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Amphicyonidae

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11 Amphicyonidae

ROBERT M. HUNT, JR.

INTRODUCTION

The Amphicyonidae occur in North America from late Eocene (~40 Ma) to early late Miocene (~9 Ma), a span of 31 million years (Fig. 11.1). In the North American land mammal biochronology, this diverse family extends from the Duchesnean to the end of the Clarendonian and is especially well represented in the Miocene (~5–24 Ma). In the Old World, amphicyonids survive no longer than in North America: The last European records are Vallesian (Dinotheriensande, Mainz Basin, Germany, Kuss, 1965, Tobien, 1980; Vallés-Penédes Basin, Spain, Crusafont-Pairó and Kurtén, 1976), and the last representative may occur at about 9 Ma at Kohfidisch, Austria (latest Vallesian, Beaumont, 1984; Mein, 1989). The group is extinct by 13 Ma in eastern Asia and by about 7 Ma on the Indian subcontinent (Barry and Flynn, 1989). In Africa, amphicyonids are no longer evident after about 11 Ma, but future discoveries may improve this sparse record as Miocene faunas become better known.

Two North American subfamilies (Daphoeninae, Amphicyoninae) have been recognized, but as commonly employed they are in fact arbitrary groupings without well-founded support. Because the Amphicyoninae simply succeeded the Daphoeninae in time, the subfamilies appeared to be evolutionary grades, but the grades in

North America were without substantiated phyletic connection between ancestral and descendant genera. In this chapter I advance a new hypothesis to account for the evolution and geographic distribution of amphicyonids. This hypothesis uses an improved knowledge of biogeography of amphicyonid fossils on the northern continents as a significant new source of information in deciphering their phylogenetic relationships, while at the same time recognizing the lack of reliable synapomorphic traits to ally subgroups within the family. Simply stated, the distribution of amphicyonid fossils in North America and Europe suggests the existence of two separate radiations of beardedogs, both initiated in the late Eocene/Oligocene, the European termed “amphicyonine,” the North American identified as “daphoenine.” Thus I employ the subfamilies as monophyletic groups arising and radiating in different geographic areas, yet sharing a common ancestral population (the stem amphicyonid stock) sometime in the Eocene. The distribution of amphicyonid genera in time in North America and Europe is central to the proposed concept of amphicyonid evolution advocated in this chapter: North American daphoenines are endemic to the New World, first appearing about 40 Ma and continuing to about 17 Ma. European amphicyonines originate about the same time (40 Ma) in the Old World and continue to 9 Ma in Europe, but amphicyonine lineages periodically invade North America as immigrants during

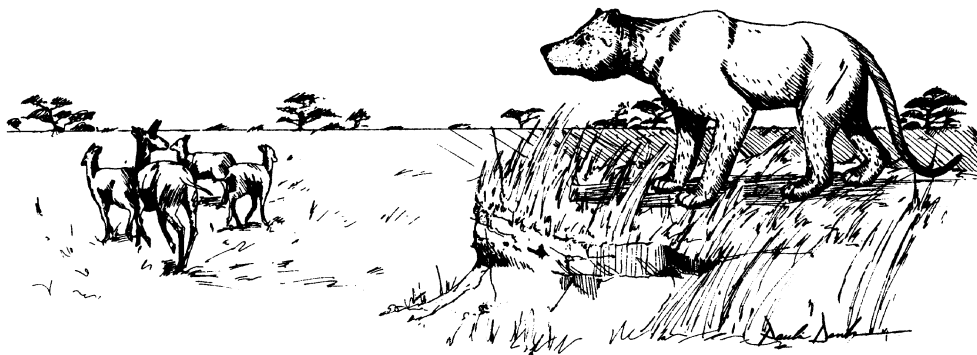


Figure 11.1. The giant amphicyonid *Amphicyon ingens* and its prey, a dromomerycid, mid-Miocene of the North American midcontinent. Restoration by Paula Denham.

the late Oligocene and Miocene. All native daphoenines are extinct by 17 Ma and are replaced by Old World amphicyonines. From this point in time until their North American extinction (~9 Ma), the beardedogs of the New World are all derived from migrant Old World amphicyonines whose roots occur in European lineages.

I also recognize two additional subfamilies, the North American Temnocyoninae and European Haplocyoninae. The dental specializations of these two groups provide distinctive synapomorphic features that allow them to be identified and set apart. New World temnocyonines are plausibly derived from a haplocyonine immigrant in the late Oligocene, although each subfamily evolves its own unique dental morphologies in Europe and North America.

Abundant amphicyonid fossils have been found in both Europe and North America where the family displays a progression from generalized species of small body size to very large forms of a more specialized nature. Amphicyonids are also known from Asia and Africa where their remains are rare but of great interest in demonstrating affinity to European taxa. No amphicyonids are known from South America, and their extinction in North America preceded the interchange of faunas that occurred in the Americas during the Pliocene-Pleistocene.

In North America, the Duchesnean (late Eocene) fossils indicate that the oldest known daphoenine amphicyonids are small carnivores less than 5 kg in body weight, about the size of a swift fox (*Vulpes velox*). Chadronian through Whitneyan (late Eocene-late Oligocene) amphicyonids lack diversity, attain only moderate body size no larger than the coyote *Canis latrans* (~25 kg), and are known primarily from rocks of the White River Group in the midcontinent and Rocky Mountain basins. However, in the Arikarean and Hemingfordian (late Oligocene-early Miocene), daphoenine and amphicyonine amphicyonids of large size (100–200 kg) appear in North America, diversifying to include wolflike and bearlike species that parallel the living canid *Canis lupus* and the ursid *Ursus arctos*. The largest North American species, which are bearlike in their postcranial skeletons, are attributable to *Amphicyon* and occur in the mid-Miocene (late Hemingfordian and early Barstovian). Such huge amphicyonine beardedogs also are recorded from Eurasia and Africa where, together with large hemicyonine ursids, they were the largest terrestrial carnivores of the Miocene.

There are no certain records of amphicyonids or hemicyonine ursids after the Clarendonian (early late Miocene) Land Mammal age in North America. The succeeding Hemphillian (late late Miocene) mammal fauna is dominated by large ursids (*Agriotherium*, *Indarctos*) that appear to fill the vacuum left by the extinction of amphicyonids and hemicyonines, and also by large felids (*Machairodus*, *Nimravides*) and hyaenalike (*Osteoborus*) and wolflike (*Aelurodon*) canids. Within the late Miocene the North American fossil record documents a significant shift in the dominant large land carnivores from the amphicyonid-hemicyonine fauna of the Clarendonian to an *Agriotherium-Indarctos-Machairodus* fauna in the Hemphillian. The disappearance of hemicyonine ursids and amphicyonids is especially striking because they were an integral part of the North American carnivore fauna since the Hemingfordian age, persisting during an interval of about 10 million years.

The amphicyonid fauna of North America changes through a succession of temporal intervals each characterized by a group of

distinctive genera. The transitions between groups occur within relatively brief periods of time. The late Eocene-early Oligocene features the plesiomorphic *Daphoenus* and several archaic beardedogs of small size (<25 kg) that comprise the Daphoeninae: This assemblage shows only a remote relationship to the initial amphicyonine radiation occurring in Europe at this same time. In the late Oligocene and early Miocene the North American record is characterized by temnocyonine amphicyonids (7–50 kg), recognizable by their distinctive dentitions. Temnocyonines are the first beardedogs to attain moderate body size and became extinct in North America by 18 Ma. They are paralleled in Europe by their sister group, the Haplocyoninae, that can be recognized by similar dental specializations.

However, in the late Oligocene and earliest Miocene (~32–22 Ma), only temnocyonine and daphoenine beardedogs are found in North America. Whether this hiatus reflects an actual absence of amphicyonines is uncertain. The 22–32 Ma interval in the Great Plains and in Oregon is represented chiefly by fine-grained volcaniclastic loessic sediments in which carnivores and mammals in general are poorly represented; hence this scarcity of fossils would not be surprising in such relatively barren sediments. At present, however, I favor the concept that the carnivore fauna of North America includes only temnocyonines and endemic daphoenines until the immigration into North America of multiple amphicyonine lineages from 18–22 Ma (early Miocene). This opinion is based on the repeated discovery of temnocyonines and daphoenines in the Great Plains and in the John Day basin and absence of other beardedogs despite over a century of collecting.

In the early Miocene of North America, a new group of amphicyonid genera (amphicyonines *Cynelos* and *Ysengrinia*, daphoenine *Daphoenodon*) appears for the first time. They are notably bigger (~20–100 kg) than earlier species and include the first large North American beardedogs. The amphicyonines are immigrants from the Old World, recognizable in the European record, but not evident as yet in Asia because of a sparser record and the scattered fragmentary nature of the Asian fossils. *Daphoenodon* is a North American endemic. These genera increased in size in North America during the early Miocene, but most became extinct by the end of this interval. In the late early Miocene, these genera are joined by a new and important amphicyonine immigrant, a true *Amphicyon* from the Old World at about 18 Ma.

By the mid-Miocene a characteristic suite of amphicyonids became established in the New World, comprising *Amphicyon*, *Cynelos*, and *Pliocyon*. Together with hemicyonine ursids, these are the common large carnivores of the late Hemingfordian and early Barstovian where some species became enormous (>200 kg). They were abruptly replaced in the late Barstovian and Clarendonian by the terminal North American beardedogs, the *Pseudocyon-Ischyrocyon* group, both genera approaching or attaining body weights of over 100 kg.

As in the case of ursids, an interesting aspect of amphicyonid evolution is the lack of phyletic continuity between North American genera. The North American record is punctuated by the repeated entrance of immigrant stocks from the Old World that persist for a time, then become extinct. Consequently, first appearances and extinctions of amphicyonids can contribute to the recognition of

important biochronologic datum events in the Cenozoic of North America.

DEFINING FEATURES OF THE FAMILY AMPHICYONIDAE

CRANIAL

Figure 11.2 illustrates some aspects of amphicyonid osteology. The structure of the basicranium is diagnostic for amphicyonids in company with key dental features. Amphicyonids for which the basicranium is known possess a primitive arctoid auditory bulla termed Type A (Hunt, 1974a). In contrast to ursids, the number of ontogenetic elements comprising the bulla is uncertain because we lack juvenile skulls demonstrating the nature and number of bulla elements. There is no doubt that an ectotympanic bone is present because it is preserved as a separate element loosely attached to the squamosal in several skeletally plesiomorphic amphicyonids (*Daphoenus*, *Cynodictis*). However, discrete rostral and caudal entotympanics have not been identified in juveniles, and well-preserved basicrania of juvenile amphicyonids are uncommon. There is reason to believe, however, that a caudal entotympanic element was incorporated in

the bulla of *Daphoenus* medial to the ectotympanic: In the genoholotype skull of *Daphoenus vetus* Leidy, the ectotympanic is separated from the petrosal promontorium by a space that would accommodate a cartilaginous caudal entotympanic plate, and in addition there is a conspicuous flange on the medial rim of ectotympanic that must have contacted the dorsal rim of such a plate. Recent new evidence demonstrates the presence of an ossified caudal entotympanic in a temnocyonine beardog: A young adult amphicyonid cranium was discovered in the Upper John Day beds of Oregon (Fingerut et al., 1993) with intact bullae displaying caudal entotympanics fused to the ectotympanic as in Type A arctoid bullae (Hunt, 1974a, Pl. 4), demonstrating that the ontogenetic elements of at least some amphicyonids were assembled as in living ursids.

In all amphicyonids, the ectotympanic is the major element contributing to the bulla, flooring the middle ear cavity. In amphicyonids the bulla does not inflate to any degree during ontogeny, and in this respect is quite similar to bulla development in ursids. We can characterize the bulla of amphicyonids and ursids as the plesiomorphic arctoid type, in which the ectotympanic is able to nearly fully encompass and cover the petrosal promontorium during development. Thus complete enclosure of the middle ear space requires only the addition of bone at the periphery of the ectotympanic as the animal grows to adulthood. This peripheral addition is currently

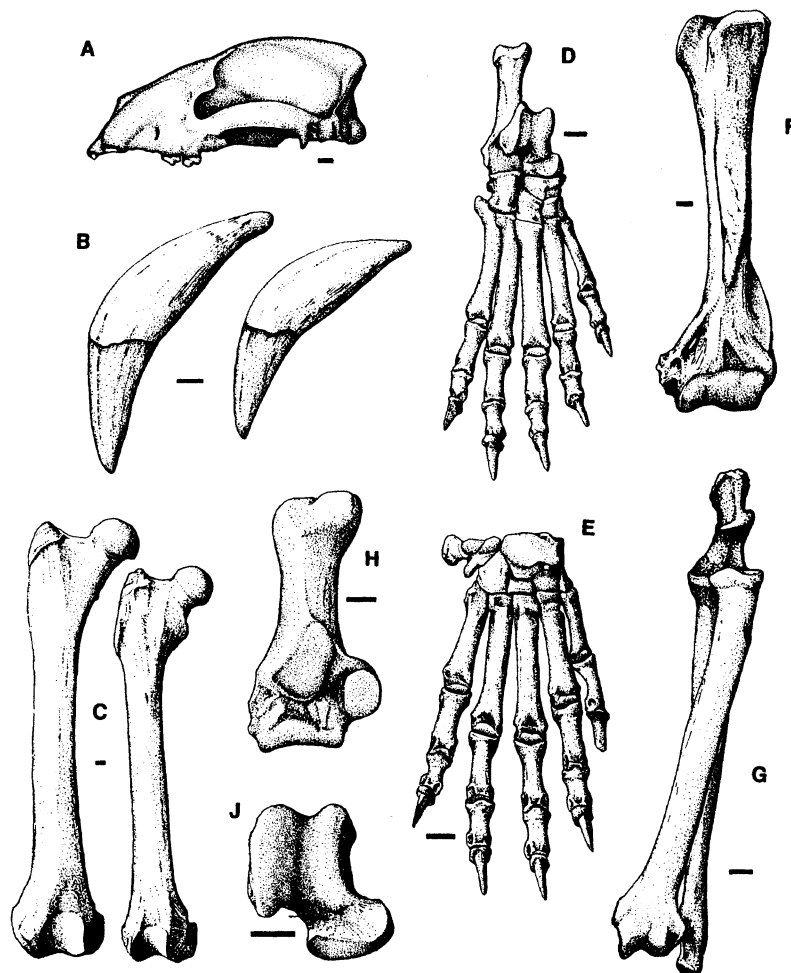


Figure 11.2. Representative skeletal elements of North American Miocene amphicyonids. A. Cranium, *Amphicyon*, early Hemingfordian, Nebraska. B, C. Sexual dimorphism in European mid-Miocene *Amphicyon* upper canines and femora (redrawn from Ginsburg, 1961). D, E. Hindfeet (D) and forefeet (E) of amphicyonids are paraxonic with the weight-bearing axis passing between digits 3 and 4 (*Daphoenodon*, early Miocene, Nebraska). F. Amphicyonid humeri have a strongly developed deltopectoral crest and epicondylar ridges permitting abduction-adduction and weight-bearing of the upper forelimb and strong extension/flexion of the lower limb and manus (*Ysengrinia*, early Miocene, Nebraska). G. In amphicyonids the radius retains the ability to rotate around the ulna allowing pronation-supination of the manus (*Daphoenodon*, early Miocene, Nebraska). H. Calcanea of large amphicyonids (*Ysengrinia*, *Amphicyon*, Miocene, Nebraska) are similar to those of large living ursids, massive, without elongation, suggesting an ambulatory gait and short bursts of speed (temnocyonine and some *Daphoenodon* species evolve elongate slender calcanea and limbs indicative of a cursorial gait). J. Amphicyonid astragali generally lack cursorial modifications such as placement of the distal condyle directly below a strongly

ridged trochlea (*Daphoenodon*, early Miocene, Nebraska). D through H modified from Peterson (1910). Scale bar in all drawings = 1 cm.

believed to occur by means of discrete entotympanic elements, as demonstrated in living ursids (Hunt, 1974a, Pl. 4), and also probably includes a small amount of peripheral extension of the ectotympanic itself. The discovery of the John Day cranium is important in suggesting that the assembly of the amphicyonid bulla closely follows the ursid pattern.

In the amphicyonid basicranium, only a simple ectotympanic crescent is known in Eocene and Oligocene species. A more hemispherical bony bulla that is the product of an ectotympanic with caudal entotympanic(s) appended to its medial and posterior edges appears for the first time in the early Miocene. In Europe such a bulla is first encountered in the amphicyonine *Cynelos* from St.-Gérand, France (Hunt, 1977); in North America in the late Arikarean daphoenine *Daphoenodon* from the den site at Agate National Monument, Nebraska (Hunt, Xue, and Kaufman, 1983); and in the John Day temnocyonine beardog from Haystack Valley, Oregon, presumed to be of Arikarean age (Fingerut et al., 1993). Middle and late Miocene amphicyonid basicrania show that this low hemispherical bulla is retained by the family and is modified in several lineages by the addition of an elongate bony external auditory meatus to produce a low, flask-shaped auditory bulla as in living and many extinct ursids. However, contrary to ursids, several amphicyonid lineages develop an extension of the hypotympanic sinus in the floor of the ectotympanic that invades the bony meatus in order to increase middle ear volume. Expansion of the auditory bulla by relative growth of the caudal entotympanic as seen in canids and most aeluroid carnivorans never occurs in amphicyonids.

Skull form in amphicyonids departs very little from a basic plan in which a short snout is associated with a long postorbital segment (Fig. 11.2), a configuration that reflects the plesiomorphic arcoid skull form. Short-skulled (brachycephalic) amphicyonids are known but are the exception; most genera are long skulled (dolichocephalic). When large body mass evolved in some lineages, the heads of these animals often became disproportionately enlarged. Consequently, the temporal muscle masses can be enormous, resulting in exaggerated development of the sagittal crest in some species (e.g., *Amphicyon ingens*).

DENTAL

The plesiomorphic dental formula of amphicyonids (I3/3, C1/1, P4/4, M3/3) is the same as the basic eutherian formula and is maintained in many amphicyonid lineages throughout their evolutionary history, modified only by premolar loss in derived species and by loss of the M3 independently in several genera. M3 loss is characteristic of an entire subfamily, the Temnocyoninae, and also characterizes the *Ischyrocyon* lineage as well as some species of *Daphoenodon*. Whereas large canines and incisors are retained in all amphicyonids, the premolars can be strongly reduced, particularly P1–3/p1–3. Such premolar reduction is typical of many amphicyonines but not daphoenines or temnocyonines.

Molar modification in amphicyonids follows one of two directions. In daphoenine, temnocyonine, haplocyonine, and plesiomorphic amphicyonine lineages, the molars decrease in size from first to third (M3 can be lost). This dental type parallels modern canids in which M2 is usually slightly smaller than M1 and the basic tri-

bosphenic character of the molars is maintained (parallel evolution of molars and carnassial form in amphicyonids and canids is largely responsible for the erroneous attribution of amphicyonids to the Canidae in earlier studies). In many advanced amphicyonine beardogs the posterior molars are enlarged to produce broad crushing platforms (M1 < M2 > M3). However, in contrast to living ursids, these platforms are not created by adding a talon to the upper molars or by anteroposterior elongation and squaring of the molars. On the contrary, in amphicyonids with enlarged posterior molars the entire tooth is proportionately increased in size so that it appears as an enlarged replica of the original (M2 may become as large or larger than M1, yet its typical plesiomorphic form is retained).

