21. Canidae

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ABSTRACT

The White River Group of the late Eocene and Oligocene age contains some of the earliest and most primitive canids in North America. These archaic canids, mainly Hesperocyon and its close relatives, gave rise to several clades that contain ancestral forms for all three subfamilies of the Canidae: the paraphyletic Hesperocyoninae which became the dominate canids during the Arikareean, the monophyletic Borophaginae which flourished during the Miocene, and the monophyletic Caninae which did not diversify until Pliocene through Recent time. The middle-late Eocene (Duchesnean to Chadronian) saw the emergence of the first canids with a fully ossified entotympanic bulla and canid dentition (3 1 4 2/3 1 4 3), as represented by Prohesperocyon wilsoni and H. gregarius, which probably evolved from primitive cynoids such as Procyonidictis. The White River canids began an initial diversification in the beginning of Oligocene (Orellan), giving rise to the earliest members of the borophagine (Cormocyon) and canine (Leptocyon) clades. At least six species can be recognized at this time: H. gregarius, "H." coloradensis, "Mesocyn" temnodon, Osbornodon renjiei, Cormocyon pavidus, and Leptocyon sp. In Whitneyean time, the majority of the hesperocyonine clades began to be readily distinguishable, and the borophagines began to develop small, hypocarnivorous taxa. The number of species in the Whitneyean had increased to nine: H. gregarius, Parahesperocyon josephi, "M." temnodon, Cynodontus howides, Osbornodon renjiei, O. sesnoni, Ectocyon antiquus, Cormocyon pavidus, and Oxetocyon cuspidatus. Near the top of the White River sequence, an early precursor of the hypercarnivorous Enhydrocyon clad, Sunkahetanka geringensis, had emerged, and most clades of the Hesperocyoninae began independently developing meso- to hypercarnivorous forms.

INTRODUCTION

Early members of the dog family (Canidae) left an abundant fossil record in the White River Group of North America with a fairly continuous presence throughout the strata. This is especially true of Hesperocyon, an ubiquitous, small fox-sized animal frequently found in the White River Group, leading some authors to speculate that it was responsible for keeping the numbers of its contemporary rodents, lagomorphs, and small artiodactyls in check (Cope, 1874; Clark et al., 1967). Less conspicuous than their contemporary large predators such as hyaenodontids and nimravids, these early canids include the ancestral stocks that went on to become the dominant carnivores of later times.

The late Eocene and Oligocene Hesperocyon has attracted the attention of vertebrate paleontologists, not only because of the well-preserved skeletal materials commonly found in the White River strata, but also because it is an important bona fide canid which possesses the right morphology and occurs at the right time to be ancestral to or close to the ancestry of all later canids. In addition to representing the basal group for the first canid radiation, the subfamily Hesperocyoninae, H. gregarius is also the closest sister-group of the presumed common ancestor of the Borophaginae and Caninae, two subfamilies which flourished in the late Tertiary and Quaternary-Recent times (Tedford, 1978).

Since the classic treatment of the White River Hesperocyon by Scott and Jepsen (1936), no systematic effort has been devoted re-evaluating the taxonomy of these early canids despite a number of attempts (e.g., Galbreath, 1953; Hough and Alf, 1956; Elliott, 1980). Meanwhile, our knowledge of fossil canids during this crucial period of time has increased considerably, thanks mainly to the Frick Collection at the American Museum of Natural History, which contains a large number of undescribed taxa and more complete materials of known taxa from the White River Group. We are now in possession of an unprecedented data base to better evaluate morphological variations and to more accurately reconstruct phylogeny. Such a wealth of information has, in recent years, stimulated a number of studies that establish a new outlook the evolutionary relationships of primitive canids (Tedford, 1978; Wang, 1990, 1993, 1994; Wang and Tedford, 1992, 1994; Tedford and Taylor, MS). It is thus opportune to update, in this volume, the current systematics of the White River canids.

The main purpose of the present review is an evaluation of the known taxonomic diversity and phylogeny of canids from the White River Group of the northern Great Plains in light of the new calibration of Eocene-Oligocene transition as recently proposed by Swisher and Prothero (1990). The nature and scope of this chapter do not allow exhaustive treatment of all White River canids, and undescribed taxa from the Frick Collection, mostly small borophagines, will not be discussed.
ABBREVIATIONS
AMNH, American Museum of Natural History, New York; F:AM, Frick Collection, American Museum of Natural History, New York; CMNH, Carnegie Museum of Natural History, Pittsburgh; KUVP, Museum of Natural History, University of Kansas, Lawrence; LACM, Los Angeles County Museum, Los Angeles; SDSM, South Dakota School of Mines and Technology, Rapid City; TMM, Texas Memorial Museum, Austin; UNSM, State Museum, University of Nebraska, Lincoln; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.; YPM-PU, Yale Peabody Museum (Princeton University Collection), New Haven.

TAXONOMIC OVERVIEW OF THE EARLY CANIDAE
Detailed systematic treatments of the hesperocyonines, borophagines, and canines are the subjects of separate studies (Wang, 1994; Tedford and Taylor, MS), and for the present purpose, only a synopsis is presented to summarize the taxonomy of early canids in the White River and equivalent strata. Since only published taxa are included, the White River canid diversity presented here is incomplete. This is especially the case for the Borophaginae, which has more undescribed taxa than has been documented. Complete synonym lists for each species of the Hesperocyoninae can be found in Wang (1994).

