C) holotype mandible with p2–m2 (F:AM 25406), lateral view; (D) p2–m2 (F:AM 25407), occlusal view, all from Dunlap Camel Quarry, Runningwater Formation, Hemingford Group, NE.

its snout was probably somewhat longer than the North American species. However, because the North American skull is probably a female, the snout can be expected to be more gracile than in the larger males. Without additional European crania, we cannot be certain of the significance of what may be minor proportional differences. The only teeth in place in the paratype are P4–M1, but the alveoli for the remaining upper teeth indicate their size. P4–M1 are like those of *A. major* from Sansan; however, M2 in *A. gal-*

ushai is smaller, and is not as enlarged as in *A. major* (compare M2 in tables 4.2, 4.3).

The second skull (UNSM 1570–59, fig. 4.3), a juvenile from Hovorka's Quarry, is not as well preserved as the paratype. It has been dorsoventrally crushed, and the greater part of the basicranium is missing. The snout is short with a broad palate. On the right, P2–M2 are present, including alveoli for M3, P1, C, and I1–3. Most of the teeth on the left side are lost or damaged. This skull is important in retaining P4–M2 in place, dem-

TABLE 4.3
Dental Measurements (in millimeters) of *Amphicyon major* (Sansan, France)^a

Mus. no.	P1	P2	P3	P4	M1	M2	M3
MNHN Sa1	9.8	—	—	31.9	27.5 × 34.3	22.0 × 32.5	—
MNHN Sa2	—	—	—	30.7	25.5 × 31.0	21.9 × 31.7	—
MNHN Sa3	—	10.5	11.7	25.9	—	—	—
	—	10.3	11.6	26.4	— × 27.2	19.0 × 27.2	—
MNHN Sa4	9.0	11.7	13.1	30.0	25.2 × 30.0	—	—
MNHN Sa5	—	—	—	30.0	—	20.7 × 31.0	—
MNHN Sa25	—	—	13.7	—	—	—	—
MNHN Sa28	—	—	—	26.3	—	—	—
MNHN Sa30	—	—	—	—	—	22.5 × 33.4	—
MNHN Sa31	—	—	—	—	—	—	12.8 × 14.9
MNHN Sa32	—	—	—	—	—	—	14.0 × 16.7
Muséum de Toulouse		10.7 × 6.5	12.9 × 7.1	25.9 × 15	23.8 × 26.9	19.0 × 27.2	12.1 × 16.6
Mus no.	p2	p3	p4	m1	m2	m3	
Muséum de Toulouse	9.8 × 5.3	12.3 × 6.5	16.2 × 9.2	30.0 × 14.5	21.1 × 15.5	17.5 × 14.3	
MNHN Sa34	9.9	12.3	—	35.0	24.5	—	
MNHN Sa35	10.9	11.4	19.5	36.7	—	—	
MNHN Sa36	—	—	18.7	34.6	25.0	20.0	
MNHN Sa45	—	—	—	31.7	—	—	

^a Data from Ginsburg, 1961; Bergounioux and Crouzel, 1973.

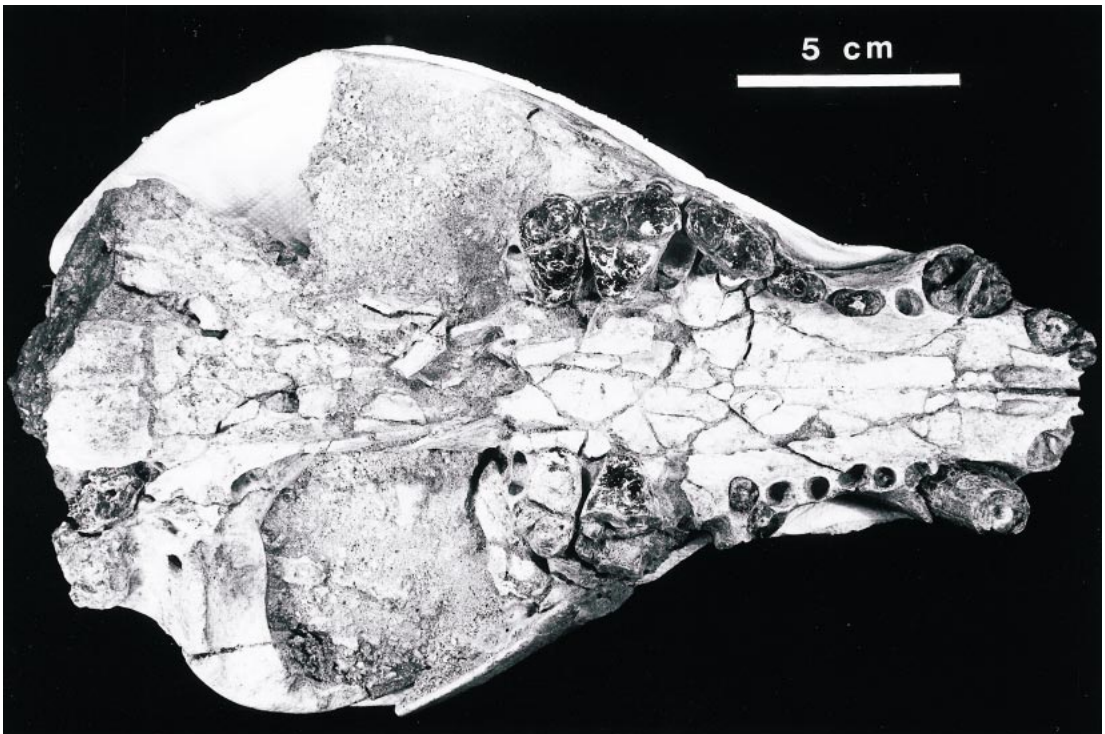


Fig. 4.3. Cranium (in palatal view) of juvenile *Amphicyon galushai* (UNSM 1570–59), Hovorka's Quarry (UNSM Loc. Bx-21), Runningwater Formation, NE.

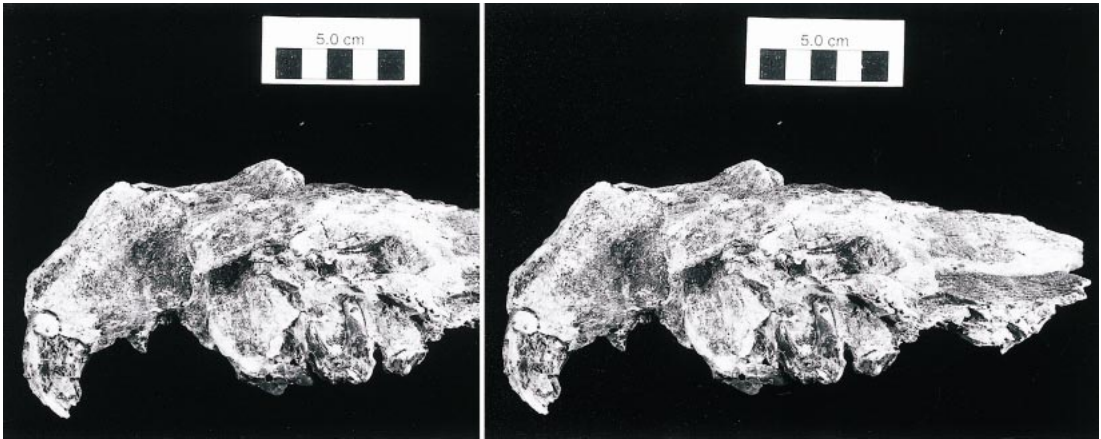


Fig. 4.4. Crushed rostrum (in lateral view) of *Amphicyon galushai* (USGS D645), Troublesome Formation, U.S. Highway 40 roadcut, Grand County, CO.

onstrating the small size of M2 relative to M1, which is diagnostic of *A. galushai*, in contrast to the enlarged M2 of *A. major*, *A. frendens*, and *A. ingens*. Both skulls of *A. galushai* show alveoli for M3 in contrast to Runningwater Formation *Daphoenodon* skulls, which have lost this tooth.

Despite the distortion produced by post-mortem crushing, the rostrum of the Trou-

blesome Formation *Amphicyon* (fig. 4.4) was also short, with a wide palate, and a slight constriction of the snout posterior to the canines, features also seen in F:AM 25400 and UNSM 1570–59.

Basilar lengths for *A. galushai* (~310 mm) are similar to those of the larger living ursids (table 4.4)—*Ursus arctos* (basilar lengths of 284–310 mm, $N = 4$), *Ursus americanus*

TABLE 4.4
Basilar Skull Length and Length of Basicranial Axis in Living Ursids and in *Amphicyon galushai* from the Runningwater Formation, Northwestern Nebraska (in millimeters)

Species	Museum no.	Basilar length	Basicranial axis length
<i>Ursus americanus</i>	ZM ^a -1869	260	76.6
<i>Ursus americanus</i>	ZM-174	242	70.9
<i>Ursus americanus</i>	ZM-283	272	82.1
<i>Ursus americanus</i>	ZM-1870	232	69.3
<i>Ursus americanus</i>	ZM-239	276	76.6
<i>Ursus americanus</i>	ZM-3253	245	71.5
<i>Ursus americanus</i>	ZM-16986	247	73.1
<i>Ursus arctos</i>	ZM-15540	310	94.8
<i>Ursus arctos</i>	ZM-5094	284	(81.3) ^b
<i>Ursus arctos</i>	ZM-190	300	76.9
<i>Ursus arctos</i>	ZM-191	307	81.1
<i>Ursus arctos</i> (Kodiak Is.)	ZM-17888	386	105.3
<i>Thalartos maritimus</i>	ZM-16938	360	102.6
<i>Helartos malayanus</i>	ZM-13875	181	60.4
<i>Amphicyon galushai</i>	F:AM 25400	310	84.3

^aZM = Mammalogy Division, UNSM.

^b() Indicates estimated measurement.

(232–276, $N = 7$), *Ursus arctos* (Kodiak Island, 386 mm, $N = 1$), and *Thalartos maritimus* (360 mm, $N = 1$).

Because the paratype skull is uncrushed, details of basicranial anatomy and general anatomical proportions of the cranium can be established with greater confidence than in the case of the crushed skull of *Amphicyon major* from Sansan described by Bergounioux and Crouzel (1973). The postorbital length is nearly two times the preorbital, indicating cranial proportions as in most amphicyonids and living and extinct ursids (similar proportions are plesiomorphic for early arctoids). The form of the cranium approaches that of some large living ursids such as *Ursus arctos*, but is most similar to the fossil skulls of its probable descendants, *A. frendens* and *A. ingens*. Skulls of *A. frendens* and *A. ingens* in the AMNH collections show variation in length of snout and in the development of the sagittal crest that are attributable to sexual dimorphism. Large males have slightly longer, more robust snouts, larger canine teeth, and, in some cases, enormous sagittal crests for attachment of massive temporal musculature.

An attempt to obtain an endocast from the cranial cavity of the paratype was made by Radinsky (1980) but was not completed; he did describe a damaged endocast of *A. frendens*, suggesting that the lineage retains a number of primitive features—unexpanded sigmoid gyri, narrow lateral gyri, absence of an entolateral sulcus, and much of the cerebellum not yet covered by the occipital lobe of the cerebrum. Radinsky was careful to point out that the greater amount of infolding of the amphicyonid neocortex observed in the family over time might not be due to actual increase in relative amount of neocortex. Because the neocortex is a sheet, it can increase only by areal expansion; as the volume of the brain below the neocortex increases, the neocortex must compensate by complex infolding. Although he could demonstrate a definite increase in relative brain size over time in the amphicyonids that he studied, it was not possible to show a gain in neocortical volume, despite the suspicion that it occurred.

At present, the principal source of information on skull form in amphicyonids that immediately precede the appearance of *Am-*

phicyon in North America are crania of late Arikareean amphicyonids from the Upper Harrison beds of northwest Nebraska and southeastern Wyoming. Nearly complete skulls are known for *Daphoenodon*, *Ysengrinia*, and an unnamed genus. All of these genera differ in their dentitions, and more conspicuously in skull form, from early Hemingfordian *Amphicyon*: (a) the skulls of *Daphoenodon* are short-faced, low crania, much smaller than the paratype skull of *Amphicyon*; (b) the skull of *Ysengrinia*, a probable male, has a robust snout but narrows behind the orbits, and has a low forehead and very small braincase; (c) the undescribed genus is the only one of these amphicyonids to attain the skull size of *Amphicyon*; however, its braincase is smaller than *Amphicyon*, its skull more elongate, and its dentition more primitive, lacking expanded posterior molars. No late Arikareean amphicyonids enlarge M2–3 and m2–3, in contrast to *Amphicyon*, which does.

Somewhat similar in skull form to *Amphicyon* is its contemporary in the Runningwater quarries, the terminal species of *Daphoenodon*. Runningwater *Daphoenodon* retains the short snout and broad skull characteristic of the genus, but the skull in this, the largest species of the genus, equals the dimensions of *Amphicyon*. This huge *Daphoenodon* can be most readily distinguished from *Amphicyon* by its teeth, but certain cranial features also differ between the two genera: in Runningwater *Amphicyon*, the frontal region is not as expanded or inflated; the braincase seems to be slightly greater in volume; the occiput is broader; and the mastoid process is more developed. Male and female skulls of the Runningwater *Daphoenodon* are known; hence these distinctions are not influenced by sexual dimorphism.

Thus, at its first appearance on this continent, *Amphicyon* is distinct in its skull form from other genera of early Miocene amphicyonids. When the form of the cranium is combined with the dentition and basicranial anatomy, the genus can be readily identified.