The shearing function of the carnassial pair is maintained in amphicyonids. This is true of even the large bearlike forms, hence contrasts with living ursids in which the shearing function of the carnassials has been lost. In large bearlike amphicyonids the carnassials become heavy and massive, losing the slender, gracile form of the carnivorous lineages, yet shear surfaces are still developed on such teeth. Blunted cusps in older individuals, however, testify to the processing of hard materials in their diet. The retracted protocone diagnostic of ursid carnassials does not occur in amphicyonids that maintain a typical, more anteriorly placed protocone (except in some temnocyonines).

Consequently, an amphicyonid can be identified using a combination of basicranial structure and molar morphology. Beardogs are characterized by a diagnostic upper molar pattern in which the M1 crown is basically triangular (not quadrate), with three principal cusps (paracone, metacone, protocone). The protocone basin does not open to the rear of the tooth and is closed by a postprotocrista; in ursids the molar crowns become quadrate, a metaconule is developed to square the tooth crown, the protocone basin opens to the rear, and the postprotocrista is not developed. The migration of the metaconule to the posterointernal corner of the tooth seen in ursids (Beaumont, 1982) and the posteriorly open protocone basin are useful diagnostic features of ursid molars not seen in amphicyonids. The talons or heels developed on the posterior edge of M2 in ursine bears never occur in amphicyonids.

Temnocyonines are the only amphicyonids to possess enlarged crushing premolars paralleling living hyaenids. No amphicyonids develop hypersectorial carnassial blades as in felids and hyaenids in which metaconid and talonid are lost, but some temnocyonines and *Ischyrocyon* evolve shearing lower carnassials in which the m1 metaconid is lost and the talonid contains only a single trenchant cusp (hypoconid). However, in the temnocyonines such lower carnassials accompany upper carnassials in which the protocone is well developed, even enlarged (in contrast to felids), indicating that these amphicyonids have developed a hybrid carnassial function combining both shearing and crushing in a manner unique to Carnivora.

POSTCRANIAL

Although amphicyonids retain a generalized postcranial skeleton in which modification of the limbs and feet for more cursorial gaits is not developed to the extent seen in specialized runners such as canids, the family nevertheless includes several independent

experiments directed toward improved cursoriality. In North America, the two most prominent were the temnocyonines, which evolved an unusual cursorial adaptation of the forelimbs, and some species of *Daphoenodon*, in which the limbs became elongate and cursorially adapted in a manner similar to large living canids such as wolves. Cursorial amphicyonids are long-limbed, long-footed, digitigrade animals but lack the extreme appression of the metapodials found in living canids.

The largest amphicyonids are in most cases scaled-up Miocene descendants of plesiomorphic Oligocene species and display massive bearlike skeletons characterized by heavier, robust limb elements lacking cursorial adaptations (Fig. 11.2). These large bearded dogs are short footed and presumably plantigrade or at most subdigitigrade just as living ursines. In canids the ability to rotate the radius around the ulna (supination-pronation) is greatly limited by bone-joint configuration, and consequently the lower limb is restricted in its motion to a fore-aft path. In amphicyonids the rotational capability of the radius and the ability to abduct/adduct the massive upper forelimb are maintained; metapodials and digits are not strongly appressed. There is herein a parallel with ursids: The ursine bears are commonly plantigrade, but the hemicyonines are exceptional among ursids in their digitigrade stance; similarly, a number of large amphicyonine amphicyonids are plantigrade, whereas temnocyonines and daphoenines are commonly digitigrade. The carnivorous shearing dentition of hemicyonines logically accompanies digitigrady, and the crushing teeth of most ursines occurs with plantigrady. Among the amphicyonids there is a similar correlation: Shearing carnivorous dentitions are usually found in digitigrade forms, and enlarged crushing molars often accompany short-footed plantigrade species.

Five toes are present in fore- and hind feet; a paraxonic stance (digits 3 and 4 of equal length) is the rule in digitigrade species. Lower limb bones are never fused, always separate mobile elements. Claws are nonretractile, but the intermediate phalanges of amphicyonids are often moderately asymmetric.

Pronounced sexual dimorphism in body size has been documented in amphicyonids. In North America, evidence of large males and smaller females is known from samples of late Eocene *Brachyrhynchocyon dodgei*, Oligocene *Daphoenus vetus* and *hartshornianus*, early Miocene *Daphoenodon superbus*, and large species of middle Miocene *Amphicyon*, all from western Nebraska. Degree of dimorphism is known to increase with body size (Kurtén, 1969), so it is not surprising that the largest amphicyonids display strong dimorphism in teeth and postcranial skeleton. Ginsburg and Telles-Antunes (1968) describe marked dimorphism in large European *Amphicyon*.

SYSTEMATICS

SUPRAFAMILY

Amphicyonids are members of the arctoid Carnivora. This placement is primarily supported by basicranial structure, particularly the

nature of the auditory bulla and petrosal, as well as the dentition. Because amphicyonids are extinct, important biochemical traits and diagnostic features of the soft anatomy (such as absence of caecum and bulbourethral glands of Cowper) cannot be determined. In keeping with other arctoid carnivorans, however, they possess a prominent baculum in males, evidence of strong sexual dimorphism, and the teres fossa on the ventral border of the scapula.

In North America, arctoid carnivorans appear in the late Eocene Duchesnean Land Mammal age where the first representatives are amphicyonids belonging to the genus *Daphoenus* (Dawson, 1980). The oldest sampling of a diverse early arctoid assemblage in the fossil record occurs in the Quercy fissures of France (late Eocene-Oligocene) where dental and cranial material record the early ancestry of amphicyonids, ursids, procyonids, and mustelids, but not canids. The oldest canids occur only in the late Eocene (Chadronian) and early Oligocene (Orellan) of North America, and this geographic isolation of ancestral canids in the New World supports the recognition of a pre-Oligocene split within caniform carnivorans into canoid versus arctoid branches.

In Asia, the oldest arctoids are (1) amphicyonodont ursids found in the Oligocene sediments of Inner Mongolia at Hsanda Gol, and (2) rare records of poorly preserved Oligocene amphicyonids. A possibly latest Eocene amphicyonid is known from the Bai-se Basin of south China, indicating that the family may be of equivalent antiquity in both Asia and Europe. Although there is as yet no evidence that diversity of Asian arctoids approached that of Quercy in Europe, this may be the result of the lack of adequate sampling in Asian sediments.

The Oligocene arctoid record in North America can be explained as the result of occasional immigration of Eurasian arctoid species into the New World. These immigrants spring from a species-rich radiation of small arctoids that developed in Eurasia during the Oligocene and Miocene. It seems likely that Eurasia acts through much of the Cenozoic as the principal staging ground of arctoid evolution, generating a diverse array of lineages, some of which migrate periodically into North America. Amphicyonids, however, appear quite early in the fossil record of both Europe and North America: Amphicyonid skulls with diagnostic basicrania and teeth occur both at Quercy in France and in the oldest levels of the White River Group of the Great Plains. Where the family originated is uncertain, except to say that the Holarctic region must have been the spawning ground for amphicyonids as well as arctoids because these groups are unknown in the early Cenozoic of the southern continents.

INFRAFAMILY

Amphicyonids radiated broadly on the northern continents from their first appearance in the late Eocene until the Miocene when they attained their greatest diversity. This diversity is manifest particularly at the generic level (Figure 11.3). The grouping of genera into higher infrafamilial categories is at best a tenuous procedure.

This situation is due to the maintenance of a conservative skeletal anatomy in most amphicyonids, amounting to the lack of strong

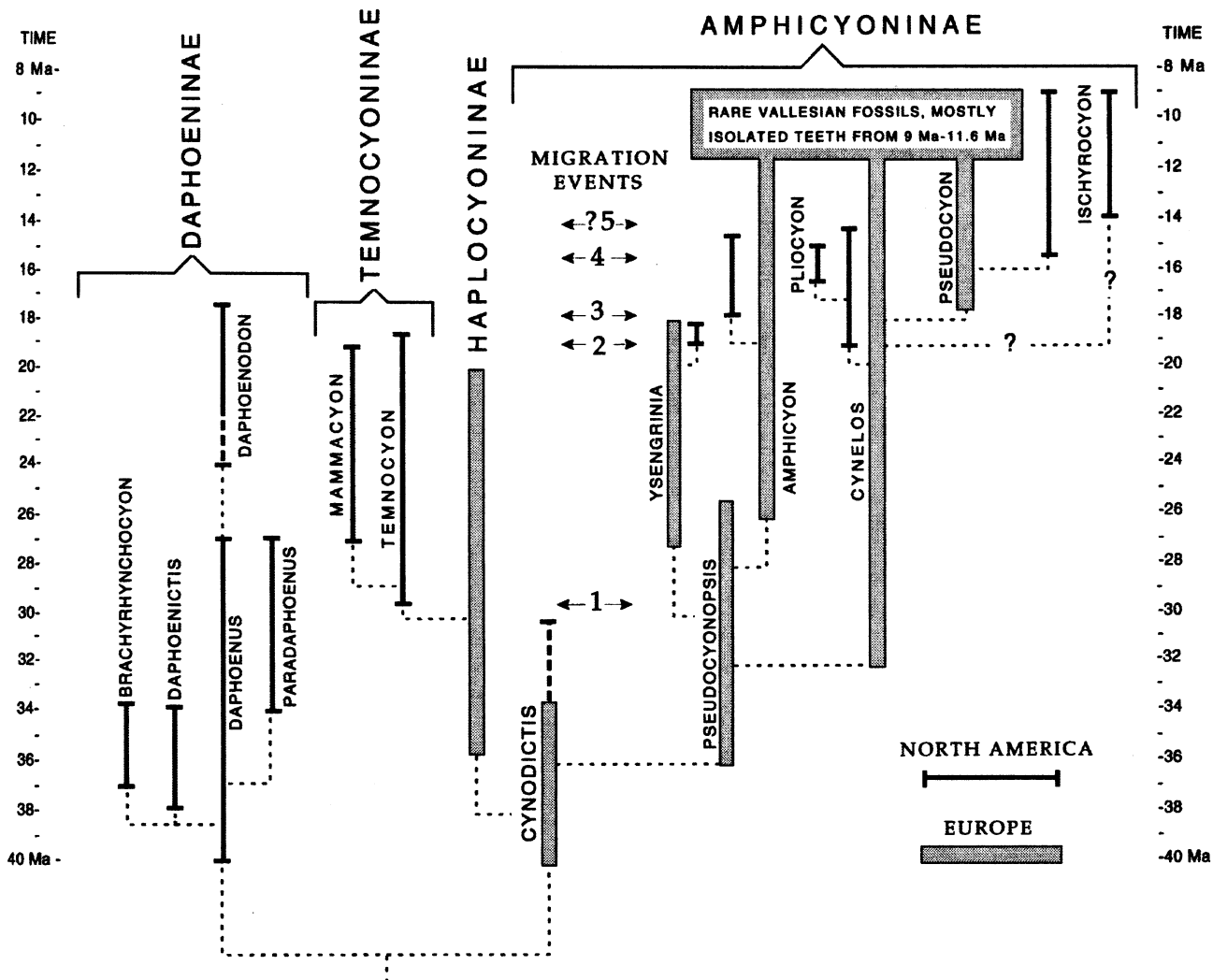


Figure 11.3. Hypothesized relationships of North American and European Cenozoic Amphicyonidae with time ranges and migration events: (1) 29.5 Ma, haplocyonines. (2) 19.2 Ma, amphicyonines *Cynelos*, *Ysengrinia*. (3) 18–18.5 Ma, *Amphicyon*. (4) 15.5 Ma, *Pseudocyon*. (5) ?14–15 Ma, *Ischyrocyon*.

skeletal specializations that would distinguish and set apart such subgroups, and the seemingly endless parallelisms that evolve in dentition and other skeletal traits. This problem has been well articulated by Beaumont (1984) in evaluating the European fossil amphicyonids: “[Their] systematics is badly obscured due to the great monotony in the morphology of the fossil remains, the fragmentary nature of the material (numerous but often isolated teeth) which hinders the definition of the diverse species and their possible variability, and finally because of the great dispersion of the fossils in collections throughout the world.”

However, among amphicyonids, the North American temnocyonines (late Oligocene–early Miocene) can be identified from derived dental features and set apart as a subfamily. Recognized by tall, robust, well-spaced premolars, by loss of M3, and by lingually hypertrophied upper molars with swollen lingual cingula that surround a centrally placed protocone, temnocyonines are closely related to

European haplocyonines, which have similar dental specializations (Fig. 11.3). The most plesiomorphic temnocyonine comes from the John Day beds, Logan Butte, Oregon, and can be derived from European haplocyonines. The European haplocyonine and North American temnocyonine radiations proceed independently, determined by regionally distinct dental patterns; however, the first temnocyonine to appear in North America is probably a late Oligocene Eurasian immigrant.

Previous infrafamilial classifications of amphicyonids have grouped the early North American genera *Daphoenus*, *Daphoenictis*, and *Brachyrhynchocyon* (= *Daphoenocyon*) in a subfamily Daphoeninae and all later genera in the Amphicyoninae. These subfamilies are essentially temporal grades, not clades: Almost no well-founded anatomical evidence has been marshaled in support of them. Daphoenines, however, can be redefined to create a monophyletic group with geographic integrity and some degree of morphological

identity. The similarity among the crania of North American daphoenines suggests they represent a local radiation. None of these genera appear in the Old World. Morphological attributes that ally the group are few because plesiomorphic features are retained and simply scaled upward in size. Nevertheless, some features unite the daphoenines: (1) Premolars do not undergo significant reduction as they do in many amphicyonines; (2) in daphoenines p4 tends to elongation, with a squared posterior border, but in amphicyonines is shorter on average with a more rounded posterior border; (3) digitigrady is common in daphoenines, less so in amphicyonines; (4) M1 tends to be longer along its labial margin in early daphoenines relative to early amphicyonines (compare *Daphoenus* with *Cynodictis*).

Beyond these morphological features, the most important evidence supporting the hypothesis of amphicyonid evolution adopted here is the geographic distribution of the fossils. The pattern of genera on the northern continents is arresting. The restriction of daphoenines to North America and confinement of early amphicyonines to the Old World, followed by the sudden appearance of Old World amphicyonine genera in the Miocene of North America, is interpreted as the principal support for the hypothesis. The early basal or stem amphicyonid stock probably underwent geographic separation in the late Eocene and early Oligocene, and subsequent migrations to the New World only became possible in the late Oligocene and at various times in the Miocene when continental connections and climatic factors became favorable. Why the exchange of species was unidirectional is unexplained, but the fossil evidence of these immigration events is convincing and unequivocal. Independent tests of this hypothesis will occur as the Asian fossil record becomes better established. Currently, Asian amphicyonids have affinities with those of Europe and can be provisionally classified as amphicyonines.

Among the daphoenines, *Brachyrhynchocyon* and *Daphoenictis* are both specialized taxa without descendants, the former a short-faced, broad-skulled carnivoran that probably was in part durophagous, the latter a hypercarnivorous, possibly catlike animal known from a single species. *Daphoenus*, in contrast, is a plesiomorphic genus with multiple species represented by large samples. It is plausibly ancestral to *Daphoenodon* of the North American early Miocene. The small *Paradaphoenus* is regarded as an early offshoot of *Daphoenus*. These five genera constitute the members of a revised subfamily Daphoeninae.

The closest morphological analogues to *Daphoenus* in dentition and cranial features are species of *Cynodictis* from the Quercy fissures of France. Skulls of *Cynodictis* from Quercy represent the oldest European amphicyonid crania, and these show the embayed basioccipital bone and characteristic petrosal, ectotympanic, and molar structure seen in North American *Daphoenus*. The highly specialized *Brachyrhynchocyon* and *Daphoenictis* are unknown in Eurasia and are considered North American endemics. Similarly, in Europe specialized endemic amphicyonine amphicyonids occur with *Cynodictis* in the Quercy fissures. The age of the larger, more advanced beardogs remains in question because some Quercy fissures appear to contain mammals as young as late Stampian or Aquitanian. Some of the more derived larger Quercy amphicyonids may in fact be descendants of more plesiomorphic taxa also found in the

fissures, but a difference in geologic age may have been obscured by combining samples from fissures of different ages in museum collections under the single designation "Quercy."

Consequently, it is possible that a Eurasian amphicyonine amphicyonid radiation stems from early species of *Cynodictis* and that North American daphoenine amphicyonids are derived from early forms of *Daphoenus*. No immigrant taxa entering Eurasia from North America can be presently identified. However, in North America several Old World amphicyonine genera (*Cynelos*, *Ysengrinia*, *Amphicyon*, *Pseudocyon*) appear abruptly in the Miocene record. There are no plausible ancestral forms on this continent for these beardogs. These must be immigrants from Eurasia and are unlikely to be derived from plesiomorphic North American genera such as *Daphoenus* because plausible ancestral species already occur at an earlier time in Europe.

INCLUDED GENERA IN THE FAMILY AMPHICYONIDAE

The locality numbers listed for each genus refer to the localities in Appendix I (for a more detailed listing of localities, see the Key to Fossil Localities at the end of this chapter). The acronyms for museum collections are listed in Appendix III. Because the species-level taxonomy of amphicyonids is in revision at the present time, localities usually are given for genera rather than species.

DAPHOENINAE

Characteristics: Small (<25 kg) to large (100 kg) arctoid carnivorans with plesiomorphic auditory bulla formed by an ossified ectotympanic element with probable cartilaginous entotympanic plate attached by its ventral margin to the medial rim of ectotympanic and by its dorsal margin to the petrosal promontorium (this is the most plesiomorphic bulla yet known among amphicyonids and is also found in European *Cynodictis*); a more advanced bulla occurs in *Daphoenodon* in which the middle ear is enclosed by a rudimentary ectotympanic bulla that may include ossified entotympanics; the bulla is unknown in *Daphoenictis* and *Brachyrhynchocyon* but was probably similar to the *Daphoenus* bulla, based on impressions made by the bulla on the basicranium. Skull dolichocephalic in *Daphoenus* and probably in *Daphoenictis* but brachycephalic in *Brachyrhynchocyon* and *Daphoenodon*; snout relatively short in all genera (considered a plesiomorphic arctoid trait). Dental formula 13/3, C1/1, P4/4, M3/3 for *Daphoenus* and *Brachyrhynchocyon* but molar number uncertain for *Daphoenictis*. M2–3/3 in *Daphoenodon* in which the youngest species lose M3.