Higher level taxonomic nomenclature (e.g., Cynoidea) follows Wang and Tedford (1994). The archaic family Miacidae is most likely paraphyletic because of its presumed ancestral relationship to more derived families of caniform carnivores (cynoids and arctoids). Unless stated otherwise, the present usage of miacids refers to the nominal genus Miacis (type species M. parvivorus). As is the case with many primitive fossil groups, paraphyly cannot be easily avoided without naming of numerous new genera. As a result, several paraphyletic genera, Hesperocyon, Mesocyon, Cervocyon, and Leptocyon, are still in use in this overview. Those that are clearly paraphyletic in view of the phylogeny presented here (Fig. 10) are enclosed in quotation marks.

Order CARNIVORA Bowditch, 1821
Suborder CANIFORMIA Kretzoi, 1943
Infraorder CYNOIDEA Flower, 1869
Family CANIDAE Gray, 1821

Diagnosis—Canids can be characterized by the following derived basicranial and dental features: an inflated entotympanic bulla that is composed of a rostral entotympanic and a caudal entotympanic; medial expansion of the petrosal which is in full contact with the basioccipital and basiphenoid; fully ossified tegmen tympani forming the roof of the facial nerve canal; extrabular position of the internal carotid artery (and thus loss of the stapedial artery) which lies between the entotympanic and the petrosal; a small suprameatal fossa anterior to the mastoid process (in primitive canids only); presence of posterior accessory cusps on the upper and lower third premolars; reduction of the M1 parastyle; and absence of M3 (Wang and Tedford, 1994). In addition, all canids, except the most basal taxon Prohesperocyon, have a low septum on the internal surface of the bulla at the suture of the ecto- and entotympanic.

Geologic and Geographic Range—Late Eocene to Recent of North America, Late Miocene to Recent of Europe, Pliocene to Recent of South America, Asia, and Africa.

Comments—The derived features in the above diagnosis easily distinguish canids from “miacids,” but some of them may have been shared with arctoid carnivores (e.g., suprameatal fossa; see this volume, Chapter 24). These basiocular and dental characteristics, conservative once acquired, permit easy recognition of canids among carnivores.

The family Canidae underwent at least two major radiations in the Oligocene and Miocene that were exclusively confined to North America: the paraphyletic Hesperocyoninae and the monophyletic Borophaginae (Tedford, 1978). A third radiation, the monophyletic Caninae, originated in North America but did not reach the Paleartic until some time in the Late Miocene. All three subfamilies appear in the White River deposits with animals smaller than a living red fox and diversified into larger, wolf-sized carnivores. There are striking ecological parallels among the three subfamilies, each with its own small predators, fruit eaters, and large hypercarnivorous predators (Tedford, 1978; Martin, 1989; Van Valkenburgh, 1991).

The ancestry of all three subfamilies can be traced back to Hesperocyon, traditionally considered the most basal canid because of its fully ossified entotympanic bulla and canid dental formula (3 1 4 2/3 1 4 3). Such easily recognized features have served well as a practical and convenient diagnosis of the Canidae. Discoveries of more archaic taxa, however, blur these distinctions, and the increased knowledge about the phylogeny of caniform “miacids” makes possible the identification of ancestral cynoids (e.g., Procynodiscus vulpiceps) lacking the above traditional diagnostic features, thus pushing cynoid origins into an early phase of caniform phylogeny (Wang and Tedford, 1994).

CANIDAE incertae sedis

Prohesperocyon wilsoni (Gustafson, 1986)
Figure 1B

Holotype—TMM 40504-126, partial skull and mandible with left C1, P3-M2, right C1-M2, left p4-m2, and right p2-m3.

Type Locality—Airstrip local fauna, in Capote Mountain Tuff, 174 m above the Bracks Rhyolite, in southern part of the Sierra Vieja area, Presidio County, Texas (Wilson et al., 1968). Middle Chirodonian.

Diagnosis—Prohesperocyon wilsoni is characterized by a mixture of derived canid and primitive “miacid” features. Derived features include: an inflated...
and fully ossified entotympanic bulla; an accessory cusp on upper and lower third premolars; a rather posteriorly positioned internal cingulum of M1; loss of a notch between the parastyle and paracone of M1; and lack of M3. Among primitive features it retains: a large, anteriorly located protocone of P4; a still large parastyle of M1; a short shearing blade of M1; a narrow talonid relative to trigonid of M1; a reduced metaconid of M2; and a posteriorly inclined ascending ramus of mandible. In addition, P. wilsoni has autapomorphies that further differentiate it from Hesperocyon gregarius and preclude it from the direct ancestry of the later canids: elongated rostrum, anteriorly expanded bulla that extends in lateral view the posterior wall of the postglenoid fossa, slender premolars, and reduced metacone of M2.

Geologic and Geographic Range—From the type locality only.

Comments—Although the presence of a fully ossified entotympanic bulla (and the essentially canid middle ear region), a posteriorly positioned internal cingulum of M1, the lack of para style notch on M1, and the loss of M3 in Prohesperocyon wilsoni signal canid affinity, its dental morphology, for the most part, is primitive. It had, in fact, been assigned to Miacis gracilis by Wilson et al. (1968). Gustafson (1986) noted this primitive similarity between P. wilsoni and Miacis but nevertheless placed P. wilsoni in the Canidae because of its complete bulla. Recent study of the basicranial anatomy of P. wilsoni reveals that it lacks a low septum on the internal surface of the bulla in contrast to the rest of canids, which have the structure (Wang and Tedford, 1994).