BASICRANIUM: Only the paratype skull of *Amphicyon galushai* (F:AM 25400) preserves the basicranium, including the auditory region and part of the right bulla (fig. 4.5). This is the only remnant of the bulla known in this species. The juvenile skull

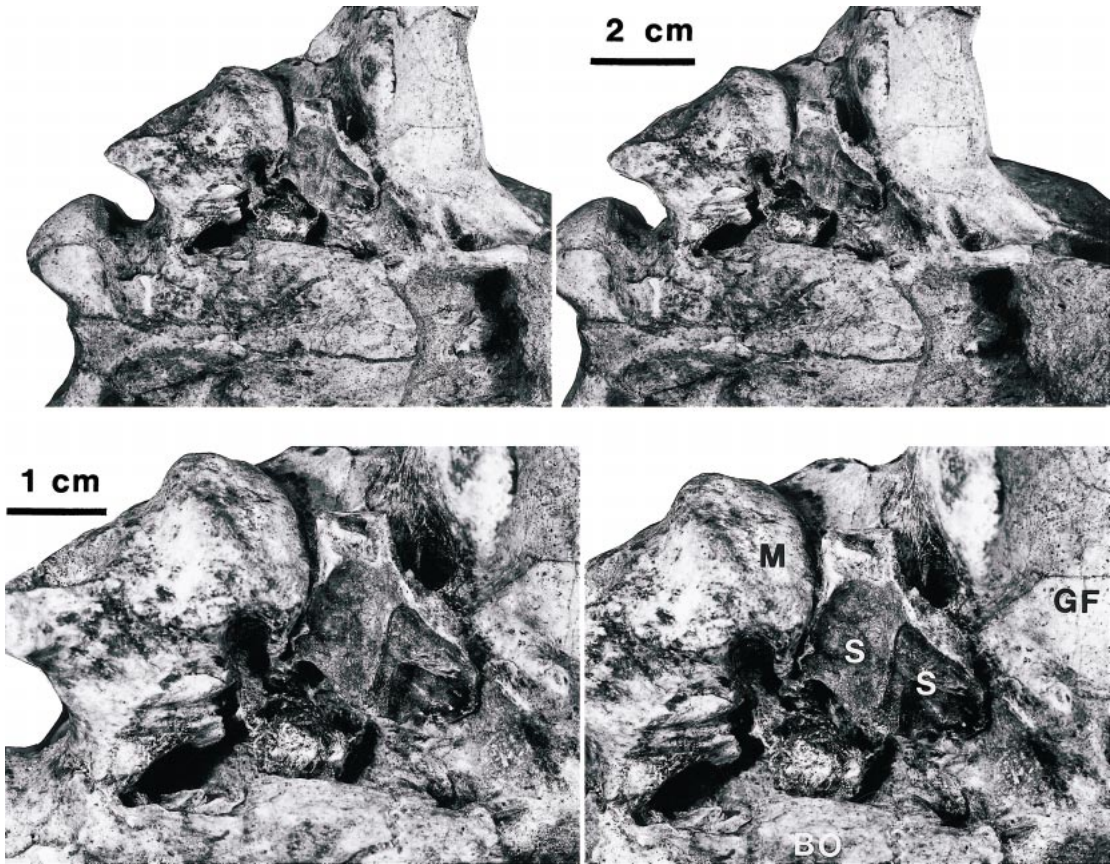


Fig. 4.5. **Above:** Stereophotographs of the basicranium of *Amphicyon galushai* (F:AM 25400, paratype), Dunlap Camel Quarry, Runningwater Formation, NE (ventral view, anterior to right). **Below:** Stereophotographs of the right auditory region (ventral view) of *Amphicyon galushai* (F:AM 25400, paratype). The ectotympanic bulla shows the specialized hypotympanic sinus (S) that invades the bony floor of the external auditory meatus in North American species of *Amphicyon*. BO, basioccipital; GF, glenoid fossa; M, mastoid process. Note the petrosal deeply recessed within the auditory region.

(UNSM 1570–59) is slightly crushed dorsoventrally and has lost the posterior cranium, including the entire occiput, but retains an intact left petrosal. The petrosal description is taken from UNSM 1570–59.

Basilar length of the paratype cranium is 31 cm, and the length of the basicranium from the base of the foramen magnum to a transverse line joining the oval foramina is ~7.5 cm; thus, the basicranial length is ~25% of the length of the skull. The basicranial width measured between the mastoid processes is 11.2 cm. Only a few pieces of the anterior cranium of *A. major* from Sansan were available to Ginsburg (1961), but in 1965, the discovery of a nearly complete skeleton of a sin-

gle individual of *A. major* at Sansan (Bergounioux and Crouzel, 1966, 1973) yielded an intact skull. Unfortunately it was crushed, preventing a detailed description of the basicranium (its basilar length of 33.6 cm is similar to the paratype skull of *A. galushai*). Consequently, the paratype skull of *A. galushai* provides the first record of an undistorted basicranium in an early species of the genus, and establishes that the basicranial anatomical pattern typical of large mid-Miocene North American species of *Amphicyon* was already in existence in the early Miocene.

As in living ursids, the basicranium displays a broad basioccipital (38.6 mm in width in the paratype, 34.5 mm in the juvenile),

flanked by deeply recessed auditory regions on either side. The lateral margin of the basioccipital is not ventrally extended as a downturned flange as in living ursids (*U. arctos*, *U. americanus*), but turns dorsad to form a thin lateral wall for the recessed inferior petrosal venous sinus that travels the basioccipital margin (Hunt, 1977). The squamosal is characterized by a weakly concave glenoid fossa that lies in the same horizontal plane as the basicranial axis. The posterior margin of the fossa is delimited by a postglenoid process of moderate height (20 mm at medial border in the paratype) that gradually decreases in height laterally. At the base of the inner margin of the process is a well-defined circular postglenoid foramen 3–4 mm in diameter, present in both skulls, indicating a viable external jugular venous drainage from the cranium. Immediately medial to this foramen is a shallowly incised Glaserian fissure adjacent to the squamosal-alisphenoid suture.

The alisphenoid contains the foramen ovale placed at the posterior end of a common depression (12 mm in length in the paratype, 9.6 mm in juvenile) that also houses at its anterior end the posterior opening of the alisphenoid canal. The posterior part of the alisphenoid (tympanic wing) descends into the deeply recessed middle ear cavity roofed by the petrosal. The petrosal can be observed in both *A. galushai* skulls (figs. 4.3, 4.5). It is deeply set into the auditory region, its ventral surface recessed 13 mm dorsal to the surface of the basioccipital in the paratype cranium. Its form is best preserved in UNSM 1570–59, where it measures 19.9 mm in length, 16.3 mm in width. In UNSM 1570–59, the bulla has been lost from the left auditory region, providing an unobstructed view of the middle ear (this area is partly covered by the bulla in F:AM 25400). The petrosals of the two Running-water skulls are extremely similar, although UNSM 1570–59 was smaller in body size, probably a young female.

The petrosal promontorium in ventral view is elliptical, low and rounded, quite small (anteroposterior diameter 12.8 mm in paratype, 11.4 mm in juvenile), and without a ventral process (fig. 4.5). A broad tegmen tympani (width, 7.3 mm in juvenile) extends laterad from the promontorium to contact the squamosal. The form and placement of the

depressions found in the tegmen (epitympanic recess, tensor tympani fossa, stapedius fossa, facial canal) of *Amphicyon galushai* are in the plesiomorphic carnivoran state. The tensor and stapedius fossae are both shallow, narrow cavities, and the epitympanic recess is only a modestly developed depression of small volume, not penetrating deeply into the squamosal. In living ursids, the epitympanic recess and tensor and stapedius fossae are found in the same rudimentary state as in *Amphicyon galushai*, and reflect the relatively unspecialized condition of the tegmen and adjacent cranial bones.

The mastoid bone and exoccipital together form a broad, massive, blocky process characteristic of all North American species of *Amphicyon* (fig. 4.5). The mastoid process is thick, wide (27.8 mm in width in the paratype, not preserved in juvenile) but does not descend ventrally, remaining at the level of the basioccipital. A nearly vertical groove for the exit of the facial nerve is present in the medial side of the mastoid bone. Its vertical orientation is due to the deeply recessed position of the petrosal that requires the nerve to descend almost directly ventrad to exit the auditory region. Appended to the mastoid process is a very short (10 mm) paroccipital process that seems inordinately small for the large skull, but which is similar in size to the short paroccipital process of living ursids. Internal to the paroccipital process is the posterior lacerate foramen for the internal jugular vein and associated cranial nerves, which has a transverse diameter of 7–8 mm; its anterior margin is ill defined because the posterior part of the auditory bulla that forms this margin is lost in the paratype skull.

The remnant of the bulla preserved in the paratype skull is of particular importance (fig. 4.5). This is the oldest known auditory bulla preserved in any species of North American *Amphicyon*. The auditory bulla and its relationship to surrounding basicranial elements distinguishes *Amphicyon* from other contemporary amphicyonids (the bulla of species of *Daphoenodon* is of entirely different shape). The bulla in *A. galushai* is formed primarily by an ectotympanic element as in other North American species of the genus. Its length was ~23 mm and width ~30 mm. Although the medial and posterior

parts of the bulla have been broken and lost, the remaining anterior and lateral parts reveal that the bulla was flask-shaped in ventral view. A short osseous external auditory meatus was present in the paratype, as in many arctoid carnivorans; but in *Amphicyon galushai* the middle ear space enclosed by the bulla extended laterad into the ventral floor of the meatal tube, creating an accessory hypotympanic sinus. In F:AM 25400, the bony meatus is deeply invaded by this sinus, which penetrates nearly to its lateral terminus. The roof of the sinus is smooth bone, traversed by two thin ridges, and was evidently covered by the mucosa lining the middle ear space. This sinus is a derived trait, and has been observed in the other species of North American *Amphicyon* (*A. frendens*, F:AM 54415, Long Quarry; *A. ingens*, F:AM 28307, Horse & Mastodon Quarry). Its occurrence in the paratype skull of *A. galushai* and also in *A. ingens* from Horse & Mastodon Quarry demonstrates that the sinus was present during the entire time span of the lineage in the New World. The sinus also occurs in North American skulls of *Pliocyon* and *Ischyrocyon*, but is only incipient in early species of *Cynelos* (Hunt, 1977, pl. 1).

The auditory bulla was apparently fully ossified and completely enclosed the auditory region, including the petrosal promontorium. However, if the plane of the posterior wall of the bulla is projected medially, it passes close to the posterior border of the promontorium, indicating little or no backward extension of the bulla, hence no posterior expansion of the middle ear space.

It is not possible to determine if entotympanic elements contributed to the ectotympanic bulla of *A. galushai*. If they were present, they were in a rudimentary state, not expanded or encroaching to any degree on adjacent basicranial bones, and probably making only a minor contribution to the medial wall and posterointernal corner of the bulla, as in a living ursid (Hunt, 1974, pl. 4). It is evident from the form of the occipital and mastoid bones that a caudal entotympanic was not closely applied to their surfaces, in contrast to the situation in canids where this occurs. The presence of the accessory hypotympanic sinus bears on the question of an entotympanic contribution to the amphi-

cyonid bulla: If one or more caudal entotympanics existed as small bony elements, forming part or all of the medial wall of the bulla as in living ursids, they were not utilized to expand the volume of the middle ear. Instead, *Amphicyon* used an alternative strategy to increase middle ear volume by invading the floor of the bony external auditory meatus.

In the skulls of *Amphicyon*, the medial margin of the petrosal contacts the edge of the basioccipital, but there is no suturing of petrosal to basioccipital as occurs in canids. The margin of the basioccipital is deeply excavated for the inferior petrosal venous sinus (Hunt, 1977; Hunt and Barnes, 1994); this excavation is evident in the paratype skull of *A. galushai* (fig. 4.5).

The form of the ectotympanic bulla, the penetration of the hypotympanic sinus into the bony meatal floor of the bulla, the relationship of the bulla to the deeply recessed petrosal promontorium, the embayed lateral margin of the basioccipital, and the lack of a sutural contact between petrosal and basioccipital distinguish *Amphicyon galushai* from contemporary carnivorans, and ally the species with the Amphicyonidae.

DENTITION: In contrast to *Daphoenodon* from the Runningwater Formation, the upper dentition of *Amphicyon galushai* is characterized by short premolars and a triangular M1 (nearly equilateral) with a large, rather flat, subrectangular M2 (figs. 4.2, 4.6, table 4.2). The form of these teeth is as in the Sansan species, *Amphicyon major*, and unlike the elongate upper premolars and transversely elongate, anteroposteriorly narrow M1–M2 of Runningwater *Daphoenodon*. Upper incisors are not known, but from the alveoli it is clear that I3 was much enlarged, whereas I1–2 were small and narrow. The canines were of average size, the root present in UNSM 1570–59 measuring 19 × 13 mm near the base, and the alveolus of the upper canine in the paratype measuring 22.3 × 15.0 mm.

P1 has a single root and was probably a small peglike tooth, judging from the form of P1 in other species of the genus.

P2 is preserved in UNSM 1570–59 as a double-rooted tooth, with low central cusp, no accessory cusps, a weak posterior ridge running directly down the posterior slope;

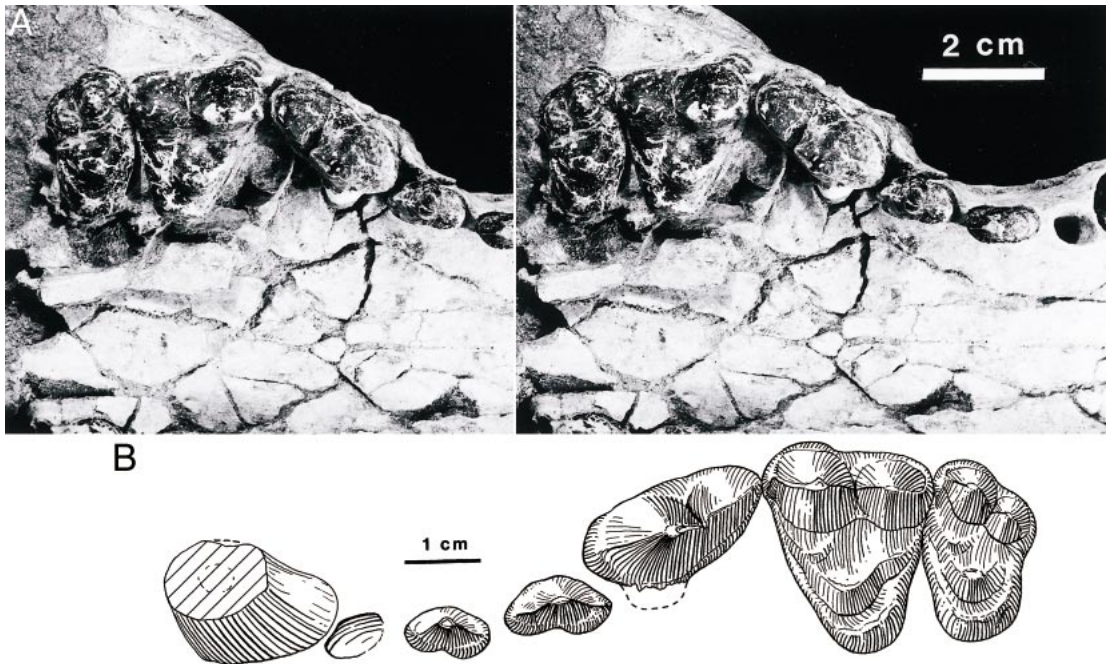


Fig. 4.6. **A:** Stereophotographs of upper dentition of *Amphicyon galushai*, UNSM 1570–59, Hovorka's Quarry, Runningwater Formation, NE. **B:** Restoration of upper dentition of UNSM 1570–59, showing relative size of M1 and M2 (reversed for comparison with paratype P4–M1, fig. 4.2).

the posterior part of the tooth is narrower than the anterior part.