The Daphoeninae is considered here as a monophyletic North American endemic subfamily and has been diagnosed in earlier studies (Hunt, 1974b, p. 1032): M2–3 relative to M1 not enlarged in contrast to amphicyonines in which M2–3 are enlarged crushing teeth with amplified surface area; no reduction of premolars; p4 unreduced, often elongate, with squared posterior border; auditory bulla preserved only as an ossified ectotympanic crescent, loosely attached to the skull, without addition of any ossified

entotympanic elements and without lateral prolongation into a bony external auditory meatus (the *Daphoenodon* bulla is evolved beyond the plesiomorphic daphoenine bulla in enclosing the middle ear by means of a hemispherical bony capsule that may include entotympanic elements); lack of expansion of the bulla posterior to the mastoid process; inferior petrosal venous sinus deeply excavated into edge of basioccipital; medial edge of petrosal in only slight contact with margin of basioccipital, not sutured to the basioccipital as seen in canids.

Hough (1948) also diagnosed the subfamily (placed by her at family rank) using plesiomorphic features: generalized "canid" (actually plesiomorphic caniform) dentition; "feline" (= unspecialized) postcranial skeleton; short facial region of skull yet cranium elongate; presence of M3; lack of accessory cusps on anterior premolars. Or she employed traits that depend on body size or sex differences, such as development of the sagittal crest and relative size of the braincase. None of Hough's characters are exclusive to daphoenines, either occurring in amphicyonines or lacking clear definition.

Morphology of the teeth indicates that *Daphoenus* and *Brachyrhynchocyon* are closely related; teeth of *Daphoenictis* appear less like those of the former two genera, but basicranial anatomy, especially the embayed basioccipital, suggests relationship. In *Daphoenus* and *Brachyrhynchocyon* the M1 is triangular to subquadrate with an expanded lingual cingulum posterointernal to the protocone. Three principal cusps (protocone, paracone, metacone) form the apices of the triangle, and both paraconule and metaconule are present as small wedge-shaped cusps at the bases of the paracone and metacone, respectively. The paraconule and metaconule are situated at the labial terminations of the protocristae and are incorporated in them. Because the protocone is placed close to the anterior edge of the M1, the postprotocrista is longer than the preprotocrista. A weak constriction in the postprotocrista lingual to the metaconule may segregate a cusplike segment of the postprotocrista just posterobuccal to the protocone. The protocone basin of the *Daphoenictis* M1, a more derived genus, opens to the rear and is not closed by a postprotocrista; this is a specialization of the sectorial dentition in this carnivore.

M2 in these daphoenines is smaller than M1, subquadrate, with less surface relief. The expression of the para- and metaconules as well as the protocone is subdued relative to M1: The conules in both genera are weakly developed or absent, although in *Brachyrhynchocyon* there are very few specimens with an unworn M2. M2 is unknown as yet in *Daphoenictis* but was probably reduced relative to M1. P4 is a shearing tooth with a prominent protocone and short metastylar blade. In the lower carnassial the paraconid blade is not advanced as it is in canids and amphicyonines; hence the trigonid cusps are more closely grouped. Premolars (except p4) lack developed posterior accessory cusps but are surrounded by distinct cingula.

Old World amphicyonid fossils from Quercy attributed to *Cynodictis* are similar in skull morphology and dentition to the North American *Daphoenus*, suggesting a common origin for amphicyonines and daphoenines in the Eocene. *Daphoenictis* and *Brachyrhynchocyon* are too specialized to give rise to any of the later amphicyonids, and both lineages terminate at the end of the Chadronian.

Daphoenines occur in abundance only in the White River Group of the central Great Plains and northern Rocky Mountains, but a small sample derives from the John Day beds of Oregon, and rare individuals are known from the Tecuya beds of California, the Vieja Group of Texas, the Cypress Hills of Saskatchewan, and the I-75 locality in northern Florida. They are unknown in Europe despite a good amphicyonid record. In Asia, the only known amphicyonid fossils of Oligocene age are a few rare fragmentary discoveries from mid-Oligocene sites attributed to *?Cynodictis* and *Amphicyon* (Russell and Zhai, 1987). This material is too poorly known to warrant comment. Thus, although late Eocene-Oligocene amphicyonids are Holarctic in distribution, little is known about Asian links between North America and Europe; the nature of early Asian amphicyonids and potential migration between the Old and New World prior to the Miocene and the center(s) of origin of the family are not clarified by Asian evidence. However, the marked endemism of European and North American late Eocene-Oligocene amphicyonids argues for absence of migration between the two geographic regions.

***Daphoenictis* Hunt, 1974b**

Type species: *Daphoenictis tedfordi* Hunt, 1974b.

Type specimen: NMC 9205.

Characteristics: Small amphicyonid carnivorans with skull lengths of about 10–12 cm. Dental formula I?/? , C1/1, P?4/4, M?2/3. Recognized by their distinctive dentition (postcranial skeleton unknown), which differs from the species of *Daphoenus* and *Brachyrhynchocyon* in the following features: p2 with prominent posterior accessory cusp; p3 taller yet anteroposteriorly shorter than p4; posterior accessory cusp on p3 well developed; prominent anterior and posterior cingulum cusps on p2–4; premolars bladelike, narrow, with accessory and cingulum cusps producing a leaflike appearance in lateral view; m1 metaconid greatly reduced, paraconid advanced, trigonid much longer than talonid, talonid reduced, with single centrally placed knoblike cusp; m2 with prominent protoconid, reduced paraconid, metaconid absent, talonid with single centrally placed cusp, talonid reduced relative to trigonid; molars more adapted for shearing than in *Daphoenus* and *Brachyrhynchocyon*.

The genus is known from (1) the teeth, either isolated or preserved in jaw fragments, and (2) a posterior cranium including the auditory region.

Lower carnassial length range: *D. tedfordi*, 14.2–16.6 mm (N = 6).

Included species: *D. tedfordi* (known from localities SB44B, CP39B, CP39C, CP43, CP98B or C, NP10B, NP24C).

***Brachyrhynchocyon* Loomis, 1936 (in Scott and Jepsen, 1936)**

Type species: *Brachyrhynchocyon dodgei* (Scott, 1898) (= *Daphoenocyon*).

Type specimen: PU 11422.

Characteristics: Small amphicyonid carnivorans with skull lengths of about 14–17 cm. Skull form exhibits strong

dimorphism, interpreted as sexual: males broad skulled, massive; female skulls narrower, more gracile. Dental formula I3/3, C1/1, P4/4, M3/3. Recognized by brachycephalic skull and distinctive dentition that differs from the species of *Daphoenus* and *Daphoenictis* in having anteroposteriorly short, wide, robust premolars relative to elongate narrow premolars in the latter two genera. In both *Daphoenus* and *Brachyrhynchocyon* the premolars increase in size from p1 to p4, and posterior accessory cusps are developed on p2–4; the posterior accessory cusp of p4 is always prominent, progressively diminishing in size in the anterior direction on p2–3 (in both genera, posterior accessory cusps on p2–3 may be weak to absent in some individuals). Also, in *Brachyrhynchocyon* the principal cusp of p2–4 is more anteriorly placed than in *Daphoenus*; that is, the short *Brachyrhynchocyon* premolars are evolved by apparent reduction of the anterior part of the premolar such that the principal cusp lies near the front of the tooth.

Daphoenictis differs from *Daphoenus* and *Brachyrhynchocyon* in its p2–4 with prominent posterior accessory cusps and p3 taller yet anteroposteriorly shorter than p4; in the latter two genera, p3 is never as tall as p4.

The m1 metaconid remains prominent and unreduced in *Brachyrhynchocyon*, and the paraconid blade is not advanced. The m1 talonid has a prominent hypoconid ridge that dominates the heel; from this ridge the talonid surface slopes downward to the lingual border without development of a strongly basined talonid as seen in *Daphoenus*.

The m2 protoconid and metaconid are equally developed (in *Daphoenus* the protoconid is larger than metaconid), the paraconid low; the hypoconid is expressed as a low ridge sloping internally to a flat talonid surface; there is no entoconid. The talonid is lower than (and the same size or somewhat smaller than) the trigonid. Thus m2 differs only in detail from that of *Daphoenus* but is much different from the derived m2 of *Daphoenictis*.

The genus is known from fossil remains of (1) 5 to 7 skulls, some with associated lower jaws; (2) numerous isolated mandibles and maxillae belonging to 40–50 individuals; and (3) a few postcranial skeletons, indicating a robust, muscular, wolverinelike carnivoran.

Lower carnassial length range: *B. dodgei*, ~13–17.0 mm (N = 32); *B. montanus*, 11.9 mm (N = 1).

Included species: *B. dodgei* (known from localities SB44C, CP39B, CP39C, CP39F, CP39G, CP40A, CP41A, CP42A, CP68B, CP83A, CP83B, CP83C, CP98B or C, CP98C, NP10B, NP29C, NP23C, NP24C, NP24E); *B. montanus* (locality NP24C).

Daphoenus Leidy, 1853

Type species: *Daphoenus vetus* Leidy, 1853.

Type specimen: USNM 658–659.

Characteristics: Very small (*D. hartshornianus*) to small (*D. vetus*) to mid-sized (*D. n. sp.*) amphicyonid carnivorans

with skull lengths of about 14–16 cm, 17–20 cm, and 24 cm, respectively. Skull form and canine teeth dimorphic, interpreted as sexual: males larger, with robust rostrum and canines; females smaller, with more gracile rostrum and canines. Dental formula I3/3, C1/1, P4/4, M3/3. Recognized by dolichocephalic skull and distinctive dentition with anteroposteriorly elongate, narrow premolars (especially P2–3/p2–3) that differ from the brachycephalic skull and short, wide, robust premolars of *Brachyrhynchocyon*. In both *Daphoenus* and *Brachyrhynchocyon* the premolars increase in size from p1 to p4, and posterior accessory cusps are developed on p2–4; the posterior accessory cusp of p4 is always prominent, progressively diminishing in size in the anterior direction on p2–3 (in both genera, posterior accessory cusps on p2–3 may be weak to absent in some individuals). Also, in *Daphoenus* the principal cusp of p2–4 is centrally placed, not anteriorly placed as in *Brachyrhynchocyon*. In *Daphoenictis* the p3 is taller than p4, and p2–4 have much more elaborately developed posterior accessory and cingulum cusps.

The lower molars emphasize the external cusps relative to the internal: The m1–2 protoconid and hypoconid are dominant. The m1 metaconid is prominent, not reduced or retracted relative to the protoconid; the paraconid blade is not advanced (contemporaneous canids have an advanced m1 paraconid). The m1 talonid is basined (no basin in *Daphoenictis* and only a weak to moderately developed basin in *Brachyrhynchocyon*): A prominent hypoconid ridge dominates the heel; the internal face of this ridge slopes downward to a basin bordered internally by a rim that includes the entoconid and adjacent cuspules. The m2 protoconid is usually more developed than the metaconid (in some individuals these cusps are nearly equally developed) and the paraconid low; the anterobuccal corner of m2 is enlarged and the posterior border squared, giving m2 a more quadrate appearance than seen in *Brachyrhynchocyon*. As in the case of m1, the m2 hypoconid is expressed as a low ridge sloping internally to a basined talonid; there is an internal enamel rim formed by a weak entoconid; the talonid is lower than the trigonid. Thus m2 of *Daphoenus* differs only in detail from that of *Brachyrhynchocyon* but is much different from the derived m2 of *Daphoenictis*.

The genus is known from fossil remains of (1) over sixty skulls, many with associated lower jaws; (2) numerous rostra, isolated mandibles, and maxillae; and (3) several postcranial skeletons, indicating in the North American midcontinent (White River Group) a large and small species of digitigrade, gracile, subcursorial arctoid carnivoran. This is the most common genus of North American amphicyonid.

Lower carnassial length range: *Daphoenus* (Whitneyan–early Arikareean, Great Plains), 15.4–18.1 mm (N = 3); (Whitneyan–early Arikareean, John Day), 14.4–18.5 mm

(N = 5); (Orellan), 13–17.1 mm (N = 81); (Chadronian–Duchesnean), 10.9–15.4 mm (N = 14).

Included species: *D. vetus*, *D. hartshornianus*, *D. lambei*, *D. transversus*, *D. socialis*, *D. n. sp.* *Daphoenus* is known from the following localities: Duchesnean (SB44B, CP29D, CP39IIA, NP9); Chadronian (CP39D, CP41A, CP83B, CP83C, CP98C, CP98B or C, NP10B); Orellan (CP40B, CP41B, CP68C, CP84A, CP99A, NP29E, NP50B); Whitneyan localities (CP84B, CP99B); Whitneyan or Arikareean (CC13, CP100II, PN6, PN6C, PN6D).

Comments: The Great Plains sample of *Daphoenus* is almost entirely derived from the White River Group of Nebraska, South Dakota, Wyoming, and Colorado. Sample size is sufficient to recognize a small *D. hartshornianus* Cope and a larger *D. vetus* Leidy. Definition of these species is greatly improved by the larger samples available after decades of collecting by various institutions in the White River beds. In particular, the nature of sexual dimorphism in amphicyonids has been clarified on the basis of these fossils.

In the John Day beds of Oregon there are two identifiable species of *Daphoenus* represented by adequate material: *D. transversus*, a small species, and *D. socialis*, a somewhat larger animal. The first-named is the size of the Great Plains *Daphoenus hartshornianus* Cope; in fact, Cope assigned the holotype rostrum to *D. hartshornianus*, but in 1899 Wortman and Matthew made the rostrum the type of “*Paradaphoenus transversus*”. This animal is not part of the *Paradaphoenus* lineage that comprises much smaller carnivorans (see *Paradaphoenus*, this chapter). It is a *hartshornianus*-sized *Daphoenus* but differs from the Great Plains species in a more sectorial dentition that mimics Oligocene canids. This dentition can be recognized by a more advanced paraconid blade and slightly retracted metaconid of m1, and by the more abbreviated protocone of p4. There also appears to be more of a difference in m2 trigonid versus talonid height. A second larger species of *Daphoenus* includes the holotype mandibles of “*Pericyon socialis*” Thorpe from the Haystack Valley area of the John Day beds. Several additional fragmentary specimens and isolated teeth can be assigned to this *D. vetus*-sized beardog. To this hypodigm I also refer a partial cranium (YPM 10064) with an inflated frontal region and broad snout similar to *D. vetus* but differing sufficiently in dental traits to warrant recognition as a distinct morphospecies, *D. socialis*. Thus two skull morphs of *Daphoenus* in the John Day region correspond to the two morphs found in the Great Plains: *D. socialis* (YPM 10064) has an inflated frontal region and broad snout, whereas *D. transversus* (AMNH 6851, the holotype of Wortman and Matthew) has a more gracile skull with less frontal inflation and a narrower snout. Based on comparison with the larger Great

Plains sample, the two John Day skull morphs are not male and female but more probably two species.

Unfortunately, the specimens of John Day *Daphoenus* were primarily collected in the nineteenth century with only minimal data as to their placement in the John Day succession. As a result we know almost nothing of the relative stratigraphic position of the fossils of the two species. However, recent collections by Ted Fremd and his associates at John Day National Monument have produced teeth of *Daphoenus* that are much younger than the upper range limit of the Great Plains *Daphoenus vetus*, and suggest that the John Day *Daphoenus* persists as a relict lineage in the Pacific Northwest.

The National Park Service John Day collections also demonstrate the existence of a third very large species of *Daphoenus* in the John Day beds low in the stratigraphic section. In Fremd’s Unit C, over 100 m below the Picture Gorge ignimbrite, a maxilla of *Daphoenus* with unusually large teeth was found in Blue Basin at John Day National Monument. This fossil (JODA 1411) establishes this large species of *Daphoenus* low in the John Day sequence; it is equivalent in size to the largest known species of *Daphoenus* from the Great Plains dated at about 28.6 Ma. Thus three species of *Daphoenus* occur in the John Day beds, and future discoveries may establish their stratigraphic range more accurately.

The continuation of the *Daphoenus vetus* lineage into the Whitneyan of the Great Plains is evidenced by several mandibles in the Protoceras channels of South Dakota. These indicate a form larger than Orellan *vetus* but smaller than the terminal Great Plains species of *Daphoenus* known from a single enormous cranium in the uppermost White River Group of Wildcat Ridge, western Nebraska, dated at about 28.6 Ma.

There is also evidence of the small *D. hartshornianus* lineage in the Whitneyan of the Great Plains. Two specimens, a maxilla with M1–2, P4, and alveoli for C–P3 (LACM 16933) and a maxillary fragment with P4–M1 (AMNH 1195b), represent the *hartshornianus* lineage in the Whitneyan of South Dakota. A fragmentary mandible with m1, p2, p4 (AMNH 85880) from the Upper Brule of Nebraska may represent this same species.

The *vetus* lineage ranges from about 35–36 Ma to 28.6 Ma as currently recognized in the Great Plains White River Group. The small *hartshornianus* ranges less certainly from 35–36 Ma to perhaps 30–32 Ma in the Great Plains. Both species are probably descended from the small Duchesnean species and therefore may extend to about 40 Ma. Thus, by combining the dating of Great Plains and John Day fossils, the range of *Daphoenus* in North America extends from about 40 Ma to about 27 Ma.

***Paradaphoenus* Wortman and Matthew, 1899**

Type species: *Paradaphoenus cuspidiger* (Cope, 1878).

Type specimen: AMNH 6852.

Characteristics: Very small amphicyonid carnivorans with skull lengths of about 9–11 cm. Dental formula I3/?3, C1/1, P4/4, M3/3. Very little change in body size and skull proportions from first appearance of the genus in the Orellan to the most advanced species from the John Day beds of Oregon (Whitneyan or early Arikareean) and Arikaree Group of the Great Plains (early Arikareean). The general form of the premolars is much like that of *Daphoenus* but smaller in size. The lower premolars are laterally compressed, blade-like, and are known in only two mandibles (UNSM 26130, AMNH 6852); they become slightly more robust in the John Day species. A prominent posterior accessory cusp is developed only on p4, may be very weakly developed on p3, and is absent on p1–2 in the two available mandibles. In *P. minimus*, the oldest and most plesiomorphic species, the m1 is distinguished from early contemporaneous canids by the closed trigonid in which the paraconid is only slightly advanced. The m1 talonid is basined, the hypoconid and entoconid forming low ridges bordering the basin. The m2 is plesiomorphic in Orellan *P. minimus* in which the trigonid and talonid are of equal size. The protoconid, metaconid, and paraconid form a small equilateral triangle; the talonid surface is slightly lower than the trigonid and is basined, bordered by low ridges formed by the hypoconid and entoconid. In the John Day *P. cuspidigerus* the enlarged M2 causes the m2 trigonid to be crowded to the front of the tooth and the basined talonid is exaggerated, forming most of the occlusal surface. This type of m2 is derived from the plesiomorphic m2 of *P. minimus* in which trigonid and talonid are the same size. A key feature of m2 is its thickened anterobuccal cingulum that forms a protuberant corner on the tooth, similar to the same feature in *Daphoenus*.

Unworn upper molars are preserved in the holotype skull of *P. minimus*: M1 is very similar in form to M1 of *Daphoenus*. Para- and metacone are placed far laterad; hence there is no styler shelf, although a small parastylar region is present. Both para- and metaconules are present, as is the small cuspule anterointernal to the metaconule that develops on the postprotocrista (also in *Daphoenus*). The V-shaped protocone is surrounded by a prominent posteromedially thickened lingual cingulum. M2 is a miniature of M1 even to the presence of tiny para- and metaconules, and the para- and metacone are similarly placed far toward the buccal margin. The upper carnassial shows a reduced protocone that is a hallmark of the genus; P4 is short and robust in both species, not elongate and bladelike, and is always surrounded by a sharply defined cingulum. The upper premolars lack posterior accessory cusps.