A monotypic genus, Prohesperocyon, was erected by Wang (1994) to preserve monophyly of the taxon and to mark its largely primitive dentition distinct from Hesperocyon of the northern Great Plains. The intermediate nature of P. wilsoni narrows the morphologic gap between canids and “miacids,” and reduces the number of characteristics of the Canidae previously regarded as first appearing together in Hesperocyon gregarius. Stratigraphically, however, P. wilsoni (middle Chadronian) occurs later than the earliest Hesperocyon (Duchesnean) from the Cypress Hills Formation of southwestern Saskatchewan, Canada (Bryant, 1992). This late occurrence of P. wilsoni and its possession of autapomorphies (above) preclude it from being in the direct ancestry of the more derived canids.

Subfamily HESPEROCYONINAE Tedford, 1978

Included Genera—Hesperocyon Scott, 1890; Mesocyon Scott, 1890; Cynodesmus Scott, 1893; Sunkahetanka Macdonald, 1963; Philotrox Merriam, 1906; Enhydrocyon Cope, 1879; Osbornodon Wang, 1994; Parahydrocyon Wang, 1994; Caecodony Wang, 1994; and Ectopyocynus Wang, 1994.

Geologic and Geographic Range—Duchesnean (late Eocene) to Early Barstovian (middle Miocene) of North America.

Comments—A cladistic diagnosis of the Hesperopyoninae is not possible because of its paraphyletic nature. A trenchant talonid of lower molars (or much smaller entoconid than hypoconid), a primitive character, is all there is to distinguish it from the two more derived subfamilies Borophaginae and Caninae, which share the synapomorphy of basined (bicuspid) talonid. Associated with this single-cusped talonid is the absence or reduced presence of a metaconule in a transversely elongated M1, in contrast to the well-developed metaconule on a quadrate M1 often present in borophagines and canines. Even this single character does not hold true for all hesperocyonines. One lineage of the hesperocyonine, Osbornodon, has acquired a basined talonid and quadrate upper molars. Despite the difficulty in diagnosing the Hesperocyoninae, it is nevertheless a useful term to encompass the basal stocks of canids that are not related to later subfamilies.

The subfamily Hesperocyoninae includes four monophyletic clades whose ancestry can be traced to a Hesperocyon-like form: Mesocyon—Enhydrocyon clade, Osbornodon clade, Parahydrocyon clade, and Ectopyocynus clade. These clades represent part of the initial radiation of the Canidae. They parallel one another or later canids in some morphological features, and tend to evolve into medium- to large-sized species that take the roles of powerful hypercarnivorous predators. Throughout most of their history, the hesperocyonines coexisted with borophagines and canines, although Oligocene members of the latter two subfamilies were mainly represented by a few small forms.

Hesperocyon Scott, 1890

Type Species—Hesperocyon gregarius (Cope, 1873a).

Included Species—Hesperocyon gregarius (Cope, 1873a), and “H.” coloradensis Wang, 1994.

Diagnosis—Compared to Prohesperocyon, Hesperocyon has the following derived characters (Fig. 10, node 2): a reduced protocone of P4; a further reduced parastyle of M1; an elongated shearing blade of M1; nearly equal metaconid and protoconid of M2; a more upright ascending mandibular ramus, and a low septum within the bulla. Compared to more derived hesperocyonines and borophagines/canines, Hesperocyon is still primitive in having a posteriorly directed paroccipital process which is not fused with the entotympanic (except in “H.” coloradensis), an unreduced metaconid of M1, and presence of a low entoconid shelf of M1.

Geologic and Geographic Range—Cypress Hills Formation, southwestern Saskatchewan, Canada; Chadron, Brule, and their correlative formations in the White River Group of southwestern Montana, eastern Wyoming, western South Dakota, southwestern North Dakota, northeastern Colorado, and northwestern Nebraska. Duchesnean to Whitneyan of North America (late Eocene to early Oligocene).

Comments—Hesperocyon is important, morphologically and stratigraphically, in the understanding of the early canid radiation. It is one of the best known early canids (Cope, 1884; Scott, 1898; Matthew, 1901;
hesperocyonine clades (e.g., *Paraehydrocyon*) and because it lacks a synapomorphy shared by its two species.

A recent study by Bryant (1992) identified isolated teeth of *Hesperocyon gregarius* in the lower part of Cypress Hills Formation in Saskatchewan, Canada, and thus extended its record into the Duchesnanean.

*Hesperocyon gregarius* (Cope, 1873)

Figures 1C, 2

**Lectotype**—AMNH 5297a, fragment of left ramus with p2–m1 and alveolus for p1.

**Type Locality**—White River Formation of northeastern Colorado, ?Orellian.

**Diagnosis**—Distinctions among species of *Hesperocyon* are quite subtle, and no single character could be used as the sole criterion of identification. *H. gregarius* tends to have a more posteriorly enlarged internal cingulum (hypocone) of M1 which often lacks the anterior segment of the cingulum. The parastral of M1, although more reduced than in "miacids," is relatively large compared with that of the borophagine *Cormocyon pavidus*. The metaconid of m2 is smaller than the protoconid; the reverse is usually true for *C. pavidus*. Compared to the larger "H." *coloradensis*, *H. gregarius* lacks a ventrally directed paroccipital process.