P3 is diagnostic: short in *Amphicyon* and long in Runningwater *Daphoenodon*. In both UNSM 1570–59 and in a referred maxilla (UNSM 25687), this tooth is extremely short, almost round, and peglike, and it lacks any accessory cusps. The main cusp is centrally placed, the lateral part of the tooth slightly convex, the medial concave, but not to the extent seen in Runningwater *Daphoenodon*. Most notably, there is little posterior widening of the tooth, which does occur in *Daphoenodon*.

P4 is also diagnostic, especially its shortness relative to width, lack of a prominent cusp on the protocone, and the presence of a parastylar cusp at the base of the anterior face of the paracone. This short, wide P4 is also seen in Sansan *Amphicyon*. In *A. major*, *A. galushai*, *A. frendens*, and *A. ingens*, P4 length is slightly greater than M1 length (tables 4.2, 4.3, 4.5).

M1 has a tall, well-developed paracone, and a slightly shorter metacone. The anterior

border of the tooth is convex, and the posterior border is straight to convex because of a swelling midway along this edge. The tooth is nearly an equilateral triangle in occlusal view, thus differing from the much more transversely extended M1 of Runningwater *Daphoenodon*. There is no notch in the anterior margin of the tooth as exists in *Daphoenodon*. The protocone is placed more toward the anterior border of M1. From the protocone to the base of the paracone there extends an unbroken ridge (preprotocrista of Van Valen, 1966) without cusps that terminates in unworn specimens in a small, low vestigial paraconule. The postprotocrista extending from the protocone toward the metacone ends at a low, distinct swelling, the metaconule, much larger and more prominent than the paraconule, and placed farther linguad. The distinct metaconule has been noted as a characteristic feature of Old World *Amphicyon major* by Ginsburg (1961). The cingulum is swollen and thickened at its posterolingual corner, just as in *Daphoenodon*, but there is no development of a cusp or

ridge that could be called a well-defined hypocone—the thickened cingulum does little to alter the triangular form of M1.

M2 occurs in place in the smaller skull (UNSM 1570–59), and in the Foster Ranch maxilla (UNSM 26393) from the lower part of the Runningwater Formation, Sioux Co., NE. It also is present in the rostrum (USGS D645) from the Troublesome Formation, CO. In UNSM 1570–59 and USGS D645, the M2 is seen in relationship to M1 and the remainder of the upper teeth (fig. 4.6). There are also two isolated M2s, a smaller one from Cottonwood Creek Quarry, and a much larger M2 from Hemingford Quarry 12D, both in the Runningwater Formation. These five M2s are all subrectangular in occlusal view, but differ among themselves in shape and size (fig. 4.7). Because M2s of UNSM 1570–59 and USGS D645 are in partial skulls of *A. galushai*, there is no doubt that they belong to that species. Although the variation in M2 size and form is greater than in any other tooth in *A. galushai*, I infer that they belong to a single species. Variation in M2 is likely the result of sexual dimorphism and also slight differences in geologic age among the various Runningwater quarries.

M2 of *Amphicyon* is easily distinguished from M2 of Runningwater *Daphoenodon* because the latter animal has a transversely elongate, anteroposteriorly short M2 which is “bent” or folded around an anteroposterior axis through the protocone basin, causing the paracone-metacone to appear to be rotated inward toward the lingual half of the tooth. In contrast, the occlusal surface of M2 of *Amphicyon* is quite flat, nearly a horizontal plane. The entire perimeter of the *A. galushai* M2 is bordered by a heavy cingulum thickened to over 6 mm in width around the lingual face of the protocone (fig. 4.7; UNSM 25578), yet separated from that cusp by a shallow groove. The M2 paracone is the largest cusp, taller than the metacone, the metacone is reduced, and the protocone low. There is a distinct and prominent paraconule; the metaconule is low, more subdued.

M3 is known only from an isolated tooth (UNSM 25762) much smaller than M2. It has a large lingual and a small labial root. The occlusal surface is essentially flat; a low paracone is placed far labiad, forming an ex-

ternal projection; posterolingual to the paracone is a low metacone. Internal to the paracone-metacone is a shallow flat protocone basin entirely surrounded by a thick lingual cingulum. M3 is represented only by alveoli in the paratype skull (F:AM 25400), in UNSM 1570–59, and in the Troublesome Formation rostrum (USGS D645).

The lower dentition is known from three mandibles; the holotype (F:AM 25406) is the best preserved and most complete (fig. 4.2). The lower premolars are separated by short diastemata, are reduced in size, and are very low and of variable form. The p1 is not preserved, but represented by a single alveolus or by two alveoli—their shape suggests that p1 was slightly elongate. It is separated from p2 by a long or short diastema, and is always separated by a diastema from the canine.

The p2 is a low tooth, oval in occlusal view, with a low central cusp, narrower behind the cusp than anterior to it (but in one individual wider behind), and with weak anterointernal and posteroexternal ridges running downward from the central cusp to the respective corners.

The p3 is slightly larger than p2 but is still low, considerably more so than p4, and with a low central cusp. However, in p3, the anterior and posterior ridges run directly to the anterior and posterior basal borders, not to the corners. The rear of the tooth is often elevated as a small cingulum cusp, and to this point runs the ridge in the Dunlap Camel Quarry mandibles (F:AM 25407, F:AM 25406). In the Cottonwood Quarry mandible, the ridge includes a posterior accessory cusp not present in the other two jaws.

The p4 is considerably taller than p1–3 as in *Amphicyon major* from Sansan. It has a posterior accessory cusp, no distinct anterior accessory cusp, is slightly wider posteriorly, and has a rounded posterior basal border, in contrast to the truncated or “squared” border of Runningwater *Daphoenodon*. The p4 abuts the anterior face of m1.

The m1 is similar to m1 of Runningwater *Daphoenodon*, and it can be difficult to distinguish isolated teeth. The paraconid is advanced anteriorly, the larger protoconid placed directly behind it. These two trigonid cusps are rather tall, swollen, and become

TABLE 4.5
Dental Measurements (in millimeters) of *Amphicyon fendens* and *A. ingens* (North America)

Mus. no.	P3	P4	M1	M2	Locality
<i>Amphicyon fendens</i>					
SHEEP CREEK FM., NEBRASKA					
AMNH 18913	—	32.4	27.0 × 35.5	(24) ^a × 35.4	Stonehouse Draw
F:AM 54424	—	26.0	23.6 × 32.1	19.9 × 31.5	Thistle Quarry
F:AM 54416	—	—	26.4 × 33.0	—	Long Quarry
F:AM 54418	—	—	—	23.7 × 36.1	Long Quarry
F:AM 54420	—	—	—	26.5 × 39.9	Long Quarry
F:AM 54417	—	—	27.1 × 34.4	—	Long Quarry
F:AM 54402	—	30.4	—	—	Long Quarry
F:AM 54415	(19)	31.8	29.3 × 35.6	— × (38.1)	Long Quarry
F:AM 54390	12.7	24.9	23.2 × 29.4	19.5 × 31.4	Thomson Quarry
F:AM 54250A	15.0	29.1	25.8 × 37.0	20.5 × 33.1	Plihippus Draw
<i>Amphicyon ingens</i>					
OLCOTT FM., NEBRASKA					
F:AM 54280	19.9	33.4	29.7 × 41.4	29.0 × 41.3	Boulder Quarry
F:AM 54260	20.2	(39)	(30) × 43.1	29.4 × 42.4	Quarry 2
F:AM 54265	—	37.1	—	—	Quarry 2
F:AM 54284	21.3	33.5	32.0 × 41.8	26.7 × 40.4	Quarry 5
F:AM 54304	15.1	32.4	28.9 × 36.7	22.0 × 34.6	Humbug Quarry
F:AM 25470	20.2	32.9	29.3 × 38.5	24.2 × 38.2	Echo Quarry
F:AM 54292	—	33.5	29.2 × 36.8	—	Echo Quarry
F:AM 54296	—	—	—	24.8 × 39.1	Echo Quarry
F:AM 54300	—	—	32.5 × 42.4	—	Echo Quarry
F:AM 54315	16.5	32.7	—	—	Echo Quarry
F:AM 54291	—	33.9	—	—	Echo Quarry
F:AM 25499	18.9	33.7	28.3 × 42.3	22.9 × 38.3	Sinclair Qu. 4, Hor. A
F:AM 54287	20.1	(33.5)	—	—	West Surface Quarry
F:AM 54264	—	—	—	30.0 × 44.1	New Surface Quarry
F:AM 54263	—	—	30.3 × 40.4	—	East Sand Quarry
PAWNEE CREEK FM., COLORADO					
F:AM 28307	18.8	(31.2)	(28.8) × 42.3	25.9 × 39.0	Horse & Mastodon Qu.
TEXAS COASTAL PLAIN					
F:AM 63280	—	—	—	26.5 × 39.7	Trinity River Pit 1
ESPAÑOLA BASIN, NEW MEXICO					
F:AM 49244	—	(32)	30.4 × 38.9	21.2 × 32.4	Arroyo Ancho Prospect
BARSTOW SYNCLINE, CALIFORNIA					
F:AM 27096	—	(33.4)	28.9 × 38.6	22.6 × 32.2	Green Hills
F:AM 23788	18.5	32.8	29.0 × 39.6	26.4 × 37.7	Valley View Quarry
F:AM 27099, 27099A	—	—	27.4 × (35)	21.8 × 31.2	Green Hills

blunted with age; they wear in mature individuals to relatively flat surfaces, not to vertical shear planes. The metaconid is somewhat reduced and is placed on the postero-internal slope of the protoconid. The talonid is shorter than the massive trigonid, a huge hypoconid dominates the labial margin of the talonid, and there is an entoconid ridge, well developed in the holotype (in contrast to

Ysengrinia, where the entoconid ridge is not developed). The tooth is widest between the trigonid and talonid, and in occlusal view has an elliptical outline. In contrast, m1 in Runningwater *Daphoenodon* is somewhat narrower in occlusal view, but to reliably distinguish the two genera, p4–m2 in place in the mandible is required.

The m2 is similar to m2 in Runningwater

TABLE 4.5
(Continued)

Mus. no.	p3	p4	m1	m2	Locality
<i>Amphicyon frendens</i>					
SHEEP CREEK FM., NEBRASKA					
AMNH 18913	—	21.6	37.9	28.7	Stonehouse Draw
F:AM 54391	13.3	18.4	34.9	24.1	Thomson Quarry
F:AM 54392	13.8	18.9	35.8	21.9	Thomson Quarry
F:AM 54423	17.7	22.1	37.0	25.5	Thistle Quarry
F:AM 54407	13.4	18.5	(33.5)	(24.3)	Thistle Quarry
F:AM 54426	lost	22.1	37.9	27.0	Thistle Quarry
F:AM 54425	14.1	20.9	39.8	28.0	Thistle Quarry
F:AM 54411	14.5	18.2	(34)	23.9	Long Quarry
F:AM 54400	15.8	18.8	37.3	25.7	Long Quarry
F:AM 54401	14.7	19.2	(35)	25.9	Long Quarry
F:AM 54403	—	—	—	27.6	Long Quarry
F:AM 54406	—	—	—	23.0	Long Quarry
F:AM 54404	—	—	—	26.9	Long Quarry
F:AM 54405	—	—	—	24.6	Long Quarry
F:AM 54430	—	—	—	32.1	Greenside Quarry
F:AM 54250A	14.1	19.1	36.4	25.0	Pliohippus Draw
<i>Amphicyon ingens</i>					
OLCOTT FM., NEBRASKA					
AMNH 18272	17.3	(25)	—	—	Snake Creek Quarries
AMNH 18273	—	—	44.8	—	Snake Creek Quarries
F:AM 54261	18.0	23.6	44.9	33.0	Quarry 2
F:AM 54270	17.2	22.8	40.9	30.9	East Sinclair Draw
F:AM 54262	17.1	22.9	41.9	32.1	West Sand Quarry
F:AM 25498	15.1	22.0	40.2	—	Sinclair Qu. 4, Hor. A
F:AM 54304	14.7	20.8	(39.9)	26.9	Humbug Quarry
F:AM 54274	—	25.4	—	31.0	Humbug Quarry
F:AM 54306	—	—	39.8	—	Humbug Quarry
F:AM 54468	15.4	20.4	36.0	—	Prosynthetoceras Qu.
AMNH 22069	16.0	24.0	43.1	31.0	Snake Creek Quarries
F:AM 25470	15.7	22.3	36.6	—	Echo Quarry
F:AM 54301	—	—	39.4	—	Echo Quarry
F:AM 54294	—	—	—	31.7	Echo Quarry
F:AM 54308	—	—	—	29.2	East Jenkins Quarry
F:AM 54299	—	—	—	30.8	Mill Quarry
F:AM 54312	—	—	42.3	—	Snake Creek Quarries
PAWNEE CREEK FM., COLORADO					
F:AM 28307	17.6	22.8	41.5	33.4	Horse & Mastodon Qu.
F:AM 28362	—	—	39.8	—	Horse & Mastodon Qu.
F:AM 28341	—	—	—	29.6	Horse & Mastodon Qu.
F:AM 28361 ^b	(18)	23.1	41.7	32.5	Horse & Mastodon Qu.
F:AM 28307A	—	—	—	34.5	"East of Camp"
ESPAÑOLA BASIN, NEW MEXICO					
F:AM 21109	—	(21.4)	(40.5)	(28.3)	Skull Ridge Member
BARSTOW SYNCLINE, CALIFORNIA					
F:AM 23788	16.9	23.6	42.4	28.5	Valley View Quarry
F:AM 50070	14.9	20.1	37.8	26.8	Steepside Quarry
F:AM 27098	14.9	21.2	38.0	—	Green Hills
F:AM 27099C	—	—	—	29.3	Green Hills
F:AM 27099D	—	—	—	28.9	Green Hills

^a () Indicates estimated measurement.^b Reported to come from "just above Horse & Mastodon Quarry".