The genus is known from fossil remains from two geographic areas: (1) six mandibles and a maxilla from the Orellan, Whitneyan, and early Arikareean of the Great Plains, including a skull (AMNH 39099) from the Orellan of South Dakota that Hough (1948) made the holotype of “*Daphoenus*” *minimus* and (2) two skulls from

the John Day beds of Oregon (AMNH 6852, 6853), one with associated mandibles, originally described by Cope in 1878, both with well-preserved basicrania. AMNH 6852 is Cope’s type of “*Canis*” *cuspidigerus*, which was made the genoholotypic species of *Paradaphoenus* by Wortman and Matthew (1899). I use the species *minimus* for the Great Plains hypodigm, distinguishing it for the present from the John Day species *cuspidigerus* by the more enlarged M2/m2 in the John Day form. No postcranials are associated with this cranial and dental material.

Lower carnassial length range: *P. minimus*, 8.3–9.2 mm (N = 6), *P. cuspidigerus*, 9.3 mm (N = 1).

Included species: *P. cuspidigerus* (known from localities in PN6), *P. minimus* (localities CP84A, CP85, CC99A, CP99A or B, CP99B or C).

Comments: The presence or absence of an M3 has been a persistent problem with this genus and led Cope initially to place the two John Day skulls in different genera. In fact, we can determine that both John Day skulls retain a small M3. The tooth itself is preserved in AMNH 6853, but only a small vestige of the M3 alveolus remains in the genoholotype skull (AMNH 6852). In Great Plains *P. minimus* there is no M3; however, on one side a vestige of an alveolus may be present.

Basicranial structure is distinct from contemporaneous canids. Canids develop a narrow basioccipital bone and a large hemispherical auditory bulla well fused to surrounding skull bones. In *Paradaphoenus* the basioccipital is wide and unstricted because there is no development of an enlarged inflated bulla. In the John Day skulls an auditory bulla is preserved and demonstrates that it is a small, slightly inflated ectotympanic element (it is doubtful if any caudal entotympanic element contributed to the bulla). The petrosal is very similar in form and placement to that of *Daphoenus*. My comparison of *Paradaphoenus* crania with Quercy *Cynodictis* reveals that both show the amphicyonid pattern, but dental features of *Paradaphoenus* differ from all *Cynodictis* known to me in details of P4, M1, and lower molar form, suggesting that *Paradaphoenus* probably evolved in North America.

Daphoenodon Peterson, 1909

Type species: *D. superbus* (Peterson, 1907).

Type specimen: CM 1589.

Characteristics: Mid-sized to large amphicyonids with skull lengths of about 23–27 cm in the oldest species ranging to about 32–34 cm in the youngest. Dental formula I3/3, C1/1, P4/4, M3/3 in oldest species, reduced to M2/3 in youngest. In adequately sampled species, dimorphism is evident. In the sample of *D. superbus* from the Agate National Monument carnivore den site, the males are significantly larger in dental and postcranial dimensions (the large *Daphoenodon periculosis* Cook is simply a male of *D. superbus*).

The premolars of *Daphoenodon* never become reduced

as they do in many amphicyonine lineages. The hallmark of the genus is its wolflike dentition, progressive size increase, and development of cursorial postcranial traits. It is the least “bearlike” of the Miocene amphicyonids, and its terminal species must have been a formidable predator best described as an enormous parallel to the modern timber wolf.

Although premolars are retained in *Daphoenodon*, these carnivorans do not develop enlarged or broadened premolars for durophagy as in hyaenids. Premolars progressively increase in size from anterior to posterior but retain “normal” proportions; p2 and p3 are of lesser height than p4, not taller as in many temnocyonines. The premolars show a prominent posterior accessory cusp only on p4.

The m1 metaconid remains prominent and is never lost, but may be somewhat reduced in size and is slightly retracted relative to the protoconid. The paraconid blade of m1 is advanced; hence the P4 protocone is forwardly placed to make room for the blade. The m1 talonid has a prominent hypoconid ridge that dominates the heel; the hypoconid ridge is laterally placed on the talonid, and internal to the hypoconid is a narrow lingual shelf lacking an entoconid. However, in a large sample from a restricted stratigraphic level (the Agate beardog den site and American Museum-Cook Quarry), we find some exceptional individuals with a basined m1 talonid produced by elevation of a low entoconid ridge, demonstrating that the m1 talonid configuration varies and should not be too rigidly interpreted.

The m2 protoconid and metaconid are both developed (the protoconid is larger than metaconid). The paraconid is a low cusp at the anterointernal corner of m2; it is connected to the protoconid by a C-shaped enamel rim on the anterior margin of the m2 trigonid. The hypoconid is expressed as a low ridge sloping internally to a flat talonid surface; there is no entoconid. The talonid is lower than (and the same size or somewhat smaller than) the trigonid. Thus m2 form is very similar to m2 form in *Daphoenus*. The prominence of the hypoconids of the lower molars and the absence of entoconids illustrates the importance of a mortar-pestle crushing mechanism confined to the molars whereby the prominent hypoconids occlude within deep protocone basins of the upper molars. This relation is typical of the *Daphoenodon* lineage.

The genus is known from (1) 8 skulls, all but one with associated lower jaws; (2) many mandibles, maxillae, isolated teeth, and postcranial bones belonging to over 45 individuals; and (3) a few entire skeletons, the most complete the genoholotype female and a juvenile male, both found in the Agate carnivoran den site by O. A. Peterson in 1905.

Lower carnassial length range: 22.7–33.4 mm (N = 35).

Included species: *D. n.sp. I* (Harrison Formation), lower carnassial length 22.7 mm (N = 1); *D. superbus* (basal Upper Harrison beds), 24.2–27.4 mm (N = 9); *D. n.sp. II* (higher Upper Harrison beds), 25.8–30.6 mm (N = 6);

D. robustum (lower Runningwater Formation), 28.6–29.0 mm (N = 2); *D. n.sp. III* (upper Runningwater Formation), 29.4–33.4 mm (N = 11). *Daphoenodon* is known from localities GC8A, GC8B, GC8C, CP51A, CP52, CP104A, CP104B, CP105.

Comments: *Daphoenodon* differs in its broader skull form from the youngest species of *Daphoenus*, but whether *Daphoenodon* is a direct descendant, hence a North American endemic, is still in doubt. We currently lack fossils linking the last known occurrence of Great Plains *Daphoenus* (at ~28.5 Ma) and the first record of *Daphoenodon* (at ~22 Ma), an interval of 6.5 million years. The teeth of *Daphoenodon* remain basically plesiomorphic as the genus increases in size and dental dimensions throughout its early Miocene range (it serves as an index taxon for the North American early Miocene, ~17–24 Ma).

TEMNOCYONINAE

Characteristics: Small to moderately large arctoid carnivorans with very small, rudimentary auditory bulla formed entirely by the ectotympanic, or with plesiomorphic Type A bulla formed by ectotympanic and bony entotympanics as in living ursids; skull dolichocephalic, frontal region often inflated. Dental formula I3/3, C1/1, P4/4, M2/3. M1 is particularly diagnostic of the subfamily: In its fully evolved form it displays a conical protocone isolated at the center of the lingual half of the tooth, in essence a knoblike cusp centered in a flat expanse of enamel. Surrounding this isolated protocone is a strongly thickened lingual cingulum, so enlarged that the tooth in occlusal view takes on a figure-eight shape, constricted at its midpoint, its buccal part the para-metacone region, its lingual part the protocone region with prominently inflated cingulum.

Temnocyonines (and their sister subfamily in Europe, Haplocyoninae) possess tall, robust premolars; this is particularly true of p2–4 and P2–3, which in older individuals often show strong, apical wear similar to that seen in living durophagous hyaenids in which the principal premolar cusps are worn to flat platforms by contact with hard materials.

The carnassial pair remains functionally prominent throughout the history of the subfamily and is always flanked by a large M1 and smaller M2 in the maxilla (M3 is always lost) and by a prominent m2 and smaller m3 in the mandible. The trigonid of m1 is strongly developed, becoming robust in derived species, and the m1 talonid is occupied by an enlarged hypoconid (there is no entoconid or basined talonid). In some species the m1 metaconid is lost, and this feature is important in the recognition of certain lineages. The buccal cusps of m1–2 are always emphasized: The strong m1 hypoconid is followed in series by a developed m2 protoconid and hypoconid, forming a line of three prominent crushing cusps on m1–2. Some species possess an m2 metaconid but never an entoconid.

An important derivative feature of the group is a digitigrade stance in which the radius and ulna become modified for restricted fore-aft motion, and both metatarsals and metacarpals are elongate. The major weight-bearing axis passes between digits 3 and 4; hence

fore- and hindfeet are functionally paraxonic. The radius-ulna pair is distinguished by an unusual bony stop mechanism in the few skeletons associated with dentitions. This stop limits the movement of the radius around the ulna, preventing any marked degree of pronation-supination. Furthermore, the form of the distal humerus indicates that the forelimb was not everted at the elbow as in the large bear-like amphicyonids but was held in a more vertical alignment as in living cursorial canids. These features produce a more restricted fore-aft movement of the forelimb, suggesting that temnocyonines were cursorially adapted. Digitigrady probably evolved once in the ancestral temnocyonine and may have been an important adaptive feature contributing to their late Oligocene–early Miocene North American radiation.

The early Miocene temnocyonine radiation includes the first amphicyonids to attain moderate to large body size. Basilar lengths of the skulls of the largest individuals of *Mammacyon* and *Temnocyon* attain 30 cm and about 34 cm, respectively (the largest species of *Daphoenus* has a basilar skull length of ~24 cm in the late Oligocene at 28.5 Ma).

Temnocyonines are found only in North America, haplocyonines only certainly identified in Europe. Asian temnocyonines have not been reported, but the dental morphology of *Gobicyon* indicates that it is a member of the temnocyonine-haplocyonine clade and may be derived from a European haplocyonine.

Temnocyonines share a common basicranial structure typical of all amphicyonids in which the basioccipital bone is embayed for an enlarged inferior petrosal venous sinus; the basioccipital embayment is seen in the oldest and most plesiomorphic temnocyonines from the John Day beds of Oregon. The auditory bulla is preserved in two individuals of different lineages (*Temnocyon*, *Mammacyon*), and in both it is an extremely rudimentary ectotympanic bone without any evident enlargement. This rudimentary bulla coupled with the derived dentition is a hallmark of most members of the group.

The most plesiomorphic auditory bulla found in living arctoid carnivores is the Type A bulla that occurs in its most rudimentary state in ursids, ailurids, and some mustelids (Hunt, 1974a). The assembly of the Type A bulla is best documented in living *Ursus americanus*, where it is formed primarily by the ectotympanic with medial and posterior walls contributed by a rostral entotympanic and two caudal entotympanic ossifications. Once these four bulla elements fuse together in the adult, the bulla takes the form of a subhemispherical bony capsule that becomes firmly ankylosed to the surrounding basicranial bones. In one as yet undescribed temnocyonine lineage from the John Day beds, a Type A bulla has evolved and represents the only temnocyonine in which such an advanced bulla has been found (Fingerut et al., 1993). Its significance is in the demonstration that a temnocyonine independently evolved the Type A bulla. In all other temnocyonine lineages the bulla remains a single small ectotympanic bone, wedged into the middle ear region, appearing too small for the space it occupies, and unfused to surrounding bones in adults.

There is no evidence of intercontinental migration of temnocyonines to the Old World. Temnocyonine dental patterns are restricted to North America. However, the origin of temnocyonines may be rooted in the European haplocyonines. Mandibles of Aquitanian

Haplocyon from France show remarkable similarity to the oldest North American *Temnocyon* from Logan Butte, Oregon, yet are somewhat more plesiomorphic in molar pattern, suggesting that *Haplocyon* migrated to North America and established the temnocyonine lineage in the late Oligocene. Despite the evident dental similarity between these subfamilies, my inspection of European fossils indicates that haplocyonines evolved in isolation in Europe, temnocyonines in North America, after sharing an initial common ancestry in the Old World.

Temnocyonines became extinct by about 19 Ma in North America, the youngest known individuals occurring in the uppermost Arikaree Group in the later early Miocene (they are known in the late Arikareean but are absent from Hemingfordian faunas). In Europe the haplocyonines are reported to persist a much longer time until the Pontian of Melchingen (Kuss, 1960), but this occurrence, based on a single tooth, is doubtful. The last reliable occurrence of haplocyonines is in the Les Bailleaux fauna of France (Ginsburg, Huin, and Locher, 1981), placed by Mein (1989) very early in European Neogene mammal zone MN3. This early interval of MN3 is dated at about 20–22 Ma (Steininger, Bernor, and Fahlbusch, 1989) and provides an upper limit to the range of haplocyonines consistent with their occurrence and stage of evolution in North America.

Temnocyon Cope, 1878

Type species: *Temnocyon altigenis* Cope, 1878.

Type specimen: AMNH 6855.

Characteristics: Small to moderately large digitigrade temnocyonines with basilar skull lengths of 18–34 cm. Species increase in body size through time (?Whitneyan through late Arikareean). Largest species are late Arikareean carnivores the size of large wolves. Known basicrania preserving the auditory bulla demonstrate (1) in a plesiomorphic species a rudimentary ossified ectotympanic bulla, and (2) in an advanced species a Type A bulla with fused ectotympanic and entotympanic elements. Distinguished from *Mammacyon* by maintenance of plesiomorphic dental traits in all species of the genus, including the large terminal Arikareean forms: These include retention of metaconid on m1, normally configured shearing P4 without enlarged protocone or massive quality of *Mammacyon*, laterally compressed elongate premolars, absence of elongate m2, and retention of plesiomorphic proportions of the teeth, more so than in *Mammacyon*. Postcranial skeleton known only in two individuals: Limb elements, including metapodials, indicate these are digitigrade cursorial carnivores.

Lower carnassial length range: *T. n.sp. I*, 17.5 mm (N = 1), *T. altigenis*, 19.0–19.7 mm (N = 4), *T. ferox*, 22.2 mm (N = 1), *T. percussor*, 23.4–24.2 mm (N = 2), *T. n.sp. II*, 29.5 mm (N = 1).

Included species: There are about six New World species, confined nearly entirely to the John Day beds of Oregon and the Arikaree Group of the central Great Plains of North America. Several New World species are not presently described but are included in a forthcoming study. The North

American species appear to be grouped in two lineages, one evolving in the John Day region of the northwestern United States, the second evolving in the central Great Plains. *Temnocyon* is known from localities CC9C, CP51A, CP103, CP104A, PN6C or D, PN6F or G, PN6G.

Mammacyon Loomis, 1936

Type species: *Mammacyon obtusidens* Loomis, 1936.

Type specimen: AM 34-41.

Characteristics: *Mammacyon* was originally described by Loomis from a nearly complete skull and partial postcranial skeleton from Arikaree rocks of the Wounded Knee area, South Dakota. Although no mandible was found with the holotype, other lower jaws in the Arikaree Group from South Dakota and Nebraska can be confidently referred to the genus. These fossils establish *Mammacyon* as a dentally more derived taxon than the dentally conservative *Temnocyon*. Species of *Mammacyon* possess an elongate m2 relative to *Temnocyon* and also tend to lose the metaconid of the lower carnassial (which is retained in *Temnocyon*). In the terminal species the premolars become more robust, wider, more massive. Several skulls indicate that the frontal region is strongly inflated, but because of small sample size it is not certain if this is simply a male trait. In addition, the upper carnassial and M1 of *Mammacyon* are specialized for crushing as well as shear: The lingual half of M1 is much enlarged and has a centrally placed isolated protocone and hypertrophied lingual cingulum. This is the first specialized crushing dentition evolved by amphicyonids. Although the upper carnassial still retains an effective shearing blade, the tooth becomes particularly massive and robust, with an enlarged protocone and internal cingulum, and is intended for crushing hard materials in company with the anterior premolars.

Elongate metapodials and limb bones associated with the holotype skull of *Mammacyon* demonstrate that it is long footed and digitigrade. Postcranial bones of two other individuals referred to *Mammacyon* from Arikaree rocks of southeastern Wyoming confirm that *Mammacyon* is a digitigrade lineage with a massive crushing dentition. The late Arikareean species of *Mammacyon* and *Temnocyon* are the largest members of their respective lineages and also the largest temnocyonines to have evolved.

Lower carnassial length range: *M. n.sp. I*, 21.2 mm (N = 1), *M. obtusidens*, 24.3 mm (N = 1), *M. n.sp. II*, 27.8 mm (N = 1).

Included species: *Mammacyon* is known from localities GC8B, GC8A, CP52, CP85C, CP86B, CP102, PN6C or D.

Comments: There is probably a single evolving *Mammacyon* lineage in North America. A small undescribed mandible from the Sharps Formation of South Dakota first shows the specialized dental traits that identify the genus in North America. In the central Great Plains, *Mammacyon* occurs throughout the Arikareean, and this sample includes the

two known skulls and all postcranials; hence the genus is defined by the Great Plains Arikaree hypodigm. A maxilla from the John Day beds (Haystack Valley) constitutes the only firm record of the genus in Oregon, but its exact stratigraphic placement in the John Day sequence is uncertain. The genoholotype, *M. obtusidens*, probably is of mid-Arikareean age, and the larger, more evolved form from the late Arikareean can be regarded as a new species descended from *M. obtusidens*.

AMPHICYONINAE

The subfamily is employed here to include a presumed monophyletic aggregate of genera stemming from the European *Cynodictis*. All Old World beardog genera are included in this category with the exception of haplocyonines. Amphicyonids that migrated in the Miocene to Africa and to southeast Asia are considered amphicyonines (*Amphicyon*, *Cynelos*). The rare beardogs recorded from central and eastern Asia (including China) and the Indian subcontinent also belong to the subfamily. The most commonly encountered amphicyonines exist as long ranging lineages in Europe and include the genera *Amphicyon*, *Cynelos*, *Ysengrinia*, *Pseudocyonopsis*, and *Pseudocyon*. All of these appear abruptly at various points in the Miocene of North America yet are unknown in the Oligocene of the New World. These unheralded arrivals in North American Miocene faunas are interpreted as migration events of importance to Neogene biochronology.

Biogeographic data provide the strongest argument for the validation of the subfamily. Derived anatomical features allying the genera are few due to the marked plesiomorphic dentition and skeleton of amphicyonids. Amphicyonines tend to reduce or lose the premolars, evolve a short p4 with rounded posterior border, enlarge the posterior molars, maintain a short-footed plantigrade to subdigitigrade stance without elongation of the lower forelimb bones, and often are markedly sexually dimorphic.

Ysengrinia Ginsburg, 1965

Type species: *Ysengrinia gerandiana* (Viret, 1929)

Type specimen: None designated, but based on an m2 from Weissenau described by Schlosser (1899) and two mandibles (one with m2) from St.-Gérard described by Viret (1929, p. 120). The m2 was considered by Viret to be particularly diagnostic, and a rostrum with a partial upper dentition was also referred.