**Geologic and Geographic Range**—Cypress Hills Formation, Saskatchewan, Canada; Renova Formation of western Montana; Chadron, Brule, and their correlative formations in Colorado, Nebraska, North Dakota, South Dakota, and Wyoming; Duchesnanean to Whitneyan.

**Comments**—The rich materials of *Hesperocyon gregarius* from the White River Group of the northern Great Plains is unsurpassed by any other group of canids from the Tertiary of North America. The species is the earliest discovered Tertiary canid and its morphology the best known among early canids.

*Hesperocyon gregarius* plays a key role in understanding the phylogeny of ancestral canids, and its central position in the early canid radiation has been recognized for more than a century (e.g., Cope, 1883). It has acquired such canid characters as a low septum inside the bulla, reduced parastral of M1, and lost M3 (a few individuals, approximately 7% of all samples, still have an M3), but is still primitive enough to be close to the ancestry of many later canids. Therefore, except for a few minor peculiarities (such as a posteriorly positioned internal cingulum of M1), *H. gregarius* possesses no diagnostic autapomorphies and serves well as a primitive morphotype of the family Canidae. However, also because of its generalized morphologies, *H. gregarius* betrays no special similarity that can link it with any particular clade of canids.

"*Hesperocyon*" *coloradensis* Wang, 1994

**Holotype**—KUVP 85067, partial skull and mandible with left I3–C1, P2–M1, right I2–C1, P2–M1, left c1–m2, right i3–m2, and partial postcranial skeleton.
Figure 2. Skull and mandible of *Hesperocyon gregarius*, USNM 437888, from Wulff Ranch, southeast of Douglas, Converse County, Wyoming, in the Oreilla Member of the Brule Formation, Orellan. A, lateral view; B, ventral view; and C, dorsal view. Scale equals 20 mm.
Type Locality—Colorado locality number 46 of University of Kansas, Cedar Creek Member of White River Formation, Logan County, Colorado. Orellan.

Diagnosis—Signifying its more advanced status than Hesperocyon gregarius, "H." coloradensis has a ventrally directed paroccipital process, although it is still primitive in its lack of fusion of the process with the entotympanic (as in Mesocyon). "H." coloradensis is also 18% larger than H. gregarius and has a more robust mandible. It tends to have a less posteriorly positioned internal cingulum than in H. gregarius.

Geologic and Geographic Range—Cedar Creek Member of the White River Formation, northeastern Colorado. Orellan.

Comments—Cope (1873b, p. 9) recognized a species from the Tertiary of northeast Colorado, Canis lippincottianus, which was frequently used to include the larger-sized individuals that could not fit comfortably into H. gregarius (Matthew, 1901; Scott and Jepsen, 1936; Elliott, 1980; Galbreath, 1953). The type of C. lippincottianus (AMNH 5327a, a ramus fragment with an isolated m2), however, may be a small Daphoenus because of the wide talonid of its m2 with a well-developed entoconid (see Wang, 1994). Nonetheless, Cope's concept of a form larger than H. gregarius is confirmed.

Intermediate in size between Hesperocyon gregarius and "Mesocyon" temnodon, "H." coloradensis is at the base of the Mesocyon-Enhydrocyon-Osbornodon clade because of its initial development of a ventrally directed paroccipital process (node 7 of Fig. 10 and Table 1). Its membership in this latter clade further renders Hesperocyon a paraphyletic taxon, a fact already apparent before the inclusion of "H." coloradensis (see comments under the genus).

Mesocyon Scott, 1890

Type Species—Mesocyon coryphaeus (Cope, 1879).

Included Species—Mesocyon coryphaeus (Cope, 1879), "M." temnodon (Wortman and Matthew, 1899), and M. brachyops Merriam, 1906.

Diagnosis—Compared to Hesperocyon and Paraenhydrocyon, Mesocyon is more derived in its robust and long paroccipital process which is directed ventrally. The two derived species, M. coryphaeus and M. brachyops, have further acquired a small fossa on the supraoccipital above foramen magnum. Mesocyon is still primitive in its lack of robust premolars and broadened M2 found in Cynodesmus. In addition, the paroccipital process of Mesocyon is not thickened at the base as seen in more derived (geologically later) individuals of Cynodesmus. Mesocyon is paraphyletic and has no autapomorphy of its own (see Comments below).

Geologic and Geographic Range—John Day Formation of central Oregon; Otay and Sespe formations of southern California; Brule-Gering and correlative formations of the northern Great Plains. Orellan to Arikareean.

Comments—Mesocyon includes primitive members of the Mesocyon-Enhydrocyon clade (M. coryphaeus and M. brachyops). Its most primitive species "M." temnodon, however, is probably a basal taxon of the larger Mesocyon-Enhydrocyon-Osbornodon clade (Fig. 10), and the genus Mesocyon is thus paraphyletic. Only "M." temnodon is summarized below, which has fossil records in the White River Group. The Arikareean species, M. coryphaeus and M. brachyops, are not considered in this paper.
"Mesocyon" tenmodon  
(Wortman and Matthew, 1899)  
Figure 3

Lectotype—AMNH 8753, partial left ramus with c1, p2–3.

Type Locality—Horizon C of Castle Rock "in either R53 or R54, T11N, Logan County" (Galbreath, 1953, p. 50), Vista Member of White River Formation, northeastern Colorado. Whitneyan.