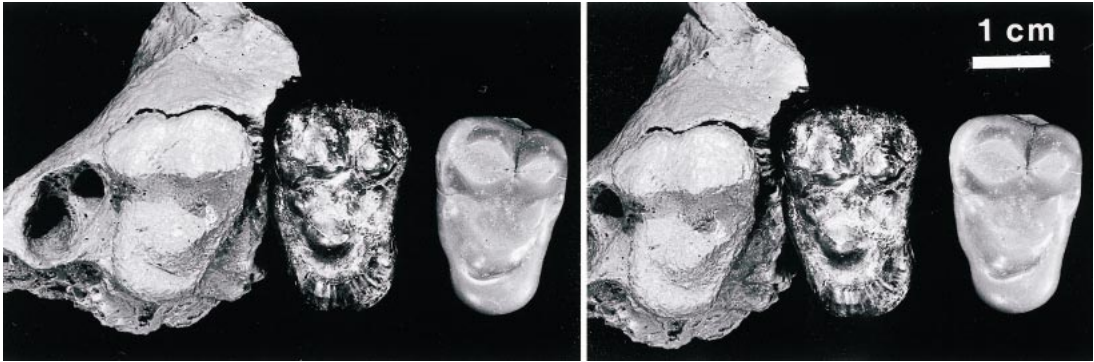


Fig. 4.7. Comparison of M2 in *Amphicyon galushai* illustrating variation in size and form: Left, UNSM 26393 (cast); center, UNSM 25578; right, F:AM 25437 (cast), all Runningwater Formation, NE. Note alveoli for M3 in UNSM 26393.

Daphoenodon, but is wider and more elliptical in occlusal view. The protoconid is quite large, the small metaconid is a discrete, low cusp placed directly internal to the posterior part of the protoconid, but the paraconid is not evident as a distinct cusp, its position being occupied by a low curved ridge. In old individuals, the m2 trigonid is worn to a flat surface without relief. The trigonid is larger than the talonid, the latter with a prominent hypoconid and a very small entoconid. The m3 is evidenced by a single, large, oval alveolus.

The middle and posterior mental foramina are placed below the anterior roots of p2 and p3, respectively. There are no demonstrable differences from Runningwater *Daphoenodon* in location of the angular process, articular condyle, or ascending ramus, except that the articular condyle itself appears to have been more transversely elongate in *Daphoenodon*.

POSTCRANIAL SKELETON: Almost all postcranial elements of *Amphicyon galushai* come from only a few quarries: Hemingford Quarries 7B and 12D, and from Cottonwood Creek Quarry. Hemingford Quarries 7B and 12D are located at the surface of the Hartville Table in northwestern Nebraska (Hunt, 1990), at a high topographic elevation, also considered stratigraphically high in the Runningwater Formation. Isolated teeth of *Amphicyon* accompany the postcranial remains at these sites. The only other large amphicyonid carnivore in these quarries in the upper Runningwater Formation is the large beardedog *Daphoenodon*, whose postcranial remains and

teeth are similar in size, but much different in form, from those of *Amphicyon*. Other than by its teeth, *Amphicyon galushai* is most easily distinguished from contemporary *Daphoenodon* by the bones of the feet and lower limbs. *Daphoenodon* has considerably more elongated lower limb bones and metapodials relative to the short, stout lower limb elements and metapodials of *Amphicyon*.

In addition to the two crania, three mandibles, and a number of isolated teeth from the Runningwater Formation, a scapula, humerus, ulna, radius, femur, astragalus, calcaneum, cuboid, metacarpals 1–5, and metatarsals 1–4 can be attributed to *A. galushai* (figs. 4.8–4.13). The sample lacks the vertebrae, pelvis, sacrum, tibia and fibula, and the smaller bones of the carpus and tarsus. Based on comparison with other species of the genus, *A. galushai* must have had a long tail, but there are no certainly attributable caudal vertebrae. Postcranial bones of *A. galushai* are extremely similar to postcrania of European *A. major* described by Ginsburg (1961).

The forelimb of *A. galushai* is represented by the scapula, humerus, radius, ulna, and all metacarpals. The proportions of scapula, humerus, lower limb, and foot bones are essentially as in *A. major*. The scapula is massive, robust, with broad surfaces of origin for the rotator cuff muscles that stabilize the scapulothoracic joint. A large infraspinous fossa, 16 cm in length and 2.5 cm in width, common to amphicyonids and ursids, occupies the ventral border of the scapula. The hu-

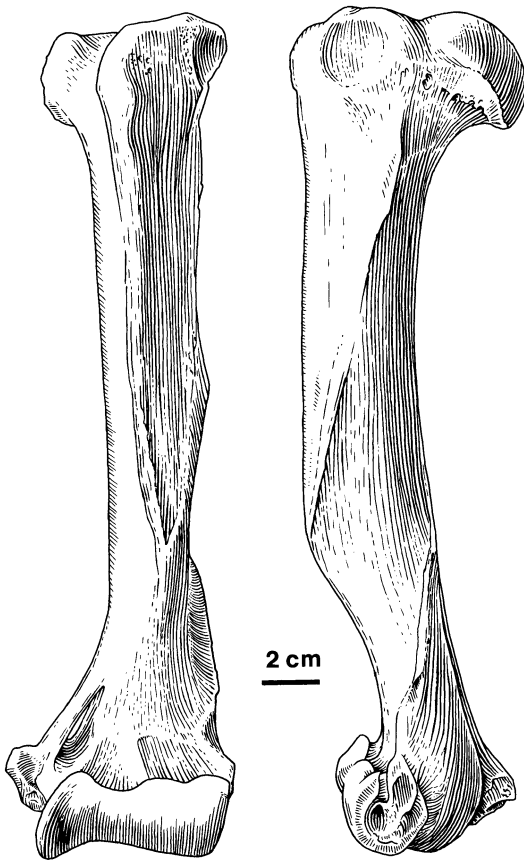


Fig. 4.8. Humerus, *A. galushai*, UNSM 26383, Hemingford Quarry 12D, Runningwater Formation, NE: anterior (left) and lateral (right) views.

merus (length, 298 mm) is remarkable for the width and ventral extent of the broad surface for insertion of the deltopectoral muscles (fig. 4.8). This surface forms a prominent V-shaped plateau on the anterior surface of the diaphysis; this is more developed and extends further ventrad than in living large urids and felids. Attachment areas for the origin of extensor and flexor muscles of the carpus are prominent on the lateral and medial condylar areas of the distal humerus. Both radius (272 mm, fig. 4.9) and ulna (321 mm, fig. 4.10) are short relative to the more elongated radius and ulna of the large Runningwater *Daphoenodon* (5 radii, mean = 303.6 mm). A radius, ulna, and humerus of *Amphicyon* from the same quarry (Hemingford Quarry 12D), although not associated,

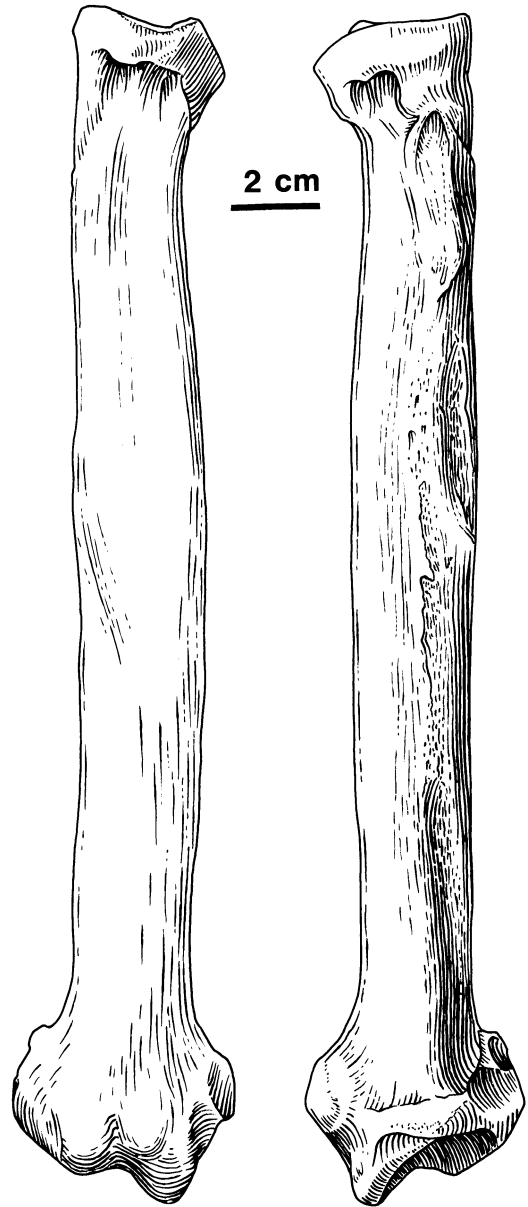


Fig. 4.9. Radius, *A. galushai*, UNSM 25557, Hemingford Quarry 12D, Runningwater Formation, NE: anterior (left) and posterior (right) views.

articulate satisfactorily, and indicate a radius shorter than the humerus. Lengths of the radius (272 mm) and ulna (321 mm) of *A. galushai* fall within the range of the radius (239–280 mm) and ulna (295–336 mm) of *A. major* (data from Ginsburg, 1961; Ber-

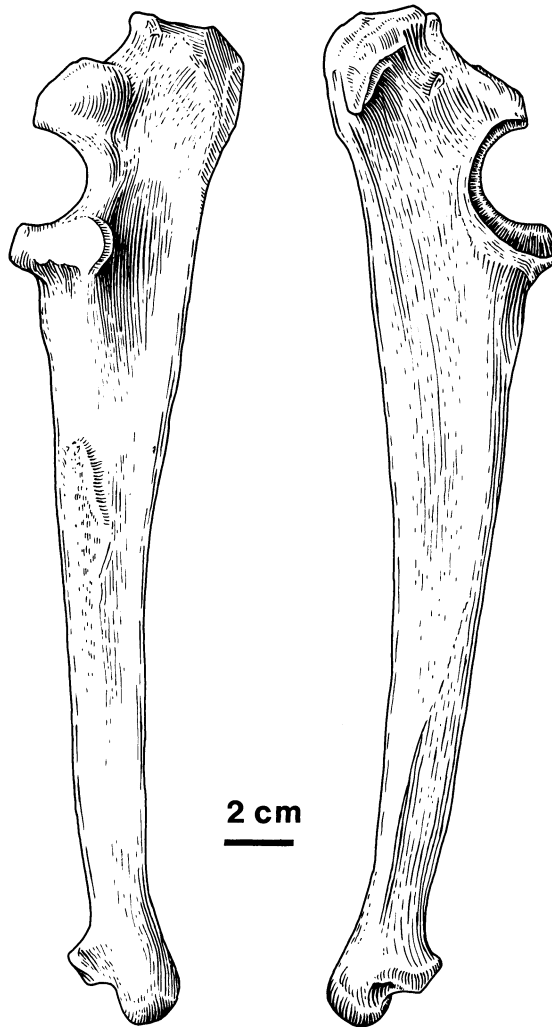


Fig. 4.10. Ulna, *A. galushai*, UNSM 25559, Hemingford Quarry 12D, Runningwater Formation, NE: lateral (left) and medial (right) views.

gounioux and Crouzel, 1973). The diaphyses of the radius and ulna exhibit elliptical rugose tracts for the anchoring of strong interosseous ligaments binding these bones together; the configuration of the proximal and distal articulations of the radius with the ulna indicate a relatively unrestricted ability to pronate/supinate the forefoot on the lower limb (more so than in living canids, where this motion is restricted). Of interest is that the ulna in *A. ingens* no longer maintains the slight curvature of the diaphysis seen in the smaller species *A. galushai*. The enormous size of *A. ingens* has modified the form of

the lower forelimb bones which function both in locomotion and as weight-bearing columns. The metacarpals are short, robust bones (fig. 4.11); when articulated, they are not tightly appressed along their shafts as in living canids, but diverge distad. Although there is no associated metacarpus to determine the relative lengths of these bones, measurements of metacarpals 1–5 (table 4.6) suggest that they are proportionately similar to those of *A. major* from Sansan, described by Ginsburg (1961). These measurements from unassociated metacarpals at first seem to indicate that the forefoot was paraxonic,



Fig. 4.11. Metapodials, *A. galushai*, Runningwater Formation, NE. **Above** (left to right): MC 2, right, female, UNSM 25568; cuboid, UNSM 26394; MC2, left, male, UNSM 25569; MC 3, left, male, UNSM 25573. **Below** (left to right): MT 1, right, UNSM 25582; MT 2, left, UNSM 26391; MT 3, left, UNSM 26378; MT 4, left, UNSM 25565.

with the central axis between metacarpals 3 and 4 (MC1, 48; MC2, ~68–76; MC3, 82.8; MC4, 85; MC5, 66.7 mm; table 4.6). However, the associated metacarpals of *A. major* from Sansan described by Bergounioux and Crouzel (1973) reveal a forefoot more like that of living bears, but with greater emphasis on digits 3 and 4 and less emphasis of digits 1, 2, and 5. The sum of these anatomical traits indicates a powerful but short forelimb, capable of bearing considerable weight, and tolerant of significant stresses during locomotion and prey capture, yet permitting a reasonable amount of manipulation with the manus.