Characteristics: Mid-sized to large amphicyonids with a basilar skull length of 31 cm in the only known North American skull, an advanced species. Although no complete European skull is known, an estimate of the basilar length of a single individual represented by a rostrum (Viret, 1929, Pl. VII, Figure 2) from St.-Gérard is 24–25 cm. Skull exhibits strong inflation of the frontal region in both European and North American examples. The North American skull is broad snouted, massive, with expanded frontal region and enlarged canines and is interpreted to be a male; female skulls are presumed to be narrower, more gracile. Sexual

dimorphism is present in both dentition and in postcranial skeleton, based on the large North American sample from the Bridgeport Quarries, Morrill County, Nebraska. Dental formula I3/3, C1/1, P4/4, M3/3.

The genus is recognized by its dolichocephalic skull, distinctive M1–2, and reduced anterior premolars. The mandible is anteriorly deep and massive in some individuals, probably males. In North America, *Ysengrinia* has been found only in the central Great Plains. This is the only large North American amphicyonid with reduced P2–3/p2–3 that occurs in the Arikaree Group before the first appearance of *Amphicyon* in the superjacent Hemingford Group.

The lower carnassial is a massive, robust tooth. The m1 metaconid remains prominent, unreduced to somewhat reduced, and is slightly retracted; the paraconid blade is advanced. The short m1 talonid has a prominent hypoconid ridge that dominates the heel; internal to the hypoconid is a lingual shelf with occasional low tubercles but no strong development of an entoconid.

The m2 protoconid and metaconid are developed, but the protoconid is larger. The paraconid is weak to absent. The short, abbreviated talonid is dominated by a strong hypoconid ridge somewhat labially placed (strongly labially placed in the European *Y. depereti*); there is no entoconid. The talonid is lower than the trigonid.

The genus is known from the remains of (1) about 7–10 individuals from the Agate Monument bone bed and stratigraphic equivalents (basal Upper Harrison), western Nebraska; (2) about 3–4 individuals from the Upper Harrison beds of southeastern Wyoming; and (3) 8 mandibles, 1 maxilla, numerous isolated teeth and postcranial elements of at least 14 individuals from the Bridgeport Quarries, Nebraska.

Lower carnassial length range: all species, 30.0–35.4 mm (N = 24).

Included species: Probably three North American species, as yet undescribed. *Ysengrinia* is known from localities CP51A, CP104A, CP106.

Comments: *Ysengrinia* was first described by Ginsburg (1965) as a European genus and was carefully distinguished by him from *Pseudocyon*. *Pseudocyon* has a differently configured m2 relative to *Ysengrinia*, the former based on a mandible from Sansan and a referred mandible from Ponsan-Soubiran. The m2 of *Pseudocyon* has a trigonid crowded to the front of the tooth, followed by a long talonid with a relatively flat surface; the hypoconid is low and placed far toward the labial border of m2. In *Ysengrinia* the m2 trigonid occupies the entire anterior half of the tooth; the talonid is short but with a low hypoconid also labially placed. The long heel of m2 and low p4 distinguish *Pseudocyon* from *Ysengrinia*. The North American sample of *Ysengrinia* has the m2 structure of European members of the genus, for example, *Y. tolosana* (Basel Museum Pa 951, Paulhiac).

Measurements of North American specimens indicate that the p4 is becoming shorter through time while the m1 becomes larger and more robust. Reduction in anterior premolars also accompanies this trend. In the Bridgeport Quarries sample, dimorphism is evidenced by the presence of both slender, shallow as well as massive, deep mandibles together with short, robust metapodials and limb bones of two size classes. Thus the North American *Ysengrinia* appears to be characterized by large, heavy-bodied males and more gracile, light females, similar in this respect to certain living ursids.

Outside of North America, *Ysengrinia* has been identified only in Europe. The genus was distinguished from *Pseudocyon* by Ginsburg using upper teeth (M1), supplemented by careful distinctions in the lower teeth, primarily m2 (as discussed earlier). Ginsburg based his new genus on “*Pseudocyon*” *gerandianus* Viret, and added to it two other species: *Y. tolosana* from the Aquitanian of Paulhiac and *Y. depereti* from the Burdigalian of Chilleux-aux-Bois. In Europe the skull is known only from a referred rostrum from St.-Gérard (Viret, 1929, Pl. VII). M1 in the skull is unusual, having a pear-shaped form (Ginsburg, 1965). Premolars anterior to the upper carnassial are quite reduced, just as is the p1–3 in Viret’s mandible from St.-Gérard.

Although the European material comprises few specimens, comparison with the much larger North American sample does support a relationship between the two groups of fossils. The North American sample shows the robust m1 with short talonid dominated by a labially placed prominent hypoconid; a short m2 with trigonid comprising the anterior half of the tooth; reduction of upper and lower premolars (except P4/p4); a similarity in P1–3 form between the St.-Gérard rostrum and the only North American skull from the upper Arikaree Group of southeast Wyoming; a low, nearly flat M2 with tonguelike lingual cingulum; a triangular M1, robust, with a thick tonguelike lingual cingulum appended to the posterointernal corner of the tooth.

In the North American sample, many individuals (probable males) possess massive mandibles that are nearly as deep at their anterior end as in the region below the molars: No other North American early Miocene amphicyonid shows this trait. There is also a characteristic placement of two mental foramina close together, high on the side of the mandible, one below the anterior root of p3, the other at a point between the single root of p1 and anterior root of p2.

All North American specimens are from western Nebraska and southeastern Wyoming. Upper Arikaree rocks of Goshen County, Wyoming, have produced the only known complete skull and associated mandible of the genus. It is probably a male with a massive rostrum and mandible, large canines, reduced anterior premolars, an expanded frontal region but only a small braincase. The oldest record of *Ysengrinia* in North America is from the basal Upper Harrison beds at Agate National Monument

and other waterhole bone beds at the same stratigraphic level in northwest Nebraska. It may have been an important scavenger-predator at these waterholes. From higher stratigraphic levels within the Upper Harrison beds, there are only three known occurrences: the associated skull and mandible from Goshen County; isolated teeth and postcrania from a locality east of Spoon Butte; and a partial postcranial skeleton found west of Spoon Butte.

The largest North American sample of *Ysengrinia* is also the largest in the world and comes from the Bridgeport Quarries, Morrill County, Nebraska. This appears to be the last North American occurrence of the genus, includes the largest individuals, and is of probable early Hemingfordian age (the previously mentioned North American occurrences are all late Arikareean). Known only from the Upper Harrison beds and from the Bridgeport Quarries, the estimated range of the genus in North America is from about 18–19.2 Ma.

Cynelos Jourdan, 1862

Type species: *Cynelos lemanensis* (Pomel, 1846).

Type specimen: Skull with associated mandible from Langy, near St.-Gérand, France (mid-Aquitainian); see Ginsburg, 1977, p. 59.

Characteristics: Mid-sized to large amphicyonids with diagnostic upper and lower molars and a bearlike postcranial skeleton in which the metapodials are short in earlier species, somewhat longer in later North American forms. Limbs and feet not elongate as in *Daphoenodon* but rather short, less cursorial. Basilar skull length about 24–27 cm in Aquitainian species of Europe, 30 cm in North American early Hemingfordian species, 33–34 cm in the late Hemingfordian species *C. idoneus*, and 39–44 cm in the terminal North American species *C. sinapius* of early Barstovian age.

Skull form and canine teeth dimorphic: males larger with robust canines; females smaller, with more gracile canines. Dental formula I3/3, C1/1, P4/4, M3/3. Recognized by dolichocephalic skull, narrow rostrum, and characteristic molars in which the M2–3/m2–3 are enlarged relative to M1/m1 yet remain smaller in size when compared to contemporaneous species of North American *Amphicyon*. Premolars are reduced in some forms. The auditory bulla preserved in one of the earliest species (*C. lemanensis*, Aquitainian, St.-Gérand, France, Hunt, 1977) completely encloses the middle ear space and is configured as in the Type A bulla of living ursids (Hunt, 1974a). This is the first European amphicyonid lineage to develop a completely ossified Type A bulla, appearing between 20–23 Ma.

Cynelos in North America and Europe is easily recognized by its teeth: It is the first amphicyonid to enlarge the second and third molars relative to the carnassials and M1. This already occurs in relatively small early Miocene species in Europe, North America, and Africa (basilar skull length, 22–23 cm, *C. lemanensis*, Hunt, 1977). In these early Miocene species the length of M1–M3 is nearly

twice the length of P4, and the enlarged rectangular M2 approaches the size of the more triangular M1. In both early and mid-Miocene *Cynelos* from North America, the M1–3/P4 length ratio is remarkably constant at 1.9–2.0, whereas in North American *Amphicyon* this ratio is 2.3–2.4, indicating the relatively greater enlargement of the second and third molars in *Amphicyon*.

Other dental features of *Cynelos* include a tendency in some species to reduce the size of p3 so that it is the same size or smaller than p2, which does not occur in *Amphicyon*. The slender, elongate mandibles have p1–3 without accessory cusps, p4 with or without a posterior accessory cusp. The premolars are slender, laterally compressed teeth without any enlargement for durophagy; in mid-Miocene species the first premolar may be lost.

The m1 has a medially inflated protoconid with a small metaconid situated on its posterointernal slope. The m1 talonid is long, developed, and dominated by a prominent hypoconid laterally placed in the early Miocene species and more central in the North American mid-Miocene forms. The m1 entoconid is smaller than the hypoconid and may be little developed; an anteroposterior basin is present between hypoconid and entoconid that opens to the rear of the talonid and is not closed by a talonid ridge. The m2 is rectangular, with trigonid cusps crowded toward the anterior end of the tooth, the protoconid slightly larger than metaconid, the two cusps separated by a constriction and often joined anteriorly by a smoothly curving C-shaped crest. The paraconid is absent or vestigial. The m3 is rectangular with two closely apposed roots.

The upper molars have prominent paracone, somewhat smaller metacone, and a distinct but much lower protocone, all surrounding a protocone basin. A small paraconule and often pronounced metaconule are present. A tongue-like lingual cingulum characterizes M1–2. These traits are found in both *Cynelos* and *Amphicyon* so that it is primarily the much larger M2 (and M3) that separates the latter larger bearded dog from *Cynelos*. The terminal species of *Cynelos* in North America (*C. sinapius*) from the early Barstovian of western Nebraska has developed the largest M2 of the lineage relative to M1, but this tooth still does not attain the size found in North American large species of *Amphicyon* (*A. frendens*, *A. ingens*).

The metapodials of *Cynelos* are short as in living ursids, especially in the earlier species, becoming more elongate in the mid-Miocene *C. idoneus*. This contrasts with the uniformly short, massive metapodials of North American and Old World *Amphicyon*.

Lower carnassial length range: *C. sp.* (Agate Monument bone bed), 21.3 mm (N = 1); *C. n.sp. I* (Bridgeport Quarries), 21.0–25.3 mm (N = 12); *C. n.sp. II* (Runningwater Formation), 26.4–27.1 mm (N = 2); *C. idoneus* (Sheep Creek Formation), 25.6–30.2 mm (N = 5); *C. sinapius* (early Barstovian of Nebraska, Colorado, New Mexico, Texas), ~31–39.7 mm (N = 17); *C. caroniavorus* (Thomas Farm), ~15 mm (N = 1).

Included species: Probably six North American species, three as yet undescribed. *Cynelos* is known from localities GC4E, GC8D, NB6B, SB32B, CP75B, CP104A, CP105, CP106, CP108A, CP108B, CP110.

Comments: In North America, *Cynelos* is found in the early and medial Miocene, in Europe in the Oligocene to late Miocene (Ginsburg, 1977), and in the early Miocene of Africa (Schmidt-Kittler, 1987). The African fossils were first named *Hecubides* by Savage (1965), but the fossils from east Africa clearly are immigrant forms of *Cynelos* from Eurasia: *Hecubides* is a junior synonym of *Cynelos*. *Cynelos* is an immigrant to North America and Africa in the early Miocene, appearing almost simultaneously on both continents at about 19–20 Ma. Because of its presence in North America it also must have occupied parts of Asia, but no fossil record yet exists.

Cynelos first appears in North America as a single isolated carnassial (CM 2200, Hunt, 1972) from the water-hole bone bed at Agate National Monument, Nebraska, late Arikareean (19.2 Ma). It is represented by a large sample from the Bridgeport Quarries, Nebraska, early Hemingfordian (~18–18.8 Ma) and also occurs in the lower part of the early Hemingfordian Runningwater Formation, Nebraska. It next appears in the Sheep Creek Formation (*C. idoneus*, late Hemingfordian) and ends in the Olcott Formation (*C. sinapius*, early Barstovian). Nearly the entire North American sample of *C. idoneus* and *C. sinapius* comes from the Snake Creek-Sheep Creek district in Sioux County, Nebraska, and the Pawnee Buttes area, Colorado.

A small species of *Cynelos* (*C. caroniavorus*) occurs at the early Hemingfordian Thomas Farm site in north Florida (Tedford and Frailey, 1976) but is found nowhere else in North America. It is probably allied to the small *C. schlosseri* of Europe.

In Europe, *Cynelos* first occurs in the Quercy fissures (*C. piveteaui*, *C. crassidens*) and in numerous Aquitanian sites of France (*C. lemanensis*, *C. rugosidens*). The Burdigalian species *C. schlosseri* and *C. helbingi* are best known from the Bavarian fissures at Wintershof-West where large samples were described by Dehm (1950), but they are also present in the Orleanian of the Loire Basin (MN3–4, *C. schlosseri-helbingi*; MN5, *C. bohemicus*, Ginsburg, 1989) where the genus extends to upper MN5 (~16 Ma). Some European authors suggest that the lineage may continue as “Amphicyon” *steinheimensis* in MN7, persisting into the late Miocene (Ginsburg, 1977, p. 94).

***Pliocyon* Matthew, 1918**

Type species: *P. medius* Matthew, 1918.

Type specimen: AMNH 17207.

Characteristics: Mid-sized amphicyonids with skull lengths of 29–30 cm (only three crania known, all from Sioux County, Nebraska). Dental formula I3/3, C1/1, P4/4, M2/3 with *en echelon* crowding of premolars common in a short-

ened rostrum, and P3 rotated into transverse alignment in two of the three known crania, p3 likewise turned outward in some mandibles. Frontal region of cranium slightly expanded. Vestigial M3 occurs in some individuals. Strong dimorphism is not evident, males averaging about the same in skull size relative to presumed females. In the upper dentition, I3 is large, I1–2 much smaller. Premolars (P1–3, p1–4) tend to be low and lack anterior or posterior accessory cusps. P4 is small relative to M1 as in *Cynelos*. There is a prominent P4 protocone but no parastyle. M1 is subquadrate with a low protocone connected to very weak meta- and paraconules by low protocristae. M2 is smaller than M1, and its paracone is considerably larger than metacone. The lingual half of M2 is flat with a prominent thick lingual cingulum. The molars are reminiscent of *Cynelos*. The short rostrum observed in the three known skulls is correlated with the length of the upper toothrow, ranging from 87–92.8 mm. The palate is broader than in *Cynelos* despite a relatively shorter skull in *Pliocyon*.

The lower carnassial is robust, wide, with an inflated protoconid and reduced metaconid. Its talonid is as wide as the m2 trigonid and has a dominant trenchant hypoconid placed slightly laterad and an internal talonid shelf without a developed entoconid. The m2 trigonid has a prominent protoconid, slightly lower metaconid, and no paraconid: Only a smooth arcuate C-shaped crest forms the front of the trigonid as in *Cynelos*. The m2 talonid can be squared off or tapered; the hypoconid is the sole cusp and is laterally placed.

Postcranials from the Olcott Formation include slightly elongated metapodials, somewhat longer than those of *Amphicyon*. Its skeleton was robust, slightly elongated in the limbs, but without the heavy and massive elements and short proportions of Sheep Creek and Olcott *Amphicyon*.

Lower carnassial length range: *Pliocyon medius* (early Barstovian, Nebraska), 26.3–31.7 mm (N = 12); (early Barstovian, California), 28.9–31 mm (N = 2); *P. robustus* (Bone Valley, Florida), 33.2 mm (N = 1); *P. sp.* (Sheep Creek Formation, Nebraska), 30.3–~32 mm (N = 2).

Included species: *P. medius* (late Hemingfordian to early Barstovian, Nebraska and California, known from localities NB6C, CP108A, CP108B, CP110, CP111); *P. robustus* (?Barstovian, Florida, locality GC10B).

Comments: *Pliocyon* was recognized and is currently defined almost entirely on the basis of the large sample from the Sheep Creek-Snake Creek District of Sioux County, Nebraska. Rather poor material including several fragmentary mandibles is known from the late Hemingfordian Sheep Creek Formation; however, the genus is firmly established on the well-preserved crania, mandibles, and postcranials collected from various quarries in the Olcott Formation of early Barstovian age, belonging to the “Lower Snake Creek” fauna of Matthew.

Pliocyon also occurs in the Barstow Formation, Mojave Desert, California, where it is known from several mandibles. The genus was also reported from the Bone Valley Formation of Florida (Berta and Galiano, 1984): The mandible on which a new species was based measures larger in various dental dimensions than Great Plains or California *Pliocyon* and may be a larger and/or younger form, but does seem best referred to the genus.

The teeth of *Pliocyon* are similar to those of *Cynelos*. It is likely that *Pliocyon* is a derivative of the *Cynelos* lineage, possibly diverging in the early Hemingfordian.

Pliocyon is unknown in Eurasia or Africa and is regarded as a short-lived endemic North American group confined to the mid-Miocene.

***Amphicyon* Lartet, 1836**

Type species: *A. major* Blainville, 1841.

Type specimen: MP Sa 1.

Characteristics: Mid-sized to very large amphicyonids with skull lengths of 23–25 cm (early Hemingfordian), 37–39 cm (late Hemingfordian), and about 42–52 cm (early to mid-Barstovian). Dental formula I3/3, C1/1, P4/4, M3/3 with reduction of premolar size and height but without loss of premolars. There is no premolar crowding as seen in *Pliocyon*. Marked hypertrophy of posterior molars (m2–3, m2–3), producing the largest such teeth evolved within the family. M1–3 length commonly greater than two times the length of P4 as a result of molar expansion. 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 weak to moderate development of protocone and small parastylar cusp. The lower carnassial has a swollen inflated appearance, always retains a metaconid, and has a wide talonid with prominent, somewhat laterally placed, ridgelike hypoconid. The m2 is rectangular, with trigonid elevated above talonid, protoconid larger than metaconid, and a small vestigial paraconid (the arcuate crest at the anterior end of the m2 trigonid of *Cynelos* is absent). A somewhat laterally placed low hypoconid dominates the m2 talonid. M3/m3 are flat massive teeth with a subdued occlusal topography.

Sexual dimorphism is present, particularly developed in the youngest and largest species. The postcranial skeleton is important to identification of the genus: The limb skeleton is massive and robust, very similar to the limb elements of large living ursids. Metapodials and digits are short, never elongate, and specializations for cursoriality such as lengthened lower limb segments and elongate metapodials are absent. The gait was ambulatory, the limbs and feet with powerful heavy musculature.