Diagnosis—Compared to "Hesperocyon" coloradenisis, the paroccipital process of "Mesocyon" tenmodon is fully ventrally directed so that its base touches and fuses with the posterior surface of the entotympanic, a derived character shared by all subsequent taxa of the Mesocyon-Enhydrocyon-Osbornodon clade. In contrast to M. coryphaeus and M. brachyops, "M." tenmodon possesses primitive features such as a well-developed anterior cingulum of P4, the absence of a pair of round fossae above the foramen magnum, and the lack of strong elongation of the paroccipital process.

Geologic and Geographic Range—Whitneyan of northeastern Colorado and western Nebraska; Orellan to early Arikareean of southwestern South Dakota.

Comments—Since its first establishment by Wortman and Matthew (1899), "Mesocyon" tenmodon has largely remained in obscurity because of the lack of adequate description and clear assignment of a type. "M." tenmodon is now known from larger numbers of specimens and more complete material, and has a long geologic history spanning the Orellan to early Arikareean. This species is at the base of a clade which includes such meso- and hypercarnivorous taxa as Mesocyon, Cynodesmus, Sunkahetanka, Philotrox, Enhydrocyon, and Osbornodon (Fig. 10, node 8).

Cynodesmus Scott, 1893

Type Species—Cynodesmus thooides Scott, 1893.

Included Species—Cynodesmus thooides Scott, 1893; and C. martini Wang, 1994.

Diagnosis—Compared to Mesocyon, Cynodesmus has more robust and closely spaced premolars and a larger protocone of P4. Furthermore, Cynodesmus has two autapomorphies: a strong paroccipital process with a posterior keel and a transversely broadened M2.

Geologic and Geographic Range—Whitneyan to early Arikareean of Nebraska, South Dakota, and Montana.

Comments—Considerable confusion exists in the taxonomy of Cynodesmus and 13 species had been assigned to this genus (see Wang, 1994). It is now restricted to two species. Only the type species, C. thooides, occurs in the White River Group and is summarized below.

Cynodesmus thooides Scott, 1893  
Figure 4

Holotype—YPM-PU 10412, partial skull with nearly complete upper dentitions and partial mandible with left i1–h3 and right i1–p3.

Type Locality—Fort Logan Formation of western Montana, early Arikareean.

Diagnosis—Cynodesmus thooides has derived characters that distinguish it from Mesocyon: stronger premolars, heavy paroccipital process with a keel, and broad M2. However, it has many primitive features compared to its sister-species C. martini: smaller size, less robust skull and teeth, slender rostrum, lower sagittal crest, and presence of a P1.

Geologic and Geographic Range—Whitneyan to early Arikareean of western Nebraska, South Dakota, and western Montana.

Comments—Cynodesmus thooides is of the same size as Mesocyon coryphaeus west of the continental divide. Morphological differences between them are rather subtle, and this species pair probably played the same ecological roles. C. thooides is a primitive species of the Mesocyon-Enhydrocyon clade, and is at the basal stem of a series of progressively more hypercarnivorous taxa in the Arikareean such as Sunkahetanka and Philotrox, terminating in Enhydrocyon.

Sunkahetanka geringensis  
(Barbour and Schultz, 1935)

Holotype—UNSM 1092, nearly complete skull, mandible, and postcranial skeleton.

Type Locality—Redington Gap, west of Bridgeport, Morrill County, Nebraska. Brown Siltstone beds, uppermost Brule Formation, earliest early Arikareean.

Diagnosis—Sunkahetanka geringensis has two synapomorphies that distinguish it from Cynodesmus: more massive premolars that tend to be imbricated and reduced metaconid on lower molars. In addition, S. geringensis possesses some subtle features that further differentiate it from Cynodesmus and Mesocyon: larger postorbital process; posteriorly extended nuchal crest that does not overhang the occipital condyle; deep and laterally arched zygomatic arch; bulla narrowed anteriorly; slightly antero-posteriorly constricted M1 trigon; crowded lower incisors; and wider m1.

Geologic and Geographic Range—Uppermost part of the Brule Formation in western Nebraska, and lower Sharp's Formation of western South Dakota. Early Arikareean.

Comments—Following the study by Tedford et al. (1985, 1987), the sandy rocks containing the type of Sunkahetanka geringensis are now regarded as the channel facies of the Brown Siltstone in the uppermost part of the Brule Formation, instead of the traditional Gering Formation. S. geringensis is thus properly discussed here, even though it is already in the Arikareean. Corresponding to this young age, S. geringensis is the largest and most hypercarnivorous among all White River canids, and shows indications of robustness more fully developed only in Enhydrocyon. It is otherwise transitional between Cynodesmus and the Philotrox-Enhydrocyon clade in cranial and dental morphology.
Figure 4. Skull, mandible, and dentitions of *Cynodesmus thooides*, F:AM 63382, from west side of Potato Creek, 3 miles east of Morgan Ranch near the head of east branch of Red Water Creek, Washabaugh County, South Dakota, in the Brule Formation, Whitneyan. A, lateral view of skull and mandible; B, occlusal view of upper left dentition, P3–M2 drawn from right side; and C, occlusal view of lower left dentition (reversed from right side).
Osbornodon Wang, 1994

**Type Species**—*Osbornodon fricki* Wang, 1994.

**Included Species**—*Osbornodon fricki* Wang, 1994; *O. renjieii* Wang, 1994; *O. sesnsoni* (Macdonald, 1967); *O. iamonensis* (Sellards, 1916); and *O. brachypus* (Cope, 1881).