The hindlimb is represented by the femur, cuboid, calcaneum, astragalus, and metatar-

sals 1–4. The femur (fig. 4.12, length 363 mm) takes the same form as that bone in Sansan *A. major* but is somewhat shorter, and more robust. As in that carnivore, it is likely that the tibia and fibula were short, much more so than the tibia-fibula of Runningwater *Daphoenodon*. The cuboid (fig. 4.11) is dorsoventrally short, lacking the elongation seen in cursorial carnivorans such as living canids, felids, and Runningwater *Daphoenodon*. Its dorsal articular surface for the calcaneum slopes laterad as in large ursines, and it lacks the flat, horizontal dorsal surface of living cursors. The calcaneum (fig. 4.12) is most similar to that of large living ursids, and is distinct from the more elongate calcaneum of large living felids; the lack of elongation

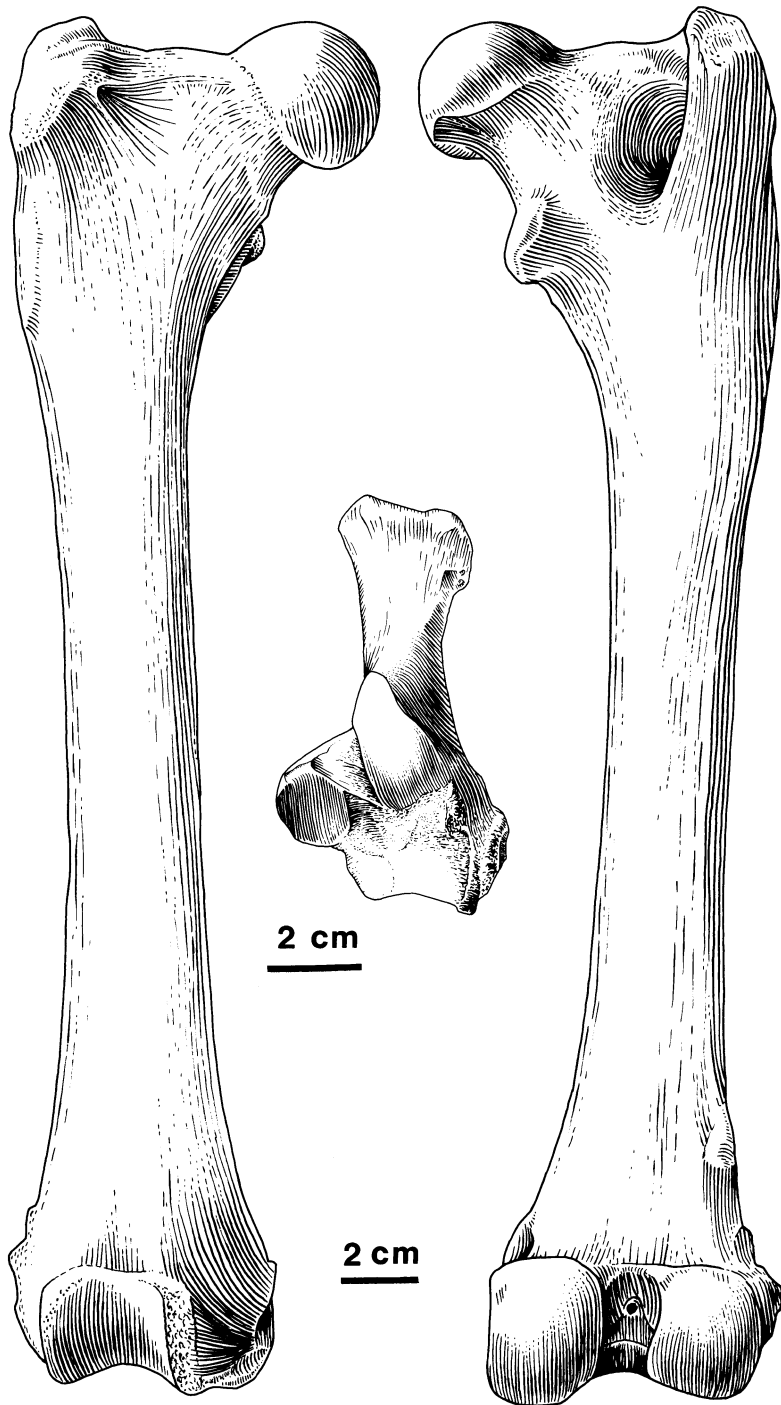


Fig. 4.12. Femur, UNSM 25560, and calcaneum, UNSM 26386, of *A. galushai* from Hemingford Quarry 12D, Runningwater Formation, NE. Anterior (left) and posterior (right) views of femur, anterior view of calcaneum.

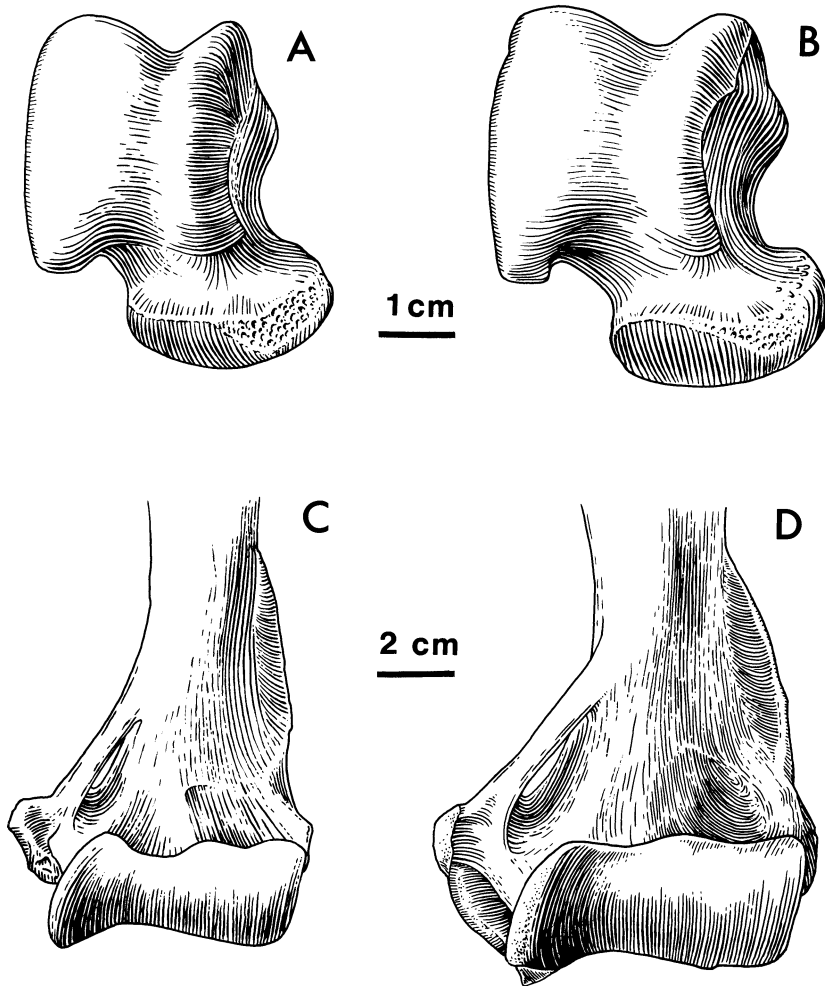


Fig. 4.13. Dimorphism in *A. galushai*: (A) female astragalus, UNSM 26389; (B) male astragalus, UNSM 26387; (C) female distal humerus, UNSM 26383; (D) male distal humerus, UNSM 26375. (A), (B), and (C) are from Hemingford Quarry 12D; (D) is from Hemingford Quarry 12B, Runningwater Formation, NE.

of the distal calcaneum, the distal placement of the sustentaculum, and the modest grooving of the posterior surface of the sustentaculum for flexor tendons of the hindfoot all demonstrate less vertical orientation of the *A. galushai* hindfoot than seen in large felids. However, the form of the astragalus (fig. 4.13) is intermediate between that of large living ursids and felids, and in its totality, the hindfoot was probably placed in an intermediate position between the fully plantigrade stance of living bears and the more vertically oriented hindfoot of large felids.

This is supported by the metatarsals (fig. 4.11), which are longer than the metacarpals; the metatarsals diverged distad and were not closely appressed, but the hindfoot was incipiently paraxonic. The lack of an associated metatarsus of *A. galushai* prevents the determination of exact proportional relations among the metatarsals; however, table 4.6 shows that metatarsals 3 and 4 were the longest; in fact, the metatarsals are similar in length to those of *A. major* at Sansan (Ginsburg, 1961). The skeleton of *A. major* described by Bergounioux and Crouzel, prob-

TABLE 4.6
Comparison of Metapodial Lengths of *Amphicyon galushai* (North America) and *Amphicyon major* (France) in millimeters

<i>Amphicyon major</i> ^a	<i>Amphicyon major</i> ^b	<i>Amphicyon galushai</i>
MC1 49.6, 49, 48.9, 44.5, 44.3	41	48.0
MC2 —	59	76.0, 72.5, 68.7
MC3 84.3, 84.2, 82.2, 80.1, 80, 79.5, 78.8, 71.1	68.5	82.8
MC4 87.8, 83.8	68	85.0
MC5 67	60	66.7
MT1 —	47	50.9
MT2 64.5, 64.4	60	73.6, 64.1
MT3 80.8	66.5	83.1, 82.1
MT4 95.4	71	93.5
MT5 —	67	—

^a Measurements from Ginsburg, 1961: 12–13.

^b Measurements from Bergounioux and Crouzel, 1973: 58, 69.

Abbreviations: MC, metacarpal; MT, metatarsal.

ably a female on the basis of size (table 4.6), also has metatarsals 3–4 as the longest. As remarked by Ginsburg, the slight elongation of the hindfoot coupled with the hindlimb anatomy suggests the capability for powerful forward propulsion in keeping with a sudden, explosive rush from cover, similar to that observed for living lions (*Panthera leo*).

The calcaneum, astragalus, and cuboid of *A. galushai* are much different from those bones in Runningwater *Daphoenodon*. These elements are elongated in *Daphoenodon* and are indicative of the more vertical orientation of the fore- and hindfoot in that genus. In *Daphoenodon*, the calcaneum is narrow, with a more dorsally placed sustentaculum deeply grooved on its posterior surface for the flexor tendons of the hindfoot; the distal process of the astragalus is elongated, and more directly beneath the proximal trochlea; the cuboid is taller, with a nearly horizontal articular surface with the calcaneum. In *Amphicyon*, the calcaneum is wider, with a more ventrally placed sustentaculum that is not as deeply grooved on its posterior surface; the distal process of the astragalus is shorter, not moved beneath the proximal trochlea; the cuboid is short, robust, and retains a sloping dorsal surface (described as a “surface oblique” by Ginsburg, 1961: 37) for articulation with the calcaneum. These features in-

dicates that the long axis of the hindfoot of *A. galushai* was not as vertically oriented as in the hindfoot of *Daphoenodon*. The metatarsals and digits were somewhat more divergent in *Amphicyon*, but more closely apposed in *Daphoenodon*. In the hindfoot, *Amphicyon* could be termed subdigitigrade and *Daphoenodon* digitigrade.

DIMORPHISM IN THE POSTCRANIAL SKELETON AND TEETH: Ginsburg (1961) and Ginsburg and Telles-Antunes (1968) noted the pronounced dimorphism in teeth and postcrania of European *Amphicyon*. There is no doubt that this also occurs in the species of North American *Amphicyon*, and is first evident in *A. galushai* (fig. 4.13), but also is present in the larger *A. frendens* and *A. ingens*. Dimorphism in *A. galushai* is based on significant size differences in the following teeth and postcranials: P4, M1, M2, humerus, astragalus, metacarpal 2, and metatarsal 2. This dimorphism has been considered sexual, the larger morph the huge males, suggesting that these species are polygynous. In polygynous carnivorous species, the males are usually highly territorial and solitary, and compete among themselves for females during the breeding season. This is probably true of both Old and New World species of *Amphicyon*, and contributed to the large size at-

tained by these animals in Europe and North America during the Miocene.

DISCUSSION

The fossils of early Hemingfordian *Amphicyon* come from two principal geographic areas: (1) the Runningwater Formation of northwest Nebraska, comprising (a) specimens from the Hemingford Quarries of UNSM in Box Butte County, (b) from quarries of the Frick Laboratory (AMNH) in Dawes County; and (c) the isolated maxilla from Foster Ranch, Sioux County, which comes from the lower part of the Runningwater Formation and represents the oldest occurrence of the genus in the Great Plains; (2) the U.S. Highway 40 roadcut in tuffaceous siltstones of the Troublesome Formation, Grand County, north-central Colorado, deposited in the Middle Park intermontane basin, west of the Rocky Mountain Front Range (Izett, 1968).

Fossils from the lower part of the Runningwater Formation, Nebraska (the Foster Ranch maxilla), and from the Troublesome Formation, Colorado (the crushed rostrum), mark the first appearance of *Amphicyon* in the New World. These are the westernmost occurrences of North American *Amphicyon* in the early Hemingfordian, and belong to the smallest species of the genus yet identified in North America, here placed in the new species, *A. galushai*. With the exception of these two specimens, all other fossils come from quarries or isolated outcrops of the Runningwater Formation farther east in Dawes County and Box Butte County, Nebraska. Most *A. galushai* specimens were discovered from 1934 to 1941 by American Museum and UNSM field parties in northwest Nebraska; the two oldest records, however, were found in 1965 and 1982, and the smaller of the two known skulls in 1959. The species is rare, and no complete skeleton or even an associated skull and mandible has been found despite extensive quarrying in fluvial channel fills of the Runningwater Formation, sediments that have produced large population samples of early Miocene ungulates.

The paratype skull and the holotype mandible from Dunlap Camel Quarry in the Runningwater Formation are the best preserved

cranial remains of *Amphicyon galushai*, and retain the most plesiomorphic dentition attributable to *Amphicyon* in North America. Although the paratype cranium lacks many teeth, the referred cranium (UNSM 1570–59) from Hovorka's Quarry has most of the upper dentition in place. Only three mandibles of the species are known, two from Dunlap Camel Quarry and one from Cottonwood Creek Quarry, and these show considerable wear on the molars, slight wear on the main cusp of p4, and no wear on p1–3. These mandibles demonstrate that over time the molars become blunted with wear, lose their shear surfaces, and in later life must be primarily limited to crushing. This toothwear pattern, however, does not preclude active carnivory because this type of molar wear also develops during the lifetime of living carnivorous canids such as North American wolves (*Canis lupus*).