Lower carnassial length range: *Amphicyon* n.sp. (early Hemingfordian, Nebraska), 31.2–32.2 mm (N = 3); *A. fren-*

dens (late Hemingfordian, Nebraska), ~33.5–39.8 mm (N = 11); *A. ingens* (early to medial Barstovian, Nebraska, Colorado, New Mexico, California, and Oregon), 36–44.9 mm (N = 20).

Included species: Three North American species, one of these as yet undescribed (early Hemingfordian to medial Barstovian of Nebraska, Colorado, New Mexico, and California, ~14.5–18 Ma in North America). *Amphicyon* is known from localities GC4C, NB6C, NB6D, SB32B, CP75C, CP105, CP108A, CP108B, CP110, PN8B.

Comments: The oldest fossils legitimately attributed to *Amphicyon* are of Stampian age (mid- to late Oligocene) in western Europe (Ginsburg and Telles-Antunes, 1968). In Asia the oldest record of *Amphicyon* is from the early Miocene of Vietnam (Ginsburg et al., 1992). The majority of Asian specimens attributed to the genus need restudy to determine their true relationships. In Africa the only record of *Amphicyon* is in the mid-Miocene Arrisdrift fauna of Namibia (Hendey, 1978) where a magnificent mandible with teeth demonstrates that large species of *Amphicyon* migrated to the limit of the continent, the southernmost point colonized by amphicyonids anywhere in the world.

In North America there is no plausible New World ancestor for *Amphicyon* at its first appearance in the early Hemingfordian of Nebraska at about 18 Ma. This earliest North American species is undescribed, is a probable immigrant from the Old World, and can be compared with early Burdigalian *Amphicyon* from Europe discussed by Ginsburg and Telles-Antunes (1968). They placed the European fossils in *A. giganteus*, a long-ranging European species known from early Burdigalian to early Helvetian. Late Hemingfordian *Amphicyon* is represented by a sample of the large *A. frendens* from the Sheep Creek Formation of Nebraska. Its descendant in the early Barstovian faunas of Nebraska and Colorado is the giant *A. ingens*, the largest of the North American amphicyonids. The youngest fossils of this species in North America occur in faunas from the early part of the late Barstovian (or medial Barstovian) such as the Horse and Mastodon Quarry, Pawnee Creek Formation, Colorado (~14–15 Ma).

These large *Amphicyon* must have been formidable predators, weighing over 200 kg, with massive skulls, robust shearing carnassials, great crushing molars, and powerful limbs capable of short bursts of speed in pursuit of prey. Following the appearance of *Ysenegrinia* in the early Miocene, these are the first large bearlike carnivores to evolve in North America, attaining maximum size in the mid-Miocene. *Amphicyon* was replaced in the late Barstovian and Clarendonian by other large amphicyonids of the *Pseudocyon-Ischyrocyon* group, and they in turn were supplanted by the huge ursids *Agriotherium* and *Indarctos* of the Hemphillian. During the mid-Miocene, *Amphicyon* was accompanied in the central Great Plains by large

species of *Cynelos*, the latter averaging somewhat smaller in size. Both genera are Old World immigrant stocks that reached North America in the early Miocene and became extinct in the mid-Miocene in the New World.

European *Amphicyon* is best known from the genoholotypic species *A. major* from Sansan, France (Ginsburg, 1961). Referred postcranials accompanying the type dentition indicate a carnivore with ambulatory gait, lacking cursorial specializations: short stout metapodials and radius, astragalus and calcaneum, all similar to those elements in North American *Amphicyon*.

Pseudocyon Lartet, 1851

Type species: *P. sansaniensis* Lartet, 1851.

Type specimen: MP Sa 207.

Characteristics: Mid-sized to large amphicyonids with the only known skull having a basilar length of 37 cm (early Clarendonian, Nebraska). Dental formula I3/3, C1/1, P4/4, M3/3 (M3 is retained contrary to terminal forms of *Ischyrocyon*). Sexual dimorphism highly probable. Identified by dental features, especially a diagnostic pattern of wear facets observed on the carnassials and molars produced by vertical shear. In the Old World this has been termed the “thaumastocyonine” pattern and is found in European specimens of *Pseudocyon* (Kuss, 1965). The anterior premolars (P1–3, p1–3) are strongly reduced, to a greater degree than those of *Ischyrocyon*, and this premolar reduction is already present in the geochronologically oldest *Pseudocyon* from North America. The p4 has both anterior and posterior accessory cusps, whereas *Ischyrocyon* lacks the anterior cusp. The m2 trigonid is shifted anteriorly and is elevated above the talonid (this forward shift and elevated trigonid are absent in *Ischyrocyon*). The subrectangular M2 is always smaller than the triangular M1, differing in this respect from *Amphicyon* in which M2 > M1.

No postcranials are certainly associated with dentitions in the North American sample.

The genus is known from (1) a skull without associated lower jaws, and a damaged but associated partial mandible and maxilla, and (2) at least eight mandibles, a few isolated teeth, but no certainly associated postcranial bones.

Lower carnassial length range: 30.9–~40 mm (N = 10).

Included species: In North America there appears to be a single lineage that at present has not been formally named. In Europe a similar situation seems to occur: members of the European lineage are placed in *P. sansaniensis* (Kuss, 1965). *Pseudocyon* is known from localities SB32D, CP110, CP114A, CP114B, CP114D, CP115B, CP116A, CP116B.

Comments: *Pseudocyon* is a European amphicyonid, originally described from Sansan (France), first appearing in zone MN4 and continuing into MN7, hence from about 13–17.2 Ma. It was recognized in North America from amphicyonid dentitions in late Barstovian and Clarendonian

sites of north-central Nebraska that display the characteristic “thaumastocyonine” wear pattern, reduced premolars, and the carnassial and molar morphology of the European specimens. The wear pattern is produced by extremely tall paracones on M1–2 and a tall M1 metacone. In the lower teeth the m1 trigonid and talonid are also high, as is the m2 trigonid. During the bite, the tall m1 trigonid fits into a deep embrasure in front of M1, shearing against the broad internal surface of the upper carnassial. P4 protocone is reduced, and the m1 paraconid cuts a wear groove in its posterior face. The typical “thaumastocyonine” pattern, however, is created by the tall M1 paracone that cuts a wear groove in the anterolateral face of the m1 talonid. Behind this facet the M1 metacone, not quite as tall as the paracone, cuts a prominent wear surface on the anterolateral face of the m2 trigonid (a facet is also cut by the metacone down the posteroexternal corner of the m1 talonid just below the m1 hypoconid). Finally, the tall M2 paracone creates a wear groove on the outer face of m2 between its trigonid and talonid. The elevated massive m1 hypoconid fits firmly into the M1 protocone basin: a dental mortar-pestle device. The high m2 trigonid is focused to an edge formed by its protoconid-metaconid: this edge fits between the posterior border of M1 and anterior border of M2, and the heel of the m2 is applied to the shallow protocone basin of M2. The three primary wear grooves found on the m1–2 are cut by the tall, nearly vertical labial cusps of M1–2 and constitute the essence of the “thaumastocyonine” pattern. This wear pattern is so distinctive that Viret (1929) created the genus *Amphicyonopsis* for an m1 from La Grive that displayed it: the tooth was later assigned to *Pseudocyon* by Kuss (1965, p. 134) and *Amphicyonopsis* placed in synonymy.

There is no doubt that some mandibles with teeth showing the “thaumastocyonine” wear pattern from early Clarendonian sediments of Nebraska (e.g., Lucht Quarry, F:AM 96627) are nearly identical in mandibular and dental morphology to specimens of *Pseudocyon sansaniensis* from Europe (MN7, Ponsan-Soubiran, Kuss, 1965, Figure 78). Upper teeth from early Clarendonian sites in Nebraska duplicate the upper molar of the Ponsan-Soubiran individual, including the tall M1 paracone that creates the principal m1 wear groove. *Pseudocyon* ranges in North America from the early Barstovian Olcott Formation fauna and medial Barstovian Hottell Ranch quarries (UNSM Loc. Bn-12) of western Nebraska to the medial and late Barstovian sites in the Valentine Formation of north-central Nebraska, ending in early and late Clarendonian sites of the Ash Hollow Formation in northern Nebraska. This range is estimated to span an interval from about 15.5–9 Ma.

A problem in the recognition of *Pseudocyon* in North America arises because of the dental and cranial similarity to North American *Ischyrocyon*. *Ischyrocyon* was originally defined using the youngest forms from the late Clarendonian, which are enormous animals with massive shearing dentitions (Matthew, 1902; Matthew and Gidley,

1904). Whereas the large late Clarendonian species is easily recognized, Barstovian and early Clarendonian fossils are sometimes difficult to distinguish from contemporaneous *Pseudocyon*. However, various lines of evidence derived from examination of the large American Museum sample of these amphicyonids, as well as key specimens in the University of Nebraska collections, allow definition of two separate lineages, *Pseudocyon* and *Ischyrocyon*.

The reasons for segregating the two genera are as follows:

- (1) Mandibles with well-preserved dentitions from the Burge Quarry (early Clarendonian, Nebraska) represent both genera: (a) a mandible (F:AM 54225) similar to the genoholotypic mandible of *Pseudocyon* from Sansan, with extreme reduction of p1–3, small p4, deep “thaumastocyonine” wear groove on m1 (made by M1 paracone), and other typical facets present on m2. The m2 trigonid cusps are anteriorly shifted and the talonid is a low, long shelf as in European *Pseudocyon*; (b) a second mandible (F:AM 54212) with p1–4 all present (p2–3 low but well developed), worn m1 without pronounced “thaumastocyonine” wear groove, and a large, broad m2 with longer trigonid than in *Pseudocyon*. This jaw appears to be *Ischyrocyon*. Both animals are old, based on tooth wear, yet in *Ischyrocyon* wear has flattened the m1 talonid and m2; in *Pseudocyon* the m1 talonid remains trenchant, and m2 retains the high anterior trigonid and low talonid. In addition, F:AM 54212 duplicates the morphology of the late Clarendonian giant *Ischyrocyon gidleyi* but is simply smaller.
- (2) A large sample of amphicyonids of a single species derived from the Hemicyon Stratum and Quarry, Barstow Formation, California, by Frick Laboratory field parties, shows a uniform dental morphology of the *Ischyrocyon* pattern, without the features typical of *Pseudocyon*. These fossils occur below a tuff dated at 13.4 +/- 0.7 Ma that occurs above Hemicyon Quarry (Tedford et al., 1987). This sample is an excellent ancestral population preceding in time the Clarendonian *Ischyrocyon* of Nebraska: it correlates well with *Ischyrocyon* from the Valentine Formation of Nebraska (Cornell Dam, Crookston Bridge, and Devil’s Gulch members).

The European time range of *Pseudocyon* (~13–17.2 Ma) slightly precedes the time range of the genus in North America (~9–15.5 Ma). The genus conceivably immigrated to North America about 15.5 Ma. At its first appearance in North America, it occurs at a single early Barstovian site in Nebraska. In the medial Barstovian it is represented by very large carnivores from at least three localities: a huge mandible from the Hottell Ranch quarries (UNSM Loc. Bn-12), Nebraska; a comparably large pair of mandibles from the Espanola Basin, New Mexico (Pojoaque Bluffs); and a partial mandible and enormous proximal femur from Norden Bridge Quarry, Nebraska.

The last North American occurrence appears to be an isolated m1 (F:AM 54232) from the late Clarendonian Xmas-Kat Quarries local fauna of Nebraska (~9 Ma).

In North America the *Pseudocyon-Ischyrocyon* group abruptly replaces the large *Amphicyon* in the 14–15 Ma interval. *Amphicyon* appears to be extinct by 14.5 Ma in North America. This is a striking change in the large carnivoran fauna and occurs during the transition from early to medial Barstovian faunas of the Great Plains region.

Ischyrocyon Matthew and Gidley, 1904

Type species: *I. gidleyi* (Matthew, 1902).

Type specimen: AMNH 10671.

Characteristics: Mid-sized to large amphicyonids with skulls having basilar lengths of 28–36 cm (Barstovian, N = 8) and 34–47 cm (Clarendonian, N = 6). Dental formula I3/3, C1/1, P4/4, M2–3/3 (M3 is lost in many Clarendonian animals). Sexual dimorphism present based on two sizes of teeth at several sites. Identified by dental and cranial features, especially low, robust, unreduced premolars (may be crowded), shearing carnassials in which P4 rotates labiad with increasing age so that the protocone root protrudes out of the palate as an exposed strut, M1 > M2 > M3, M2 subrectangular and more of a flat crushing tooth. The m1 metaconid is gradually lost in time (absent in all late Clarendonian *Ischyrocyon*), and the m1 talonid is eventually dominated by a large centrally placed hypoconid. The m2 possesses a lower trigonid than in *Pseudocyon*, and the trigonid is not crowded to the front of m2 as in the latter genus.

The wear facets observed on the carnassials and molars produced by vertical shear can simulate the “thaumastocyonine” pattern, particularly on m1, but the pattern is not developed as strongly as in *Pseudocyon*. The final wear stages in old individuals produce flat wear surfaces on the m1 talonid and the m2 trigonid and talonid, thereby differing from the “thaumastocyonine” pattern of aged *Pseudocyon*. Although the M1 para- and metacones are tall as in *Pseudocyon*, the m2 para- and metacones are not as tall as in that genus. The terminal Clarendonian form of *Ischyrocyon* has a large robust skull with shortened basicranial region (thus distinct from *Amphicyon* and *Cynelos*), expanded frontal region, and a broadened snout with incisors arranged in an arc. The I3 is enormous, nearly as large as the canine. In *Pseudocyon* the upper canine has a thin, sharp posterior ridge, and the tooth itself is laterally compressed; the *Ischyrocyon* canine is without the sharp posterior ridge and is more rounded in cross-section. The plesiomorphic amphicyonid dentition is simply enlarged in *Ischyrocyon* without the development of the widened crushing molars of large *Amphicyon*. Large hypotympanic sinuses occur in the floor of the auditory bullae of *Ischyrocyon* as in *Amphicyon* and *Cynelos*, which is a parallel development in these large amphicyonids.

Ischyrocyon ranges in time from small forms from the Hemicyon Stratum of the Barstow Formation, California,

and the Norden Bridge fauna of the Valentine Formation, Nebraska, to the huge animals of the Gidley Horse Quarry in the Clarendon beds, Texas. Its temporal span is approximately 14–9 Ma. These are the youngest well-sampled amphicyonids in North America. In the late Barstovian and Clarendonian, *Ischyrocyon* and *Pseudocyon* are the principal amphicyonid lineages in North America. A smaller animal as yet undescribed comes from this same time interval but is known from only two specimens. No certain records of beardogs have been documented in the Hemphillian.

The genus *Ischyrocyon* is known from (1) numerous skulls: of particular note is the Barstovian sample from the Hemicyon Stratum, Barstow syncline, California, and a Clarendonian sample from (a) the Ash Hollow Formation of northern Nebraska and southern South Dakota, and (b) the Clarendon beds, Texas. Some skulls are accompanied by associated mandibles; (2) over thirty mandibles, many isolated teeth, and postcranial elements.

Lower carnassial length range: Hemicyon Stratum sample, 27.3–31.5 mm (N = 15); Crookston Bridge and Devil's Gulch members of Valentine Formation, 29.5–35 mm (N = 6); Burge member of Valentine Formation, 33.6–40.2 mm (N = 7); late Clarendonian sites, Texas, Nebraska, South Dakota, 38.6–46.1 mm (N = 10); late Clarendonian Ricardo fauna, California, 44.0 mm (N = 1).

Included species: In North America there is a single lineage, *I. gidleyi*, ranging from the medial Barstovian to the late Clarendonian, based on the holotype skull and partial skeleton described by Matthew. *Ischyrocyon gidleyi* could be considered as a single lineage extending back in time to the first appearance of the genus in North America. Whether it is necessary to name the earlier part of the *Ischyrocyon* lineage as a separate species is an open question. The genus is unknown outside of North America. *Ischyrocyon* is known from localities NB6D, NB6E, NB7B, NB27II, SP2, CP90A, CP114B, CP114C, CP114D, CP115B, CP116A.

Comments: An *Ischyrocyon* was first described from a partial mandible from northwest Nebraska named "Aelurodon" *meandrinus* by Hatcher (1894). I follow Webb (1969) in considering Hatcher's species a nomen dubium due to the fragmentary state of the teeth. Although it is evident that the fossil is probably *Ischyrocyon*, the jaw could not be used to define a species within the genus. Therefore, "Dinocyon" *gidleyi* (AMNH 10671) becomes the genotypic species, based on a skull and partial skeleton described by Matthew (1902). The genus itself is based on a juvenile mandible with nearly complete dentition from the Little White River drainage of South Dakota, AMNH 10802, the holotype of *I. hyaenodus* Matthew and Gidley (1904). The species *gidleyi* has priority over *hyaenodus* for this large late Clarendonian beardog. "Pliocyon" *walkerae* Johnston and Christian (1941), based on a skull from the Clarendon beds, Texas, is also a synonym of *Ischyrocyon*

gidleyi. In addition, *Hadrocyon* Stock and Furlong (1926) from the Ricardo fauna, California, is a junior synonym of *Ischyrocyon*.

Ischyrocyon and *Pseudocyon* share a similar skull form, including a common molar morphology, broad rostrum and frontal region, and abbreviated basicranium. Both genera also have developed a massive, united mastoid/paroccipital process. The ancestry of *Pseudocyon* probably lies in *Cynelos*: both genera share a derived m2 morph in which the trigonid is crowded to the anterior end of the tooth. The earliest North American *Ischyrocyon* also has molars and carnassials like those of *Cynelos*, but it lacks the "crowded" m2 trigonid of *Pseudocyon*. The origin of *Ischyrocyon* is uncertain but may lie in an early form of North American or Asian *Cynelos*. Late Barstovian *Ischyrocyon* from Nebraska shows a pronounced correspondence in its dentition to the contemporaneous European *Cynelos steinheimensis* from Germany (MN7, ~13.4 Ma).