**Diagnosis**—*Osbornodon* is mainly distinguished from other hesperocyonines by 2 synapomorphies: antero-posteriorly elongated (thus more quadrate) upper molars and enlargement of M2 and m2; and basined (bicuspids) talonid of m1–2. Later species of *Osbornodon* progressively acquire additional derived characters that set the genus further apart from other lineages of hesperocyonines: long rostrum; large frontal sinus; posteriorly expanded paroccipital process; short, mediodiasternally flattened angular process; and enlarged p4 relative to p3.


**Comments**—*Osbornodon* represents one clade of hesperocyonines with independently acquired many skull and dental features commonly found in the subfamilies Borophaginae and Caninae. It is superficially closer to the Caninae with such features as: slender rostrum, elongated premolars, quadrate M1s, and basined talonids. However, the talonid basin, a key synapomorphy of the sister-taxon Borophaginae and Caninae, is fundamentally different in *Osbornodon* from that of the two later subfamilies. The bicuspids talonid in *Osbornodon* lacks a transverse ridge between the hypoconid and entoconid, present in most borophagines and canines, and the talonid basin is surrounded by crestlike entoconid on the lingual side rather than a cuspprestructured entoconid as in borophagines and canines.

*Osbornodon renjieii* Wang, 1994

**Figure 5**

**Holotype**—F:AM 63316, maxillary and mandible fragments with right P4–M1, left c1–p3, and right p2, p4–m2.

**Type Locality**—Leo Fitterer Ranch locality, 13 miles south and 8 miles west of Dickinson, Stark County, North Dakota, late Orellan.

**Diagnosis**—*O. renjieii* is the most primitive species of *Osbornodon* and has no additional synapomorphy besides those for the genus (quadrate, enlarged M1–2 and basined talonid). In addition to its small size, *O. renjieii* is distinct from *O. sesnsoni*, the next more derived species in *Osbornodon* clade, by its relatively broad premolars (primitive). Compared to "Hesperocyon" coloradensis, *O. renjieii* has a completely ventrally directed paroccipital process, a derived character shared with the Mesocyon–Enhydrocyon clade.

**Geologic and Geographic Range**—Orellan of southwestern North Dakota; Whitneyan of southwestern South Dakota and western Nebraska.

**Comments**—Smallest of all *Osbornodon*, *O. renjieii* is also the earliest and most primitive species of the genus. Besides the above diagnostic characters, it is little different from such primitive hesperocyonines as "Hesperocyon" coloradensis and "Mesocyon" temnodon, which are also of approximately the same size as *O. renjieii*.

*Osbornodon sesnsoni* (Macdonald, 1967)

**Holotype**—LACM 17039, partial broken skull and mandible with left P1–M2, right I3–C1, P2–M2, left c1, p2–m3, and right c1, p3–m1; postcranial fragments.

**Type Locality**—Wolff Ranch, Shannon County, South Dakota. Poleslide Member of the Brule Formation, Whitneyan.

**Diagnosis**—Larger than *O. renjieii*, *Osbornodon sesnsoni* has one derived character distinguishing it from the former: slender upper and lower premolars (high length/width ratio). The overall skull proportion of *O. sesnsoni* is also slightly more robust than in *O. renjieii*. Compared to later species of *Osbornodon* (*O. iamonensis*, *O. brachypus*, and *O. fricki*), *O. sesnsoni* shows the following primitive characteristics: relatively short rostrum; low sagittal crest; lack of an inflated frontal sinus; a round infraorbital foramen; unredced bulla; paroccipital process not posteriorly expanded; mastoid process not reduced; p4 not enlarged; and a M2 less enlarged relative to M1.

**Geologic and Geographic Range**—*Osbornodon sesnsoni* is known only in the Poleslide Member of Brule Formation, Whitneyan of southwestern South Dakota.

**Comments**—Beside its larger size and slender premolars, *Osbornodon sesnsoni* is little different from the basal species *O. renjieii*. It is a transitional species that gave rise to the successively larger *O. iamonensis*, *O. brachypus*, and *O. fricki* in the late Arikareean to early Barstovian. There is a long hiatus of fossil record between *O. sesnsoni* and the first occurrence of *O. iamonensis* in the Marsland Formation of western Nebraska. This is also reflected in the large morphological gap between these two species (see Diagnosis).

**Paraenhydrocyon Wang, 1994**

**Type Species**—*Paraenhydrocyon wallovianus* (Cope, 1881).

**Included Species**—*Paraenhydrocyon wallovianus* (Cope, 1881); *P. josephi* (Cope, 1881); *P. robustus* (Matthew, 1907).

**Diagnosis**—Members of *Paraenhydrocyon* can be distinguished from other genera of hesperocyonines in having three synapomorphies: a deeply pocketed angular process, a long, slender mandible with a deepmasseteric fossa, and a dorso-ventrally compressed paroccipital process. The two more advanced species, *P. robustus* and *P. wallovianus*, are further derived in their narrow premolars with reduced/absent accessory cusps and in their reduced/absent metaconids on m1–2. *Paraenhydrocyon* retains a posteriorly directed paroccipital process, a
Figure 5. Mandible and teeth of *Osbornodon renjiei*, F:AM 63316, holotype, from Leo Fitterer Ranch, 13 miles south and 8 miles west of Dickinson, Stark County, North Dakota, Orellan. A, lateral view of upper P4–M1 and mandible (the anterior part between c1–p3 is reconstructed from that of left side); B, occlusal view of the upper teeth; and C, occlusal view of the lower teeth.
primitive character in contrast to ventrally oriented processes in most clades of hesperocyonines.