Amphicyon galushai may be ancestral to *A. frendens* of the Sheep Creek Formation and *A. ingens* of the Olcott Formation, both Nebraska. Premolars and molars of these three species are similar in form but differ in size (compare tables 4.2, 4.5): All have a reduced P1–3/p1–3, p4 is prominent and conspicuously larger than p3, and the molars are adapted for crushing. P4 in these three species is a robust, rectangular, massive carnassial with a low, reduced protocone and small parastylar cusp. However, these species differ in the degree of enlargement of the molars. Figure 4.14 shows that M1 progressively increases in size from *A. galushai* through *A. frendens* to *A. ingens*. Similarly, M2 is relatively small in *A. galushai*, but in *A. frendens* and *A. ingens*, this tooth has considerably increased surface area (fig. 4.15), as does M3. In these large species of North American *Amphicyon*, the rear molars form broad crushing platforms, and the carnassials become blunted by wear in older individuals as the result of a mortar/pestle action that drives the m1 trigonid into the embrasure between P4 and M1 in the upper jaw. The anterior premolars do not take part in this crushing occlusion, and remain greatly reduced, essentially nonfunctional teeth.

COMPARISON WITH OLD WORLD AMPHICYON: Teeth and mandibles of *Amphicyon galushai* most closely resemble those of Burdigalian

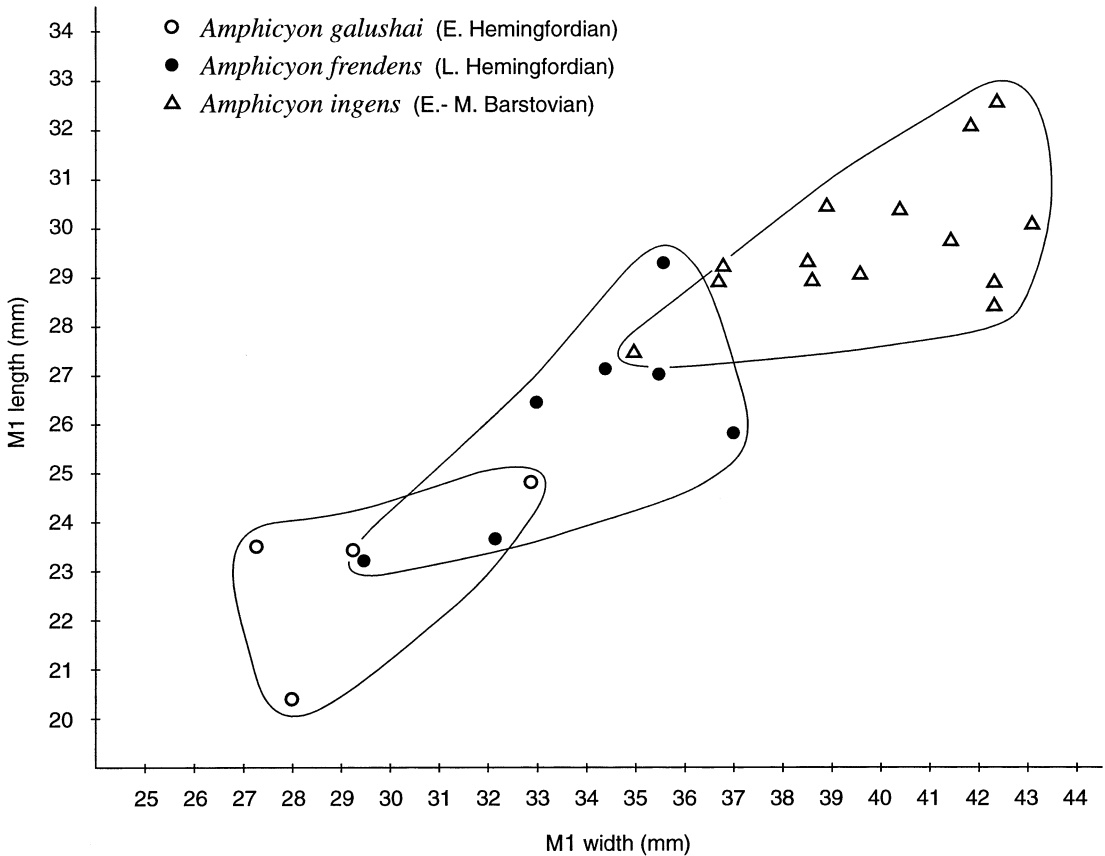


Fig. 4.14. Comparison of M1 dimensions among North American species of *Amphicyon*.

Amphicyon in Europe. Ginsburg and Telles-Antunes (1968) at first placed most fossils of Burdigalian *Amphicyon* in the species *A. giganteus*. They divided *A. giganteus* into three types that correspond to the increasing age of the samples (table 4.7): (a) “un type primitif” of early Burdigalian age, (b) “une forme typique” of mid- to late Burdigalian and early Helvetian age, and (c) the early Helvetian sample from the locality of Pontlevoy, France. *A. galushai* is most similar in dental traits to “un type primitif, d’age burdigalien inférieur.” Both *A. galushai* and the early Burdigalian fossils of *A. giganteus* share several primitive traits: the m1 talonid is slightly basined with a wide internal shelf, and m2 narrows posteriorly in width and retains a distinct paraconid. Nevertheless, *A. galushai* is clearly distinct from these early Burdigalian fossils of *Amphicyon* in its

smaller, narrower, and more plesiomorphic carnassials and molars. Recently, Ginsburg (1999) has restricted *Amphicyon giganteus* to specimens from MN zones 4–5, and now places the late Aquitanian-Burdigalian specimens from MN zones 2b–3 in a new species, *A. laugnacensis* (Ginsburg, 1989: 104).

The form of the *A. galushai* mandible and the cusp pattern of m1–m2 are very much like those of the late Burdigalian *Amphicyon* fossils from La Romieu, France (MN4a), first assigned to *A. major* by Roman and Viret (1934) and later placed in *A. giganteus* by Ginsburg and Telles-Antunes (1968). The La Romieu specimens include a small mandible, probably female, and a large mandible, probably male (Roman and Viret, 1934, pl. I, figs. 1–2). The molars in these mandibles are larger than the molars of the *A. galushai* sample (figs. 4.16, 4.17, tables 4.2, 4.7), and repre-

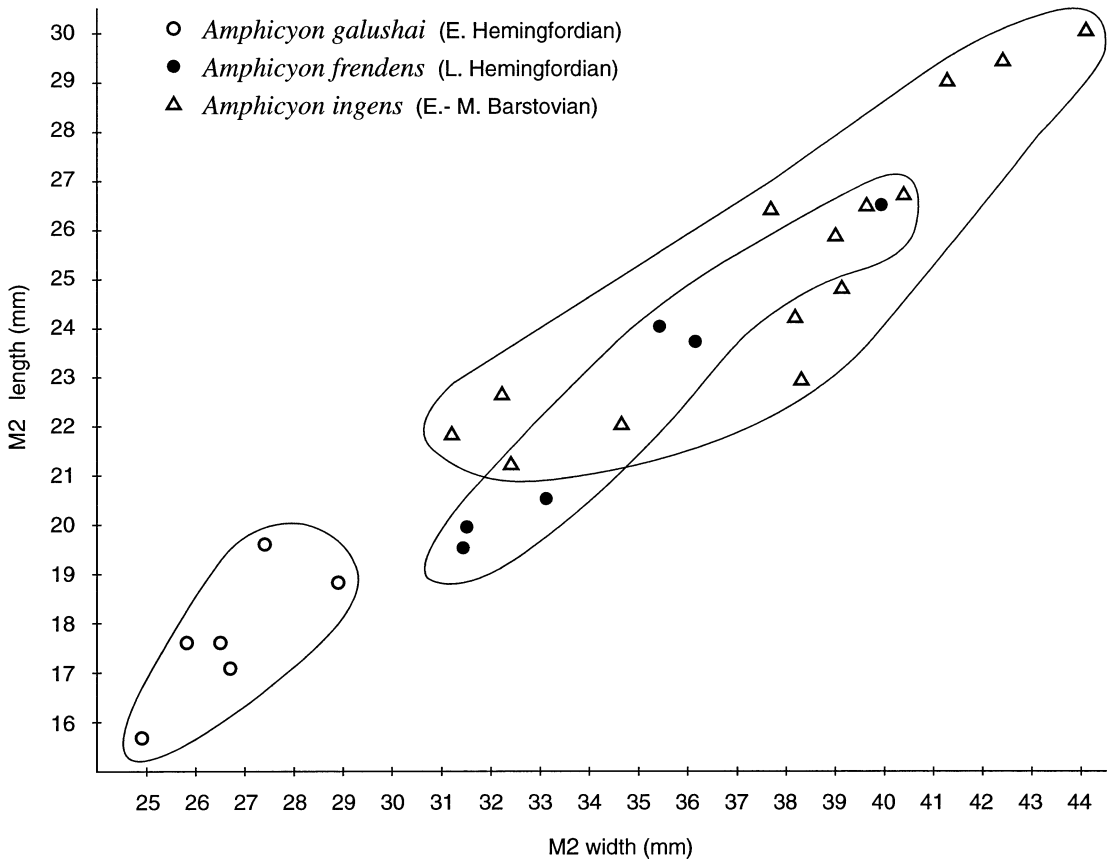


Fig. 4.15. Comparison of M2 dimensions among North American species of *Amphicyon*.

sent a species more dentally advanced than the Runningwater *Amphicyon*, yet apparently closely related. Early Burdigalian sites at Neuville and Chilleurs in France also have produced *Amphicyon* that measures somewhat larger in m1–2 dimensions than *A. galushai*, consequently suggesting that *A. galushai* displays more plesiomorphic molars than European *Amphicyon* of the Burdigalian *A. giganteus*-*A. laugnacensis* group.

An m1 and two terminal molars (M3, m3) from the early Burdigalian locality of Wintershof-West, Germany (Dehm, 1950, fig. 54, Munich 12297; figs. 55, 56, Munich 13565, 13570) were attributed to *A. giganteus* by Ginsburg and Telles-Antunes (1968); m1 is similar in size to lower carnassials of *A. galushai*, but no other similarly sized material was reported from these fissures. The terminal molars of this Wintershof-West *Amphicyon*, if they are correctly allocated, are enor-

mous teeth (Dehm, 1950, figs. 55, 56), much larger than M3/m3 in *A. galushai* (table 4.2). Consequently, if these terminal molars belong to the same species of *Amphicyon* as the Wintershof m1, then the Bavarian *Amphicyon* differs from *A. galushai* in its more enlarged posterior molars, and the New World *A. galushai* seems more primitive in its molar battery than any of the Burdigalian or Helvetian Old World species of the genus.

Another Burdigalian amphicyonid often placed in *Amphicyon* is found at several sites in Europe, and can be compared with *A. galushai*. This species, *Amphicyon bohemicus*, has been variously called *Amphicyon steinheimensis bohemicus* by Kuss (1965) or *A. dietrichi* by Dehm (1950). Specimens from the Burdigalian of Wintershof-West, Tuchorice, and Feisternitz are said to belong to this taxon (see Kuss, 1965: 46). I have been able to study casts of the material described by

TABLE 4.7
Dental Measurements (in millimeters) of *Amphicyon giganteus* from Europe^a

Mus. no.	P2	P3	P4	M1	M2	M3	Locality
EARLY BURDIGALIAN							
Munich 13570	—	—	—	—	—	14.7 × 20	Wintershof
Basel SO360	—	—	24.9 × 15.5	—	—	—	Chilleurs
Basel SO5898	—	—	—	— × 27.2	—	—	Chilleurs
MEDIAL BURDIGALIAN							
Graz, Austria	—	—	29.0 × 18.5	—	—	—	Eibiswald
Graz, Austria	—	—	27.5 × 15.5	—	—	—	Eibiswald
Graz, Austria	—	—	—	—	22.0 × 29.6	—	Eibiswald
Graz, Austria	—	—	—	—	22.3 × 29.5	—	Eibiswald
LATE BURDIGALIAN							
Basel SO2793	15.5 × 8.3	—	—	—	—	—	Baigneaux
Basel SO1700	—	16.6 × 10.5	—	—	—	—	Baigneaux
Basel SO874	—	—	26.4 × 16.1	—	—	—	Baigneaux
MNHN Ba9	—	—	30.6 × 19.5	—	—	—	Baigneaux
MNHN Ba10	—	—	(29.4) ^b × 18.3	—	—	—	Baigneaux
MNHN Ba11	—	—	27.5 × 17.3	—	—	—	Baigneaux
Basel SO1275	—	—	—	24.4 × 32.6	—	—	Baigneaux
Basel SO6587	—	—	—	26.1 × 32.9	—	—	Baigneaux
Basel SO3338	—	—	—	21.3 × 25.9	—	—	Baigneaux
MNHN Ba14	—	—	—	24.1 × 28.8	—	—	Baigneaux
MNHN Ba15	—	—	—	26.8 × —	—	—	Baigneaux
Basel SO2461	—	—	—	—	16.7 × 23.4	—	Baigneaux
Basel SO873	—	—	—	(24) × 32.7	19.7 × 23.4	—	Baigneaux
Mus. no.	p2	p3	p4	m1	m2	m3	Locality
EARLY BURDIGALIAN							
Munich 12297	—	—	—	32.5 × 16.4	—	—	Wintershof
Munich 13565	—	—	—	—	—	21.5 × 18	Wintershof
Basel SO6521	—	—	18.2 × 7	35.0 × 17.2	25 × 18.7	—	Chilleurs
Basel SO282	—	—	—	33.5 × 17.3	—	—	Chilleurs
MNHN Ch1	—	—	—	35.6 × 17.6	—	—	Chilleurs
Basel SO4377	—	—	—	33.4 × 17.9	—	—	Neuville
MEDIAL BURDIGALIAN							
Basel SO3424	—	—	—	39.2 × 20.8	—	—	Artenay
Basel SO3551	—	—	—	35.9 × 19.1	—	—	Artenay
Basel SO3525	—	—	—	—	27 × 21.1	—	Artenay
MNHN Ar12	—	—	—	—	—	× 18.1	Artenay
Vienna, Austria	9.4 × 5	13 × 7.4	18 × 10	31 × 16.6	—	—	Eibiswald
LATE BURDIGALIAN							
Fac. Sci. Bordeaux	—	—	—	—	27.5 × 19.9	—	Captieux
Basel SO3339	—	—	18.7 × 9.4	—	—	—	Baigneaux
MNHN Ba8	—	—	20.6 × 11.5	—	—	—	Baigneaux
Basel SO4906	—	—	21.9 × 12.2	—	—	—	Baigneaux
Basel SO742	—	—	—	34.5 × 17.2	—	—	Baigneaux
Basel SO6729	—	—	—	(35) × 17	—	—	Baigneaux
MNHN Ba18	—	—	—	34 × 17.5	—	—	Baigneaux
Basel SO6589	—	—	—	—	24.8 × 17.1	—	Baigneaux
Basel SO1863	—	—	—	—	25.9 × 17.9	—	Baigneaux
MNHN Ba21	—	—	—	—	20.5 × 13.7	—	Baigneaux
Fac. Sci. Lyon	(12.9)	(15)	(20)	33.3 × 17	23.5 × 17.5	—	La Romieu
Fac. Sci. Lyon	—	—	—	38.0 × 20.8	27.0 × 22.0	—	La Romieu

^a Data from Ginsburg and Telles-Antunes, 1968; Roman and Viret, 1934.