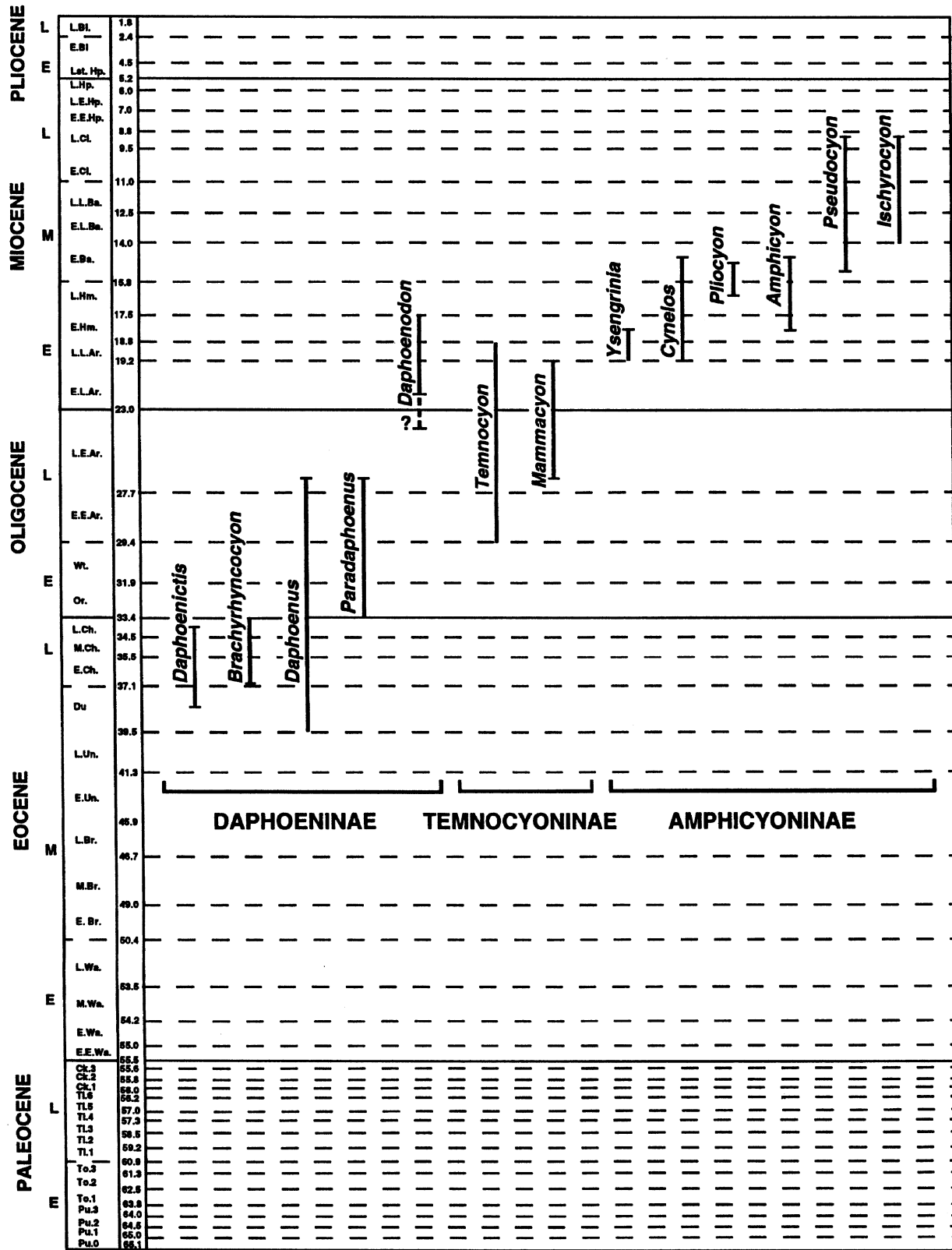
It is striking that the North American amphicyonids of the late Barstovian and Clarendonian are carnivores with enlarged plesiomorphic shearing dentitions, in essence hypercarnivores, and are not the large hypocarnivorous beardogs with crushing molars typical of the late Hemingfordian and early Barstovian interval (*Amphicyon*, *Cynelos*). The replacement of the large crushing-toothed beardogs by the seemingly more dentally plesiomorphic *Pseudocyon-Ischyrocyon* group remains unexplained. However, these large Clarendonian amphicyonids are succeeded in the Hemphillian by large ursids (*Indarctos*, *Agriotherium*) which must have adopted much the same niche among the large predatory Carnivora as utilized by the great beardogs.

In the Old World, amphicyonids survive no longer than in North America: the last European record is about 9 Ma at Kohfidisch, Austria (Beaumont, 1984). The family is apparently extinct by 13 Ma in eastern Asia and by about 7 Ma on the Indian subcontinent (Siwaliks). In Africa, amphicyonids are not found after about 11 Ma, but future discoveries may establish the survival of relict species as in the Siwaliks.

In Europe the youngest amphicyonids are Vallesian species documented primarily by isolated teeth (Kuss, 1965; Beaumont, 1984): (1) huge carnassials and enlarged crushing posterior molars referred to *Amphicyon*; (2) smaller molars reminiscent of *Cynelos*; and (3) occasional M2s that call to mind M2 in *Pseudocyon* and *Ischyrocyon*, which is transversely wide and anteroposteriorly narrow, yet smaller than M1. These teeth suggest that large hypercarnivorous beardogs much like the *Pseudocyon-Ischyrocyon* group also existed in Eurasia in the Vallesian interval but are poorly known.

BIOLOGY AND EVOLUTIONARY PATTERNS

The 30-million-year history of amphicyonids demonstrates their longevity as a viable group of predatory carnivorans (Figures 11.3, 11.4).



Bl.=Blancan, Hp. = Hemphillian, Cl.= Clarendonian, Ba.= Barstovian, Hm.= Hemingfordian, Ar. = Arikarean, Wt. =Whitnean, Or.= Orellan, Ch. = Chadronian, Du.= Duchesnean, Un. = Uintan, Br. = Bridgerian, Wa. = Wasatchian, Ck. = Clarkforkian, Tl. = Tiffanian, To. = Torrejonian, Pu. = Puercan.

Figure 11.4. Temporal ranges of North American amphicyonid genera.

They first appeared on the northern continents, spreading southward into Africa and southeastern Asia in the early Miocene, but failed to enter South America due to their extinction before the establishment of a land connection between the Americas in the Pliocene. The earliest species are animals of small body size, less than 20 kg. Progressive size increases are evident in most lineages, culminating in medial and late Miocene carnivorans exceeding 200 kg.

The replacement of amphicyonids in the late Miocene of Europe and North America by large ursids, felids, and canids may be nearly synchronous at about 9 Ma. Relict species survive into the latest Miocene in south Asia (7 Ma) and perhaps Africa. There is no reliable Pliocene record of the family anywhere in the world.

Feeding preferences of beardogs must have ranged widely from carnivorous to omnivorous and would have been adjusted to the size of prey based on the average size of the beardog. The strong sexual dimorphism, particularly for the larger species, may indicate that the males were polygynous and wide ranging. Postcranial skeletons demonstrate that locomotor patterns differed, based on

adaptive features of limbs and feet. Two broad skeletal categories appear to have evolved from the generalized amphicyonid postcranial skeleton found in *Daphoenus* and other early species: (1) Some lineages (daphoenines, temnocyonines) emphasized cursorial adaptations: elongation of lower limb segments, limitation of ability to pronate/supinate the forelimb, and elongation of the feet including appression of the metapodials; (2) others maintained the proportions of the plesiomorphic postcranial skeleton yet scaled its dimensions for large body size, resulting in a massive, heavily muscled, bearlike skeletal frame (amphicyonines).

In contrast to living ursids, amphicyonids never entirely lose the shearing function of the carnassials, most maintaining a plesiomorphic arctoid dentition in which shear is focused at the carnassial locus and crushing/shearing are accomplished by postcarnassial molar teeth. Dental reduction in amphicyonids is commonly restricted to loss or size decrease of the premolars. Scavenging of carcasses was probably within the domain of many amphicyonid species; whether some of these animals favored such a life mode is not known from the fossil evidence.

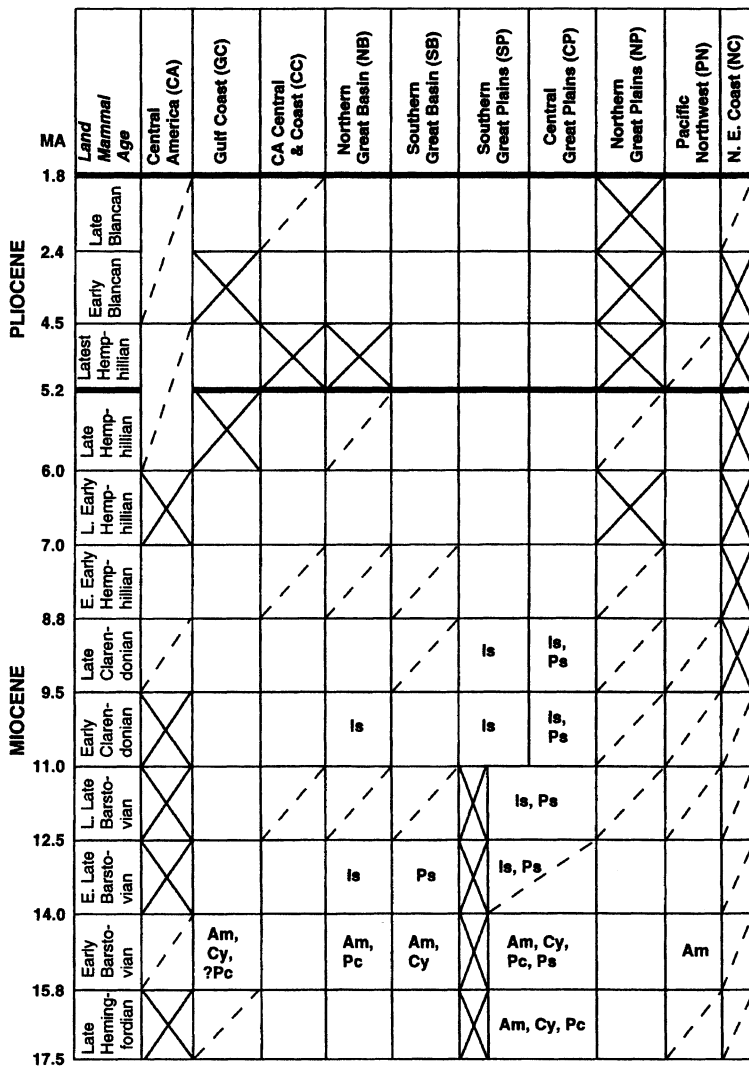


Figure 11.5. Biogeographic ranges of North American amphicyonid genera. A "box" (for a particular time period in a particular biogeographic region) that has a cross through it means no fossil localities are known for that time period from that area; a single dashed line through the box means only scant fossil information is available (usually only a single, small, locality). Key: Daphoeninae are in roman type: Br = *Brachyrhynchocyon*, Dd = *Daphoenodon*, Di = *Daphoenictis*, Ds = *Daphoenus*, Pd = *Paradaphoenus*. Temnocyoninae are in italics: Ma = *Mammacyon*, Te = *Temnocyon*. Amphicyoninae are in boldface: Am = *Amphicyon*, Cy = *Cynelos*, Is = *Ischyrocyon*, Pc = *Pliocyon*, Ps = *Pseudocyon*, Ys = *Ysengrinia*.

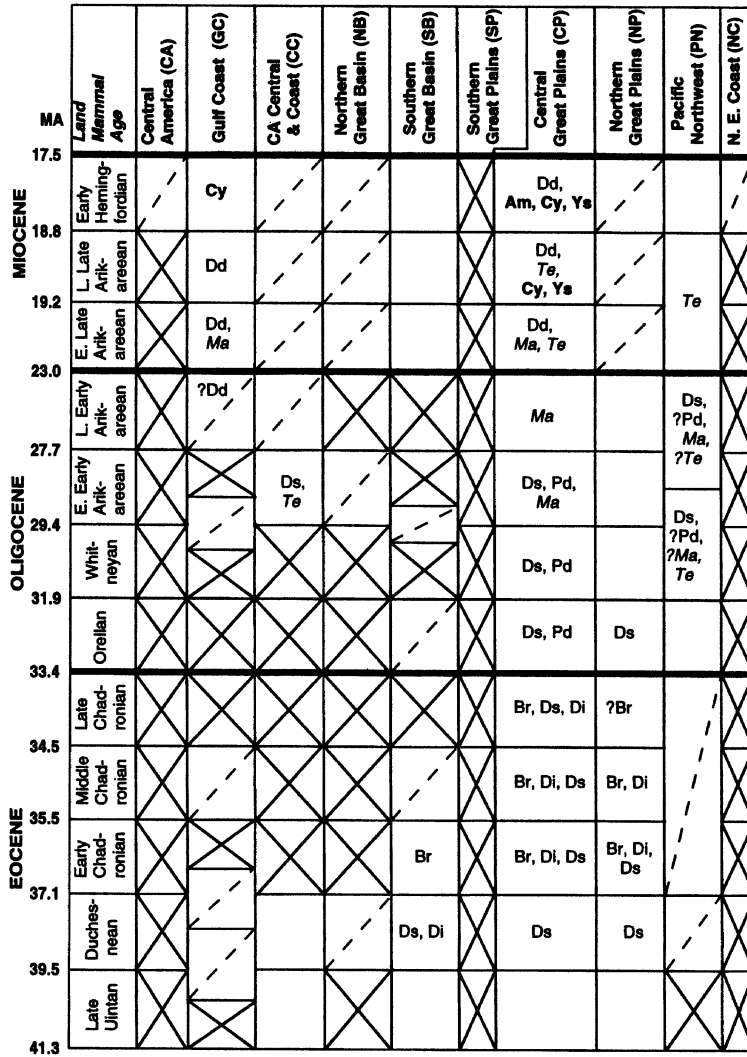


Figure 11.5. (Cont.)

The European Oligocene radiation of amphicyonids produced distinct species not seen in North America; similarly the less species-rich North American Oligocene radiation is marked by its own endemic taxa (Figure 11.5). Despite this, the strong similarity in cranial anatomy between *Daphoenus* and *Cynodictis* is evidence of the unity of the family and their descent from a common ancestor at some time in the Eocene. Most Miocene amphicyonids in Europe can be traced directly into Oligocene European species, demonstrating the continuity of these lineages on that continent (the amphicyonine radiation). As the Asian record improves, one would predict a diverse amphicyonine fauna that may or may not be diluted to some degree by New World daphoenines. But in North America the early amphicyonid record is dominated by daphoenines and temnocyonines, and amphicyonines are absent. Then, in the early Miocene, when only a single daphoenine lineage (*Daphoenodon*) remains in North America, typical Old World amphicyonine genera appear almost simultaneously in the North American midcontinent. This apparent movement of amphicyonids to the New World in the early Miocene

is followed in the later Miocene by additional amphicyonine migration events (Figure 11.3).

The influx of amphicyonines into North America is not matched by invasion of the Old World by North American species. Thus the abrupt appearance of amphicyonid and ursid carnivores in North America during the Miocene epoch seems to mark a series of important migration pulses from Eurasia, a unidirectional movement of arctoid carnivores in which earlier species are periodically replaced by new arrivals during the Neogene. North America seems incapable of evolving its own large arctoid carnivores in the Miocene, relying at times of faunal turnover on resupply from the arctoid homeland of Eurasia.

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Appendix: Key to fossil localities

Numbers in parentheses indicate the unified localities for the entire volume listed in Appendix I.

Duchesnean (*Daphoenus*)

1. Wagon Bed Formation, Badwater Loc. 20, Fremont Co., Wyoming (CP29D)
2. Wagon Bed Formation, Badwater Wood Locality, Fremont Co., Wyoming (CP29D)
3. West Canyon Creek, Beaver Divide, Fremont Co., Wyoming (CP39IIA)
4. Cypress Hills Formation, Lac Pelletier lower fauna, Cypress Hills, Saskatchewan (NP9A)
5. Chambers Formation, Porvenir local fauna, Presidio Co., Texas (SB44B)

Duchesnean (*Daphoenictis*)

6. Chambers Formation, Porvenir local fauna, Presidio Co., Texas (SB44B)

Chadronian (*Daphoenus*)

7. Chadron Formation, Chadronia Pocket, Dawes Co., Nebraska (CP98C)
8. Chadron Formation, Arner Ranch area, Sioux Co., Nebraska (CP98B or C)
9. Chadron Formation, sect. 15, T.33N, R.53W (Sx-35), Sioux Co., Nebraska (CP98B or C)
10. Chadron Formation, Pasture 34 (Dw-107), Dawes Co., Nebraska (CP98B or C)
11. Chadron Formation, Everson Ranch, Sioux Co., Nebraska (CP98B or C)

12. Chadron Formation, Crazy Johnson Member, Indian Creek, Pennington Co., South Dakota (CP83B)
13. Chadron Formation, Peanut Peak Member, Shannon Co., South Dakota (CP83C)
14. Chadron Formation, Seamen Hills area, Niobrara Co., Wyoming (CP41A)
15. White River Formation, Shirley Basin, Natrona Co., Wyoming (CP39D)
16. Cypress Hills Formation, Calf Creek local fauna, Cypress Hills, Saskatchewan (NP10B)

Chadronian (*Daphoenictis*)

20. Chadron Formation, Norman Ranch local fauna, Sioux Co., Nebraska (CP98B or C)
21. Chadron Formation, Brecht ranch local fauna, Dawes Co., Nebraska (CP98B or C)
22. White River Formation, Mink Creek local fauna, Teton Co., Wyoming (CP43)
23. White River Formation, Flagstaff Rim, 10' above Ash E, Natrona Co., Wyoming (CP39C)
24. White River Formation, Flagstaff Rim, Dry Hole Quarry, Natrona Co., Wyoming (CP39B)
25. Renova Formation, Pipestone Springs Main Locality, Jefferson Co., Montana (NP24C)
26. Cypress Hills Formation, Cypress Hills, Saskatchewan (NP10B)

Chadronian (*Brachyrhynchocyon*)

30. Chadron Formation, Arner Ranch area, Sioux Co., Nebraska (CP98B or C)
31. Chadron Formation, Whitehead Creek, Sioux Co., Nebraska (CP98B or C)

32. Chadron Formation, near Sugarloaf, Sioux Co., Nebraska (CP98B or C)
33. Chadron Formation, Brecht Ranch local fauna, Dawes Co., Nebraska (CP98B or C)
34. Chadron Formation, Chadronia Pocket, Dawes Co., Nebraska (CP98B or C)
35. Chadron Formation, Rook Ranch (Dw-104), Dawes Co., Nebraska (CP98B or C)
36. Chadron Formation, Pasture 34 (Dw-107), Dawes Co., Nebraska (CP98B or C)
37. Chadron Formation, Bartlett West #1, Dawes Co., Nebraska (CP98B or C)
38. Chadron Formation, Ahearn and Crazy Johnson Members, Indian Creek, Pennington Co., South Dakota (CP83A, CP83B)
39. Chadron Formation, Hutemacher Table, Peanut Peak Member, Pennington Co., South Dakota (CP83C)
40. Chadron Formation, Breaks, Crazy Johnson Member, Custer Co., South Dakota (CP83B)
41. Chadron Formation, Seamen Hills area, Niobrara Co., Wyoming (CP41A)
42. Chadron Formation, Yoder local fauna, Goshen Co., Wyoming (CP42A)
43. Chadron Formation, Irvine Bridge area, Converse Co., Wyoming (CP40A)
44. White River Formation, Flagstaff Rim, below Ash B, Natrona Co., Wyoming (CP39B)
45. White River Formation, Flagstaff Rim, lower part (Ash B to F), Natrona Co., Wyoming (CP39C)
46. White River Formation, Flagstaff Rim, upper Part (Ash F to J), Natrona Co., Wyoming (CP39F)
47. White River Formation, Bates Hole/Ledge Creek, Natrona Co., Wyoming (CP39G)
48. White River Formation, Cedar Creek area, Logan/Weld Cos., Colorado (CP68B)
49. Renova Formation, Pipestone Springs Main Locality, Jefferson Co., Montana (NP24C)
50. Renova Formation, Sage Creek, Beaverhead Basin, Montana (NP24E)
51. Climbing Arrow Formation, Thompson Creek, Three Forks Basin, Montana (NP23C)
52. Unnamed unit, Hadcock Ranch, Sewell Lake area, Montana (NP29C)
53. Cypress Hills Formation, Calf Creek local fauna, Cypress Hills, Saskatchewan (NP10B)
54. Chambers Formation, Little Egypt local fauna, Reeves Bone Bed, Presidio Co., Texas (SB44C)