**Geologic and Geographic Range**—Brule Formation of southwestern South Dakota; Gering-Marsland formations of eastern Wyoming, western Nebraska, and western South Dakota; John Day Formation of central Oregon; Delahoe Formation of Texas. Whitneyan to late Arikareean.

**Comments**—*Paraenhydrocyon* has striking parallels to *Enhydrocyon*, particularly in the development of hypercarnivorous carnassial teeth. The reduction or loss of the metaconid in lower first and second molars and the semicircular internal cingulum of the upper first molar makes isolated molars of the two genera difficult to differentiate. This dental similarity was noted by Loomis (1936), who thus placed *Temnocyon venator* (= *P. wallovianus*) under *Enhydrocyon*. However, there are some fundamental differences in the shape of the premolars and the proportions of the skulls between *Paraenhydrocyon* and *Enhydrocyon* that suggest independent evolutionary lineages. Only *P. josephi*, which has White River occurrence, is summarized below; the two more derived species of *Paraenhydrocyon* (*P. robustus* and *P. wallovianus*) occur only in the Arikareean, and will not be further discussed.

*Paraenhydrocyon josephi* (Cope, 1881)

**Figure 6**

**Holotype**—AMNH 6878, anterior half of skull with complete upper teeth except broken canines and incisors.

**Type Locality**—John Day Formation of Oregon, Arikareean.

**Diagnosis**—*P. josephi* is at the base of the *Paraenhydrocyon* clade and can be distinguished from other hesperocyonines by the synapomorphies of the genus: a deeply excavated masseteric fossa that expands downward so that the ventral margin of the fossa is closer to the ventral border of the mandible; a dorso-ventrally flattened paroccipital process; and an angular process of mandible with a deeply pocketed fossa for the superior ramus of the medial pterygoid muscle. *P. josephi* is distinct from the more advanced *P. robustus* and *P. wallovianus* mostly in such primitive dental structures as: a distinct anterior and posterior cingular cusp and a posterior accessory cusp in most of the premolars; presence of a small cingulum-like parastyle on P4; M1 trigon basin not deeply excavated; and relatively large metaconid on m1–2.

**Geologic and Geographic Range**—Brule Formation of southwestern South Dakota; Arikareean Group of eastern Wyoming and western Nebraska; John Day Formation of central Oregon. Whitneyan to Late Arikareean.

**Comments**—Except for its larger size and the derived characters listed above, *P. josephi* is quite similar to *Hesperocyon*. Furthermore, *P. josephi* retains a primitively posteriorly oriented paroccipital process as opposed to ventrally directed ones in all other derived clades of hesperocyonines. *P. josephi* is postulated to be directly derived from *Hesperocyon gregarius* (Fig. 10). In fact, isolated individuals of *H. gregarius* may exhibit tendencies toward a pocketed angular process, a synapomorphy of *Paraenhydrocyon*. *P. josephi* gave rise to *P. robustus*, an intermediate species that eventually leads to the hypercarnivorous *P. wallovianus*.

**Ectopocynus** Wang, 1994

**Type Species**—*Ectopocynus simplicidens* Wang, 1994.


**Diagnosis**—*Ectopocynus* is distinguished on the basis of its short, blunt, and robust lower premolars with extremely reduced or absent accessory and cingular cusps, derived characters unique to the genus. Such simple cusp patterns of the premolars are distinct from those of *Enhydrocyon* which has similarly robust premolars but has well-developed accessory and cingular cusps. Except for one referred individual of *E. antiquus* from the Whitneyan, all have lost their p1s (derived). The metaconids of m1–2 are also significantly reduced even in the basal species *E. antiquus*, in contrast to other lineages of hesperocyonines which reduce their metaconids only in larger-sized, highly derived forms.

**Geologic and Geographic Range**—Poleslide Member of Brule Formation, western South Dakota; Lower Arikareean Group of eastern Wyoming; and Runningwater Formation of western Nebraska. Whitneyan to Middle Hemingfordian.

**Comments**—This rare lineage is known only from mandibles and a few upper teeth (all in the Frick Collection of the AMNH). The limited materials available do not permit a precise assessment of the phylogenetic position of *Ectopocynus* to other hesperocyonines. No synapomorphy unites it with any other clades, although a few characteristics associated with the robust mandible and teeth (e.g., loss of metaconids, loss of p1 and m3, etc.) are also found in derived species of *Enhydrocyon*. These characters are most likely to be independently derived, not only because of the present recognition of the primitive species *Ectopocynus antiquus* that does not possess these derived characters, but also because of the detailed anatomical differences between *Ectopocynus* and *Enhydrocyon* (see Diagnosis).

Only one specimen (F:AM 63376) is referred to *Ectopocynus antiquus* from the Brule Formation of South Dakota, which will be discussed below. The two later (Arikareean to Hemingfordian) and more advanced species, *E. intermedius* and *E. simplicidens*, are not further discussed.

**Ectopocynus antiquus** Wang, 1994

**Holotype**—F:AM 54090, partial right ramus with i3–c1, p2, p4–m3.

**Type Locality**—From Little Muddy Creek locality, in Lower Arikareean Group, southeast of Lusk, 20
miles south of Keeline and west of Spanish Diggings, Niobrara County, Wyoming. Early Arikareean.