^b() Indicates estimated measurement.

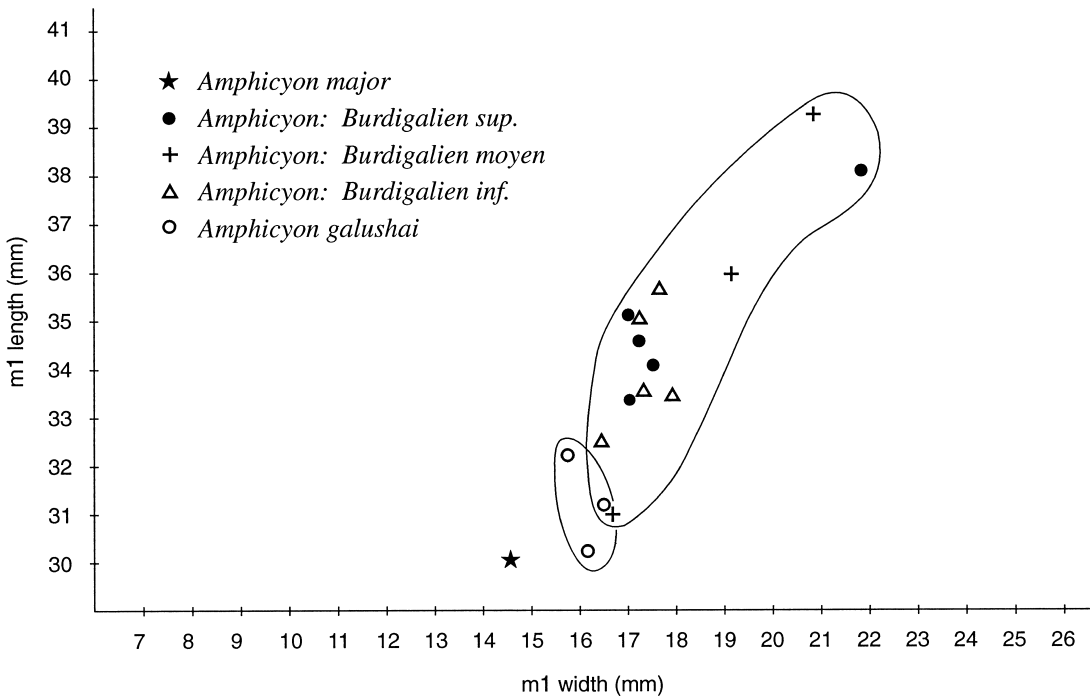


Fig. 4.16. Comparison of m1 dimensions of North American *Amphicyon galushai* and European *Amphicyon*.

Dehm from Wintershof-West: This carnivore is not as large as *A. galushai*, and has a more compressed snout with smaller carnassials and molars, and more narrow m1–m2 (table 4.8). Ginsburg (1999: 116) regarded *Amphicyon bohemicus*–*A. steinheimensis* as a European Miocene lineage, and has placed these two species in the subgenus *Heizmannocyon*. It may be more closely related to the amphicyonine *Cynelos* than to *Amphicyon*.

Before the Hemingfordian North American Land Mammal Age (NALMA), there is no record of *Amphicyon* in the New World. However, prior to the late Aquitanian and Burdigalian in Europe (Neogene mammal zones MN2b–MN3), *Amphicyon* has been reported at several early Aquitanian (MN1) sites in southern France (Kuss, 1962; Ginsburg and Telles-Antunes, 1968; Bonis, 1973). These fossils, placed in *Amphicyon astrei* or *A. cf. astrei*, were found at Garrouch, Hauterive, and Paulhiac. This species is acknowledged as the oldest representative of the genus in Europe (Ginsburg, 1999). Based on mandibles from Paulhiac and Garrouch, illustrated by

Bonis (1973, pl. 8) and by Kuss (1965, fig. 72), this is a conservative species in which the posterior molars have not yet enlarged. A maxilla with P4–M2 (Muséum de Toulouse) from Hauterive (Haute-Garonne) figured by Kuss (1965, fig. 56) is similar in proportions to these teeth in *A. galushai*, indicating that the Old and New World species are at a similar stage of molar evolution; however, the MN1 fossils are much older (22.8–23.8 Ma; Steininger et al., 1996) than early Hemingfordian *A. galushai*.

Ginsburg's (1999) recent summary of European *Amphicyon* identifies *A. astrei* in MN1 as the earliest species in western Europe; later in MN2b, *A. laugnacensis* appears at Laugnac, and continues into MN3; in MN4–5, large *A. giganteus* is the commonly encountered representative of the genus; in MN6, this large species is no longer present, and is replaced by the smaller *A. major* at Sansan and correlative sites. Ginsburg and Telles-Antunes (1968), however, noted a number of isolated teeth in the Burdigalian and early Helvetian that they believed could

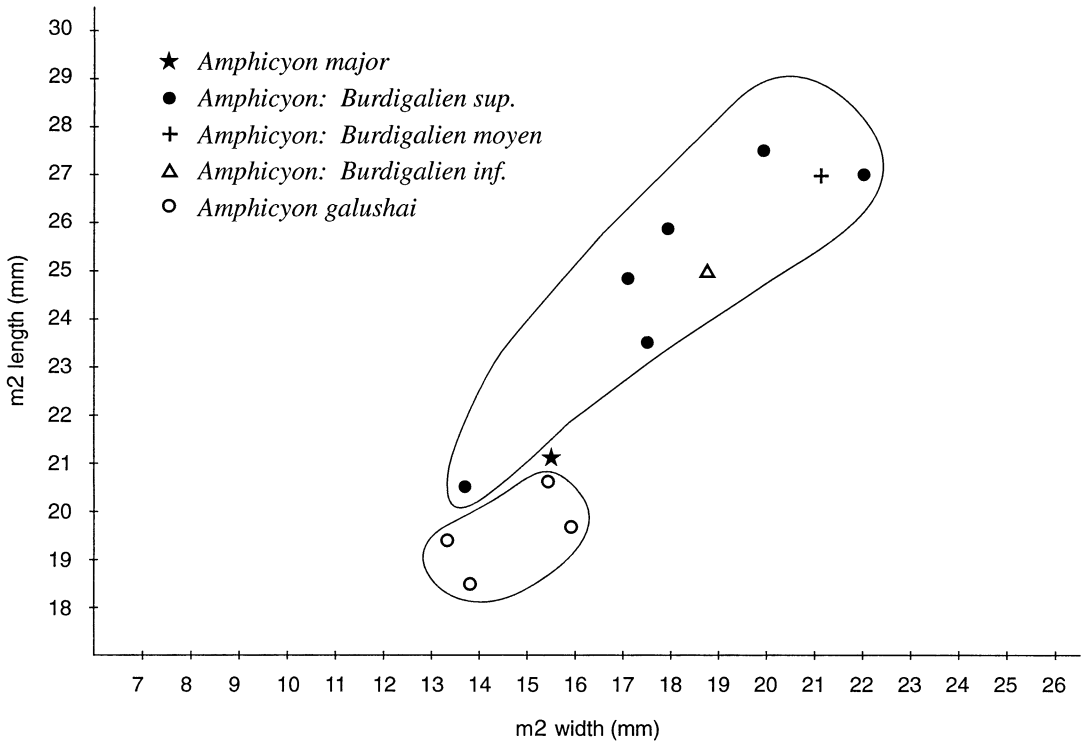


Fig. 4.17. Comparison of m2 dimensions of North American *Amphicyon galushai* and European *Amphicyon*.

represent *A. major*, coexisting with the larger *A. giganteus*. Were the two European species evolved in situ from European Oligocene amphicyonids, or were *A. major* and *A. giganteus* immigrants that entered Europe in the Burdigalian, accompanying the equid *Anchitherium* and proboscideans? Ginsburg concluded that *Amphicyon astrei* was the an-

cestor of the great European amphicyons of the Burdigalian and Helvetian. *Amphicyon astrei* in turn is said to have evolved from a Stampian species of the amphicyonid *Pseudocyonopsis* (Ginsburg, 1966). Thus, these European species of *Amphicyon* are seen as endemic forms, evolved in place in the region.

TABLE 4.8
Dental Measurements (in millimeters) of *Amphicyon bohemicus* from Europe^a

Mus. no.	P1	P2	P3	P4	M1	M2	Locality
—	—	—	—	21.5 × 13.2	—	—	Tuchorice
Munich 12296	6.2 × 4.6	(11.2)	13.3 × 6.6	22.2 × 12.2	22.1 × 27.8	—	Wintershof
Mus. Graz	—	—	11.1 × 5.8	23.0 × 12.8	21.9 × —	17.5 × 25	Feisternitz
Mus. no.	p2	p3	p4	m1	m2	Locality	
GIP 4330	—	—	—	27.7 × 14.1	—	Tuchorice	
Munich 12299, 12300	9.8 × 5.5	13.1 × 6.5	16.7 × 8.4	29.0 × 12.8	19.5 × 12.4	Wintershof	
Mus. Graz	—	—	—	28.2 × 13.6	—	Feisternitz	

^a Data from Kuss, 1965.

Abbreviation: GIP, Geological Institute of Prague.

AMPHICYON—SUMMARY AND CONCLUSIONS: This report summarizes all known fossil material of the earliest North American occurrences of the Old World amphicyonid carnivore *Amphicyon*. These fossils constitute the earliest North American record of this lineage of large predatory amphicyonids (~40–200 kg) that ranged from the eastern seaboard to the Pacific coast, and from southern Canada to Texas, but whose remains are best represented in the central Great Plains. The genus includes at least three species: early Hemingfordian *A. galushai*, new species, late Hemingfordian *A. frendens* Matthew, and early and mid-Barstovian *A. ingens* Matthew. Cranium, dentition, and postcrania of the oldest New World species, *A. galushai*, are similar to these same elements found in the Old World *Amphicyon major* and *A. giganteus*, but demonstrate the existence of a distinct New World lineage of *Amphicyon* that evolved in isolation, spatially disjunct from the European species.

Amphicyon is known for its tendency to enlarge the molars in both upper and lower jaws, and reduce in size yet retain the premolars. The enlarged molars, particularly M2/m2 and M3/m3, become the hallmark of the younger species. By the mid-Miocene in both the Old and New World, these carnivores evolved massive crushing molars, reduced premolars, enormous body size, and a postcranial skeleton indicative of powerful musculature, employed in short bursts of speed to overtake and kill their smaller prey, using their great strength.

Amphicyon galushai is remarkable in showing the initial stage in the broadening of M2–3/m2–3 that preceded the marked molar hypertrophy seen in the later species of North American *Amphicyon*. Its posterior molars are the smallest on record for any species of New World *Amphicyon*.

The discovery of *A. galushai* in early Hemingfordian sediments in northwest Nebraska and north-central Colorado establishes a temporal datum for the earliest appearance of the genus in the New World, a minimum age of ~18.2 Ma, based upon the paleomagnetic determination of Chron C5En (~18.2–18.8 Ma) within the lower Runningwater Formation, northeast of Agate, Sioux County, Nebraska. The temporal range of the

genus could extend from as early as ~18.8 Ma to ~14.2 Ma. The upper range limit is somewhat uncertain; however, the last occurrence of *Amphicyon* in North America is believed to be at Horse and Mastodon Quarry, northern Colorado, of Barstovian age, where *A. ingens* is found together with proboscideans above a tuff dated at 14.3 ± 0.02 Ma (Tedford, 1999: 43, fig. 18A). The genus is last recorded along the Pacific coast at ~14.8 Ma (Skyline Quarry) in the Barstow syncline, California. Although some Barstovian occurrences cannot be reliably dated, there is little probability that *Amphicyon* survived beyond 14 Ma in the New World.

The paratype skull of *A. galushai* from a fluvial channel fill in northwest Nebraska belonged to a mature adult; it is uncrushed and adequately preserves the undistorted skull form, including the basicranium. The basicranium is typical of amphicyonids in having a relatively small ectotympanic bulla and a deep embayment of the basioccipital for the inferior petrosal venous sinus; the basicranium of *A. galushai* is similar in these features to basicrania of the New World *A. frendens* and *A. ingens*. The paratype of *A. galushai* also retains an anatomically significant part of the auditory bulla that shows the highly specialized penetration of the middle ear cavity into the bony external auditory meatus. This is found in all North American species of the genus. It remains to be determined if this accessory hypotympanic sinus occurs in European *Amphicyon*.

Despite similarities in skull form, skeleton, and dentition, the Old and New World species of *Amphicyon* appear to have evolved independently in isolation. The scarcity of adequately preserved Asian fossils definitely attributable to *Amphicyon* prevents insight into the possibility that Asian *Amphicyon* populations connect the New and Old World lineages. Only isolated teeth and a few fragmentary jaws of Neogene amphicyonids have been described from the Siwaliks of southern Asia (Matthew, 1929; Pilgrim, 1932; Colbert, 1935) and from Viet Nam (Ginsburg et al., 1992). Additional teeth and partial maxillae and mandibles are known from China and Kazakhstan, but most are inadequate for confident referral to *Amphicyon* (s.s.). East Asian fossils that may be correctly

referred to *Amphicyon* include the holotype mandibles of *Amphicyon confucianus* (Young, 1937, Shanwang) and *A. ulungurensis* (Qi, 1989, Xinjiang); a maxilla referred to *A. cf. major* from the Tongxin basin; and isolated teeth of *A. palaeindicus* from the Sivaliks (Colbert, 1935, figs. 38, 39).