Orellan (*Daphoenus*)

Orella Member, Brule Formation (all locality CP99A):

60. 2.5 miles N of Chadron, Dawes Co., Nebraska
61. Harrison Ranch, Sioux Co., Nebraska

62. Roundtop area, Dawes Co., Nebraska
63. Badland Creek, Hat Creek Basin, Sioux Co., Nebraska
64. Dry Creek, Hat Creek Basin, Sioux Co., Nebraska
65. Prairie Dog Creek, Hat Creek Basin, Sioux Co., Nebraska
66. Cedar Creek, Hat Creek basin, Sioux Co., Nebraska
67. NW of Crawford, Sioux Co., Nebraska
68. Plunkett-Parsons Ranch area, N of Harrison, Sioux Co., Nebraska
69. 10 miles N of Harrison, Sioux Co., Nebraska
70. Sect. 11, T.33N, R.54W, Sioux Co., Nebraska
71. 1.5 miles SW of Dout Ranch, Sioux Co., Nebraska
72. Brecht Ranch area, Dawes Co., Nebraska
73. Whitehead Creek, Sioux Co., Nebraska
74. Warbonnet Creek, Sioux Co., Nebraska
75. Geike Ranch, N of Harrison, Sioux Co., Nebraska

Scenic Member, Brule Formation (localities nos. 80–97 are CP84A):

80. Big Corral Draw, Shannon Co., South Dakota (Lower Nodular Zone)
81. Spring Creek Basin, Pennington Co., South Dakota
82. East side of Harney Springs Range, SE of Sheep Mountain, South Dakota
83. Chamberlain Pass, SE of Scenic, Pennington Co., South Dakota
84. 6 miles W of Interior, Jackson Co., South Dakota
85. Little Corral Draw, Shannon Co., South Dakota (Lower Nodular Zone)
86. Red Shirt Table, Shannon Co., South Dakota
87. 2 miles and 3 miles E of Scenic, Pennington Co., South Dakota
88. 11 miles S of Scenic, Shannon Co., South Dakota
89. Cain Creek, Pennington Co., South Dakota
90. Bear Creek Basin, Pennington Co., South Dakota
91. S Arrow Wound Table, Shannon Co., South Dakota
92. Sheep Mountain area, Shannon Co., South Dakota
93. Cottonwood Pass area, Jackson Co., South Dakota
94. 1 mile E of Babby Butte, Shannon Co., South Dakota
95. 6 miles S of Scenic, Shannon Co., South Dakota
96. 3.5 miles S of Scenic, Pennington Co., South Dakota
97. 7–8 miles N of Rockyford, South Dakota
98. White River Formation, NW of Whitman, S-Bar Creek, Niobrara Co., Wyoming (CP41B)
99. White River Formation, about 6 miles SE of Douglas, Converse Co., Wyoming (CP40B)
100. White River Formation, Bald Butte, Niobrara Co., Wyoming (CP41B)
101. White River Formation, Wulff Ranch, Douglas area, Converse Co., Wyoming (CP40B)
102. White River Formation, Walker Ranch area, Niobrara Co., Wyoming (CP41B)
103. White River Formation, 8 miles SE of Douglas, Converse Co., Wyoming (CP40B)

104. White River Formation, 8 miles E of Douglas, Converse Co., Wyoming (CP40B)
105. White River Formation, Greeley/Pawnee Buttes area, Weld Co., Colorado (CP68C)
106. White River Formation, N of Stone Ranch, Yuma Co., Colorado (CP68C)
107. White River Formation, Cedar Creek, Logan Co., Colorado (CP68C)
108. White River Formation, Casement Ranch, Logan Co., Colorado (CP68C)
109. White River Formation, Canyon Ferry area, Montana (NP29E)
110. White River Formation, Little Badlands, Dickinson area, Stark Co., North Dakota (NP50B)

Whitneyan (*Daphoenus*)

114. Brule Formation, Roberts Draw, NE of Harrison, Sioux Co., Nebraska (CP99B)
115. Brule Formation, Wolff Lake, South Dakota (CP84B)
116. Brule Formation, NE of Indian Stronghold, South Dakota (CP84B)
117. Brule Formation, Big Corral Draw, Shannon Co., South Dakota (CP84B)

Whitneyan or Arikareean (*Daphoenus*)

118. John Day Formation, John Day River valley, Oregon (PN6)
119. John Day Formation, Camp Watson, John Day River valley, Oregon (PN6)
120. John Day Formation, Turtle Cove, John Day River valley, Oregon (PN6)
121. John Day Formation, Haystack Valley, John Day River valley, Oregon (PN6)
122. John Day Formation, LACM Loc. 1843, Malheur Co., Oregon (PN6)
123. John Day Formation, Blue Basin, Unit C, Grant Co., Oregon (PN6C)
124. John Day Formation, Sheep Rock area, ?Unit K, Grant Co., Oregon (PN6D)
125. Tecuya Formation, Tecuya Canyon, Kern Co., California (CC13)
126. Arikaree Formation, Birdcage Gap (Mo-106), Morrill Co., Nebraska (CP100II)

Orellan (*Paradaphoenus*)

127. Brule Formation, Orella Member, UNSM Loc. Sx-14, Sioux Co., Nebraska (CP99A)
128. Brule Formation, Orella Member, UNSM Locs. Sx-25, Sx-26, Sioux Co., Nebraska (CP99A)
129. Brule Formation, Scenic Member, SW of Sheep Mt., near Scenic, South Dakota (CP84A)

Whitneyan or early Arikareean (*Paradaphoenus*)

130. John Day Formation, John Day River valley, Oregon (PN6)
131. Brule Formation, Scottsbluff Co., Nebraska (possibly Orellan) (CP99A or B)
132. Brule Formation, sect. 36, T.20N, R.56W, Banner Co., Nebraska (CP99B or C)
133. Sharps Formation, Wounded Knee area, LACM Loc. 1981, South Dakota (CP85C)

Whitneyan or early Arikareean (*Temnocyon*)

135. John Day Formation, Logan Butte, Crook Co., Oregon (PN6C or D)
136. John Day Formation, John Day valley, Turtle Cove, Grant Co., Oregon (PN6C or D)
137. John Day Formation, Morgan's Place, UCMP Loc. 874, Grant Co., Oregon (PN6C)

Arikareean (*Temnocyon*)

138. John Day Formation, McGinnis Ranch, Grant Co., Oregon (PN6F or G)
139. John Day Formation, Haystack Valley, Wheeler Co., Oregon (PN6G)
140. Harrison Formation, 0.5 miles W of Agate, Sioux Co., Nebraska (CP103)
141. Upper Harrison beds, American Museum – Cook Quarry, Sioux Co., Nebraska (CP104A)
142. Sespe Formation, Kew Quarry, Las Posas Hills, Ventura Co., California (CC9C)
143. Upper Harrison beds, near Guernsey, Platte Co., Wyoming (CP51A)

Arikareean (*Mammacyon*)

150. Sharps Formation, LACM Loc. 1872, south of Wolf ranch, Shannon Co., South Dakota (CP85C)
151. Arikaree Formation, Porcupine Creek, Shannon Co., South Dakota (CP86B)
152. Arikaree Formation, LACM Loc. 1964, Wounded Knee area, Shannon Co., South Dakota (CP86B)
153. Monroe Creek Formation, Warbonnet Creek, Sioux Co., Nebraska (CP102)
154. John Day Formation, Haystack Valley, Wheeler Co., Oregon (PN6C or D)
155. Arikaree Formation, N of Keeline, Niobrara Co., Wyoming (CP52)
156. Unit 9 Limestone, Martin-Anthony Roadcut, Marion Co., Florida (GC8B)

157. SB-1A local fauna, 1 mile N of Live Oak, Suwanee Co., Florida (GC8A)

Medial and late Arikareean
(*Daphoenodon*)

158. Brooksville, Hernando Co., Florida (GC8B)
159. Franklin Phosphate Co. Pit no. 2, Alachua Co., Florida (GC8C)
160. Buda local fauna, Alachua Co., Florida (GC8A)
161. Harrison Formation, Van Tassell Creek, Niobrara Co., Wyoming (CP52)
162. Upper Harrison beds, Agate Monument den site (Quarry 3), Sioux Co., Nebraska (CP104A)
163. Upper Harrison beds, Harper Quarry, Sioux Co., Nebraska (CP104A)
164. Upper Harrison beds, American Museum-Cook Quarry, Sioux Co., Nebraska (CP104A)
165. Upper Harrison beds, University Quarry, Sioux Co., Nebraska (CP104A)
166. Upper Harrison beds, Carnegie Quarry 1, Sioux Co., Nebraska (CP104A)
167. Upper Harrison beds, 18-Mile District, Goshen Co., Wyoming (CP51A)
168. Upper Harrison beds, Royal Valley District, Niobrara Co., Wyoming (CP51A)
169. Upper Harrison beds, 5 miles SE of Chugwater, Platte Co., Wyoming (CP51A)
170. Upper Harrison beds, ?Niobrara Canyon, Sioux Co., Nebraska (CP104B)

Early Hemingfordian (*Daphoenodon*)

171. Runningwater Formation, Brown Quarry, Sioux Co., Nebraska (CP105)
172. Runningwater Formation, Whistle Creek-Niobrara River divide, Sioux Co., Nebraska (CP105)
173. Runningwater Formation, Aletomeryx Quarry, Cherry Co., Nebraska (CP105)
174. Runningwater Formation, Marsland Quarry, Box Butte Co., Nebraska (CP105)
175. Runningwater Formation, Dunlap Camel Quarry, Dawes Co., Nebraska (CP105)
176. Runningwater Formation, Hemingford Quarries 7A, 7B, 12B, 12D, 23, Box Butte Co., Nebraska (CP105)

Late Arikareean (*Ysengrinia*)

180. Upper Harrison beds, University Quarry, Agate Monument, Sioux Co., Nebraska (CP104A)
181. Upper Harrison beds, American Museum-Cook Quarry, Sioux Co., Nebraska (CP104A)

182. ?Upper Harrison beds, Morava Ranch Quarry, Box Butte Co., Nebraska (CP104A)
183. Upper Harrison beds, Harper Quarry, Sioux Co., Nebraska (CP104A)
184. Upper Harrison beds, Spoon Butte, Lay Ranch, Goshen Co., Wyoming (CP51A)
185. Upper Harrison beds, 25-Mile District, Goshen Co., Wyoming (CP51A)

Early Hemingfordian (*Ysengrinia*)

186. Unnamed lithic unit, Bridgeport Quarries, Morrill Co., Nebraska (CP106)

Late Arikareean (*Cynelos*)

187. Upper Harrison beds, Quarry 1, Agate Monument, Sioux Co., Nebraska (CP104A)

Early Hemingfordian (*Cynelos*)

188. Unnamed lithic unit, Bridgeport Quarries, Morrill Co., Nebraska (CP106)
189. Runningwater Formation, Runningwater Quarry, Box Butte Co., Nebraska (CP105)
190. Karst sinkhole, Thomas Farm Quarry, Gilchrist Co., Florida (GC8D)

Late Hemingfordian (*Cynelos*)

192. Sheep Creek Formation, Thomson, Hilltop and Long Quarries, Sioux Co., Nebraska (CP108A and B)

Early Barstovian (*Cynelos*)

194. Unnamed lithic unit, Pawnee Buttes area, Weld Co., Colorado (CP75B)
195. Olcott Formation, East and West Sinclair Draws, Sioux Co., Nebraska (CP110)
196. Olcott Formation, Echo Quarry, Sioux Co., Nebraska (CP110)
197. Tesuque Formation, Skull Ridge Member, Espanola Basin, New Mexico (SB32B)
198. Fleming Formation, Cold Spring fauna, Washington Co., Texas (GC4E)
199. Barstow Formation, "Rak Division," San Bernardino Co., California (NB6B)

Late Hemingfordian (*Pliocyon*)

200. Sheep Creek Formation, Thomson and Long Quarries, Sioux Co., Nebraska (CP108A and B)

Early Barstovian (*Pliocyon*)

- 201. Olcott Formation, East and West Sinclair Draws, Sioux Co., Nebraska (CP110)
- 202. Olcott Formation, Echo, Humbug, and Boulder Quarries, Sioux Co., Nebraska (CP110)
- 203. Unnamed lithic unit, Observation Quarry, Dawes Co., Nebraska (CP111)
- 204. Barstow Formation, "Green Hills," San Bernardino Co., California (NB6C)

Barstovian or Clarendonian (*Pliocyon*)

- 205. Bone Valley Formation, exact age uncertain, Polk Co., Florida (GC10B)

Early Hemingfordian (*Amphicyon*)

- 206. Runningwater Formation, Dunlap Camel Quarry, Dawes Co., Nebraska (CP105)
- 207. Runningwater Formation, Marsland and Hovarka Quarries, Box Butte Co., Nebraska (CP105)
- 208. Runningwater Formation, Hemingford Quarries 7B and 12B, Box Butte Co., Nebraska (CP105)
- 209. Runningwater Formation, Cottonwood Quarry, Dawes Co., Nebraska (CP105)

Late Hemingfordian (*Amphicyon*)

- 212. Sheep Creek Formation, Thomson and Long Quarries, Sioux Co., Nebraska (CP108A and B)
- 213. Sheep Creek Formation, Thistle and Greengside Quarries, Sioux Co., Nebraska (CP108A and B)

Early or medial Barstovian (*Amphicyon*)

- 215. Olcott Formation, East and West Sinclair Draws, Sioux Co., Nebraska (CP110)
- 216. Olcott Formation, Echo, Grass Roots (= Quarry 6), Boulder, Prosynthetoceras, Humbug, and Mill Quarries, Sioux Co., Nebraska (CP110)
- 217. Pawnee Creek Formation, Horse and Mastodon Quarry, Weld Co., Colorado (CP75C)
- 218. Pawnee Creek Formation, West Quarry, Weld Co., Colorado (?CP75C)
- 219. Trinity River Pit no. 1, Texas (GC4C)
- 220. Tesuque Formation, Skull Ridge Member, Espanola Basin, New Mexico (SB32B)

- 221. Barstow Formation, Green Hills fauna, San Bernardino Co., California (NB6C)
- 222. Barstow Formation, Turbin, Steepsides, and Valleyview Quarries, San Bernardino Co., California (NB6C and D)
- 223. Barstow Formation, Skyline and Oreodont Quarries, San Bernardino Co., California (NB6C and D)
- 224. Butte Creek Volcanic Sandstone, Red Basin local fauna, Malheur Co., Oregon (PN8B)

Early Barstovian (*Pseudocyon*)

- 230. Olcott Formation, Trojan Quarry, Sioux Co., Nebraska (CP110)

Medial Barstovian (*Pseudocyon*)

- 231. Ogallala Formation, Hottell Ranch Quarries, Banner Co., Nebraska (CP114A)
- 232. Valentine Formation, Norden Bridge Quarry, Brown Co., Nebraska (CP114A)
- 233. Tesuque Formation, Pojoaque Member, Pojoaque Bluffs, Espanola Basin, New Mexico (SB32D)

Late Barstovian (*Pseudocyon*)

- 234. Valentine Formation, Ripple Quarry, Cherry Co., Nebraska (CP114B)
- 235. Ogallala Formation, Hazard Homestead Loc. C, Hitchcock Co., Nebraska (CP114B)

Early Clarendonian (*Pseudocyon*)

- 236. Valentine Formation, Burge Member, Burge Quarry, Cherry Co., Nebraska (CP114D)
- 237. Valentine Formation, Burge Member, Lucht Quarry, Brown Co., Nebraska (CP114D)
- 238. Valentine Formation, Burge Member, June Quarry, Brown Co., Nebraska (CP114D)
- 239. Valentine Formation, Burge Member, Midway Quarry zone, Cherry Co., Nebraska (CP114D)
- 240. Ash Hollow Formation, Cap Rock Member, Horsethief Canyon no. 2, Brown Co., Nebraska (CP116A)

Late Clarendonian (*Pseudocyon*)

- 241. Snake Creek Formation, Laucomer Member, Olcott Quarry, Sioux Co., Nebraska (CP115B)

242. Ash Hollow Formation, Merritt Dam Member, Kat Quarry horizon, Cherry Co., Nebraska (CP116B)
 243. Ash Hollow Formation, Merritt Dam Member, Clayton Quarry, Brown Co., Nebraska (CP116B)

Medial or late Barstovian (*Ischyrocyon*)

245. Barstow Formation, First Division, Hemicyon Stratum, San Bernardino Co., California (NB6E)
 246. Barstow Formation, Leader, Mayday, Hailstone, and Hidden Hollow Quarries, San Bernardino Co., California (NB6D)

Late Barstovian (*Ischyrocyon*)

250. Valentine Formation, Ripple Quarry, Cherry Co., Nebraska (CP114B)
 251. Valentine Formation, Devil's Gulch Member, Devil's Gulch Horse Quarry, Brown Co., Nebraska (CP114C)
 252. Valentine Formation, Devil's Gulch Member, Mizner Slide, Cherry Co., Nebraska (CP114C)
 253. Valentine Formation, Devil's Gulch Member, Verdigrée Quarry, Knox Co., Nebraska (CP114C)
 254. ?Valentine Formation, upper channel S of Nenzel Quarry, Cherry Co., Nebraska (CP114)

Clarendonian (*Ischyrocyon*)

255. Valentine Formation, Burge Member, Burge Quarry, Cherry Co., Nebraska (CP114D)
 256. Valentine Formation, ?Burge Member, Paleo Quarry, Sheridan Co., Nebraska (CP114D)
 257. Ash Hollow Formation, Cap Rock Member, Little Beaver B Quarry, Cherry Co., Nebraska (CP116A)
 258. Ash Hollow Formation, Cap Rock Member, 2–2.5 miles W of Burton, Keyapaha Co., Nebraska (CP116A)
 259. Ash Hollow Formation, Hollow Horn Bear Quarry, Todd Co., South Dakota (CP90A)
 260. Ash Hollow Formation, Big Spring Canyon, Bennett Co., South Dakota (CP90A)
 261. Ash Hollow Formation, Mission local fauna, Fox Ranch, Mellette Co., South Dakota (CP90A)
 262. Ash Hollow Formation, 3 miles E of Rosebud, Todd Co., South Dakota (CP90)
 263. Snake Creek Formation, Laucomer Member, Olcott Hill, Sioux Co., Nebraska (CP115B)
 264. Ogallala Formation, Skillet Creek, L.17, Quarry 1, Donley Co., Texas (SP2A)
 265. Ogallala Formation, Adam Rizley Ranch, Donley Co., Texas (SP2A)
 266. Unnamed lithic unit, 7 miles W of Blair Junction, Esmeralda Co., Nevada (NB27II)
 267. Ricardo Formation (= Dove Spring Formation), Last Chance Gulch, Kern Co., California (NB7B)