A continuously maintained geographic connection between Old and New World lineages seems unlikely, however, because of the size discrepancy between New and Old World *Amphicyon* species at various times in the early and mid-Miocene. In Europe, a large species of *Amphicyon* already occurs in the early and mid-Burdigalian (MN3b–MN4) when only the smaller *A. galushai* occurs in North America. An enormous *A. giganteus* is present in Europe in the late Burdigalian–early Helvetian (MN5) when, in North America, *A. frendens* appears in the late Hemingfordian, preceding the huge *A. ingens* of the early to mid-Barstovian. The more modestly built *A. major* probably occurs in Europe at ~15.2 Ma in MN6 (Steininger et al., 1996: 13) at a time in North America when only the very large *A. ingens* is known. *Amphicyon ingens* exists in North America from ~15.9 Ma to at least 14.2 Ma. These populations of *A. ingens* are the final representatives of *Amphicyon* in the New World. We see, then, that the species of *Amphicyon* in North America increase in size from their first arrival in the early Hemingfordian to their last appearance in the mid-Barstovian. But in Europe, a smaller species, *A. major*, succeeds *A. giganteus*, the largest species of the genus to evolve in the Old World, and additional species of *Amphicyon* not recognized in the New World are also present in the Miocene of Europe (Ginsburg, 1999), indicating a more diverse and complex amphicyonid radiation than is evident at this time in North America.

On the northern continents during the early and mid-Miocene, a niche existed for large predatory carnivorans, following the extinction of large creodonts in Eurasia and North America. Amphicyonids were the first carnivorans to respond to this ecological opportunity, rapidly deploying a variety of lineages (amphicyonines, temnocyonines, haplocyonines, daphoenines) to exploit these niches. In the early and mid-Miocene of Eurasia and North America, amphicyonids share this me-

gapredator role with large hemicyonine ursids and a few relict creodonts.

PALEOECOLOGY OF NORTH AMERICAN AMPHICYON

A functional interpretation of the teeth, skull, and postcranial skeleton demonstrates that North American *Amphicyon* was a mid- to large-sized terrestrial omnivore lacking cursorial specializations like those seen in the limbs and feet of living canids; its postcranial skeleton shares a number of features with large living ursids and felids. Ginsburg (1961: 44–45) earlier remarked on this postcranial mosaic. However, these skeletal similarities do not indicate close relationship to either ursids or felids. The postcranial skeletons of large ursids, felids, and amphicyonids are now recognized as independently evolved solutions to the common problems of weight-bearing and efficient locomotion in large carnivores. Slightly different postcranial skeletal patterns developed in these lineages as species within each family attained large body size during the mid- to late Cenozoic.

The skeletal characteristics of North American *Amphicyon* would be compatible with a wooded habitat, whether savanna or riverine gallery forest, and it seems likely that these large carnivores ambushed prey from cover, overpowering them with their size and strength. European species of *Amphicyon* have been similarly portrayed as stalking predators, leaping suddenly on prey from cover, much in the manner of the living lions (Ginsburg and Telles-Antunes, 1968; Bergounioux and Crouzel, 1973; Ginsburg, 1999).

NEOGENE MIGRATION OF LARGE CARNIVORANS FROM EURASIA TO NORTH AMERICA

The first appearances in the geologic record of a number of large mammalian carnivores have been employed as datum points in Cenozoic biochronology (Tedford et al., 1987, fig. 6.3; Webb, 1989; Webb and Opdyke, 1995; Woodburne and Swisher, 1995, figs. 3–5). Such occurrences have been used to clarify the boundaries and temporal spans of the North America Land Mammal Ages (NALMAs). Recent research into the phylogenetic relationships of major groups of Car-

nivora, and new information as to the geologic and geographic distribution of the larger mammalian carnivores, both in North America and Eurasia, have resulted in revision of these earlier data. Figure 4.18 summarizes first and last appearances of selected carnivorans during the Miocene and early Pliocene in North America (relevant late Oligocene data are also included).

First appearances of fossil carnivorans are usually indicated as migrant genera, and are recorded as a first occurrence when present in the rock record at one or more localities. An acknowledged problem with this approach is that carnivores are often among the rarest fossils in collected assemblages of fossil mammals. Because of their place at or near the top of the ecological pyramid, they are commonly represented by smaller populations relative to ungulates and other primary consumers. Thus, their poorer representation in the living fauna may result in less frequent incorporation into thanatocoenoses. A number of first occurrences of Carnivora are based on single fossils.

An equally important factor in assessing immigration–extinction patterns in the fossil record is the pattern of sedimentation in time and space. If sedimentation in local basins is absent from extensive geographic areas within a continent over prolonged temporal intervals, the probability of preserving an immigration event, particularly with regard to rare Carnivora, is low. Consequently, a “first appearance” may occur in the rock record long after the carnivore enters the area. Similarly, an animal may occupy a habitat geographically removed from active areas of sedimentation on a continent well before its presence is recorded by eventual migration into an active sedimentary basin. Despite these difficulties, the pattern of first and last occurrences (fig. 4.18), whether interpreted as immigration and extinction events or simply as the currently identifiable limits of taxon ranges, directs attention to significant turnover episodes in the carnivoran fauna during the North American Neogene. Particularly useful are well-documented presence/absence data for major groups over continent-wide regions, where numerous fossil samples have been collected in a variety of depositional settings over many years; these

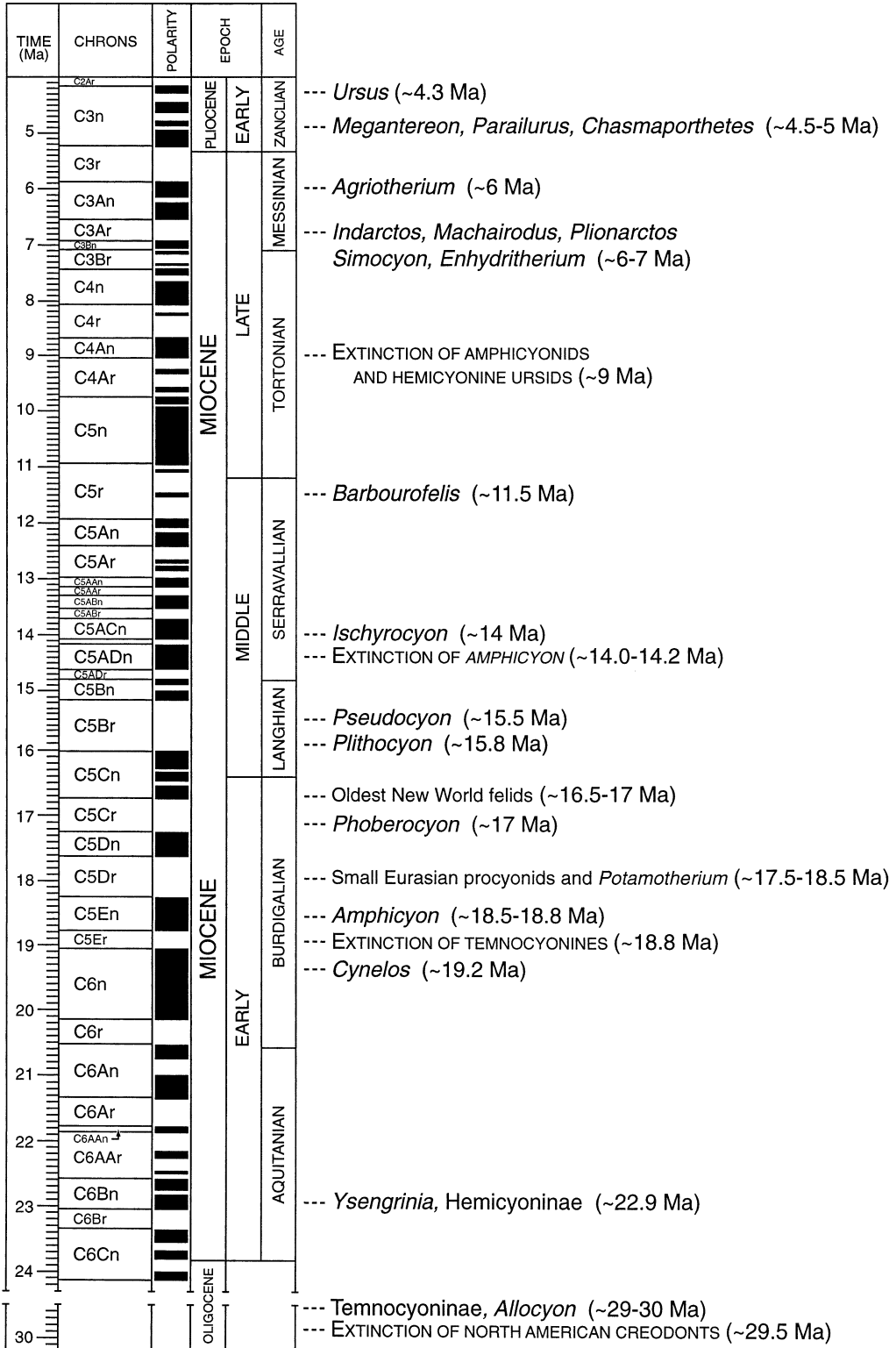
can provide reliable evidence for biochronologic datum events.

Figure 4.18 presents first and last appearance data for selected mid-sized and large carnivorans for the North American late Oligocene to early Pliocene. The initial appearance of *Amphicyon*, revised in this study, now occurs with the earliest Hemingfordian faunas in North America. The extinction of the genus takes place between 14 and 14.2 Ma; the last *Amphicyon* (*A. ingens*) is coeval with the earliest records of Proboscidea in the interior of North America.

The late Eocene to early Pliocene of North America can be subdivided into temporal intervals, each characterized by a particular large carnivoran association (Hunt and Tedford, 1993). Four associations are recognized here: (1) hyaenodont creodonts–nimravid carnivores (~40–24 Ma); (2) temnocyonine amphicyonids–large entelodonts (~29–18.8 Ma); (3) amphicyonine amphicyonids–hemicyonine ursids (~18.8–9 Ma); (4) large felids–ursids–borophagine canids (9–~4 Ma).

Hyaenodonts and nimravids define the late Eocene through late Oligocene interval in North America. Creodonts and nimravid cat-like carnivores, together with less diverse amphicyonids, are the common large carnivores of White River Group deposits in the North American interior during the late Eocene and Oligocene. Hyaenodonts are extinct by ~29.5 Ma, whereas nimravids continue to ~24 Ma and are not certainly recorded in any early Miocene sites.

With the extinction of creodonts in the New World, there is an almost simultaneous appearance of temnocyonine amphicyonids, accompanied by large durophagous entelodonts. Although artiodactyls, entelodonts were scavenger–omnivores that filled a niche later occupied by durophagous hyaenids in the Old World and by “hyaenoid” canids in North America. Temnocyonines initially are small carnivores (~10–15 kg), rapidly increasing in size in several lineages during the late Oligocene and early Miocene. From ~29–30 Ma to 24 Ma, temnocyonines coexist with nimravids, but after ~24 Ma, nimravids are extinct. The date of 24 Ma (approximating the Oligocene–Miocene boundary) marks the beginning of the North American early Miocene “cat gap,” the interval



from ~24 Ma to ~17 Ma when no nimravids or true felids are known in North American Miocene faunas, despite extensive sampling of numerous localities of appropriate age. Late Arikareean temnocyonines are now recognized as the first North American amphicyonids to attain large body size, developed in at least three separate lineages.

From ~18.8 Ma to 9 Ma, the large carnivoran fauna differs entirely from earlier ones. Large amphicyonine amphicyonids (including *Amphicyon*) and hemicyonine ursids now dominate the carnivore assemblages at early and mid-Miocene localities in North America. Almost all genera are immigrants from Eurasia at this time. Amphicyonines (*Ysengrinia*, *Cynelos*) and endemic daphoenine amphicyonids (*Daphoenodon* and a related genus) replace the temnocyonines (last recorded in the Upper Harrison beds, Arikaree Group, central Great Plains), and eventually, the large entelodonts, which become extinct at about ~17.5 Ma.

During the ~18.8 Ma to 9 Ma interval, certain important changes occur in the large carnivoran assemblage. Early in the interval, *Amphicyon* coexists with smaller hemicyonines such as *Cephalogale* and *Phoberocyon*. Later, following the extinction of *Amphicyon* at ~14–14.2 Ma, the large amphicyonids *Pseudocyon* and *Ischyrocyon* are accompanied by *Plithocyon* and a new large hemicyonine genus (Hunt, 1998). At ~9 Ma (Clarendonian–Hemphillian boundary), these large amphicyonids and hemicyonines become extinct, leaving the large carnivore niche open to lineages of felids, endemic canids, and migrant ursids that rapidly increase in body size to occupy that role.

In the North American Hemphillian, a variety of Old World Carnivora make their appearance as immigrants (Tedford et al., 1987). Conspicuous in these faunas are the large ursids *Indarctos* and *Agriotherium*, the smaller tremarctine ursid *Plionarctos*, and

the large felids *Machairodus* and *Nimravides*, joining late Miocene endemic lineages of hyaenoid canids (*Epicyon*, *Borophagus*). These carnivorans mark the ascendance of a canid–felid–ursid assemblage that continues to the present. In the Pliocene (Blancan NALMA) and early Pleistocene (Irvingtonian NALMA), important changes in this assemblage occur: (a) the Hemphillian ursids are replaced by *Ursus* and tremarctine bears (*Tremarctos*, *Arctodus*); (b) the sabertoothed felids are gradually replaced by numerous species of Felinae; and (c) the borophagine canids become extinct and are replaced by the radiation of modern Caninae.

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Fig. 4.18. First and last appearances of selected carnivorans during the Miocene and early Pliocene in North America relative to the appearance and extinction of *Amphicyon*. First appearances (FADs) are indicated by a name and date (Ma); reliably documented last appearances of genera and higher taxa are designated as extinction events. The appearance of temnocyonine amphicyonids and the amphicyonodont *Allocyon*, and the extinction of creodonts, occur in the late Oligocene (~29–30 Ma).

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