**Diagnosis**—Approximately the size of "Hesperocyon" coloradensis, *Ectopocynus antiquus* can be distinguished from the former by its loss of p1, its short but wide (in occlusal view) lower premolars, its reduced metaconid of m1, and its reduced m2–3, characters that are synapomorphies for the genus *Ectopocynus* (except the reduced metaconid, most of these characters are seen in holotype but not in F:AM 63376, see Comments below). In addition to its much smaller (21%) size than *E. intermedius*, *E. antiquus* also has relatively smaller and narrower lower premolars and molars. *E. antiquus* retains primitive characters that can be used to differentiate it from *E. simpliciden*: the presence of a small metaconid on m1 and an m3.

**Geologic and Geographic Range**—Brule Formation of western South Dakota and Lower Arikareean Group of eastern Wyoming. Whitneyan to early Arikareean.

**Comments**—The presence of this small, *Hesperocyon*-sized canid in the Whitneyan of the White River Group is indicated by a single specimen, F:AM 63376, a partial right ramus from Hay Creek of Washabaugh.

Figure 6. Skull, mandible, and dentitions of *Paraenhydrocyon josephi*, F:AM 54115, from 4 miles east of Tremain, Goshen County, Wyoming, in lower Arikareean Group, early Arikareean. A, lateral view of skull and mandible; B, occlusal view of upper left teeth; and C, occlusal view of lower left teeth, P4 restored from that of right side.
County, South Dakota. The reference of F:AM 63376 to *Ectopocynus antiquus* is mainly based on its reduced metaconids on m1–2. Although reduction of metaconid has been independently developed in other clades of hesperocyonines (e.g., *Enhydrocyon* and *Paraenhydrocyon*), most lineages that acquired it had done so in association with a number of hypercarnivorous features including large size, robust premolars, etc. The reduction of the metaconid in *Ec. antiquus* is thus unique in its lack of association with other hypercarnivorous characters, and allows the recognition of F:AM 63367 as belonging to the *Ectopocynus* clade. On the other hand, the possession of many primitive characters in F:AM 63367 (e.g., presence of a p1 and unshortened premolars) helps to link the *Ectopocynus* clade directly to *Hesperocyon*.

Subfamily BOROPHAGINAE Simpson, 1945


**Geologic and Geographic Range of White River Taxa**—Orellan through Arikareean of North America.

**Diagnosis**—The subfamily Borophaginae shares with the Caninae the following derived characteristics that distinguish them from the primitive hesperocyonines: a bicuspid talonid with a salient entoconid on the lower first molars, reduced labial cingulum and parastyle of upper molars, and metaconid larger than protoconid in m2. Borophagine after the Arikareean developed more synapomorphies, such as broadened and elongated posterior process of the premaxillary that meets the...
frontal, lateral accessory cusps on the upper third incisors, well-developed posterior accessory cusps on premolars, and transverse ridges on the talonid cusps of lower first molars.

Comments — The earliest Borophagininae can be recognized in the Orellan strata of the White River Group, although specimens of the borophagines are far less abundant than those of the hesperocyonines. Two White River species are presently known in the literature (summarized below), but additional undescribed taxa are present in the Frick Collection and the University of Nebraska.

*C Cormocyon pavidus* (Stock, 1933)

*Figure 7*

**Holotype** — LACM 466, crushed anterior half skull and mandible with left P2–M1, right P3–M2, left and right p2–m2, and alveoli for p1 and m3.

**Type Locality** — Kew Quarry Local Fauna, Las Posas Hills, Ventura County, California. Sespe Formation, early Arikareean.

**Diagnosis** — The smallest of all White River canids, *Cormocyon pavidus* can be distinguished from species of Hesperocyon on the basis of a number of subtle but significant features, which lead to the recognition of the earliest Borophagininae: reduced labial cingulum and parastyle of M1, relatively large M2, a salient encondont on m1 enclosing a talonid basin, and m2 metacodon slightly larger than protoconid. *C. pavidus* is still primitive compared to the more derived taxa in the Arikareean of John Day and Great Plains (e.g., *C. oregonensis*, *C. copei*, *C. leptodus*) in the following plesiomorphic conditions: unexpanded braincase, posteriorly directed paroccipital process, and rather transversely elongated upper molars which lack a well-developed metacone.

**Geologic and Geographic Range** — Sespe Formation, California; Cedar Creek Member of White River Formation, Colorado; Whitney Member of Brule Formation, Nebraska; Poleside Member of Brule Formation, South Dakota. Orellan to Whitney.

**Comments** — Since its initial description by Stock (1933), *Cormocyon pavidus* has remained an enigma avoided by most students of early canids. The type specimen’s geographic location far from the main occurrences of *Hesperocyon* in the northern Great Plains, and its poor condition of preservation posed special difficulties in linking *C. pavidus* with taxa from the Great Plains.

Galbreath (1953) recognized a small-sized *Hesperocyon* from the Tertiary of northeastern Colorado and informally called it “Pseudocyonidictis sp. (small form).” The Colorado specimens are here referred to *Cormocyon pavidus*. In addition, a few Whitneyan specimens from Nebraska and South Dakota are also referable to this species. In particular, F:AM 63970, a slightly crushed skull and mandible from the Whitneyan of Nebraska, represents the most complete individual available (Fig. 7). Little different from that of *Hesperocyon*, the skull of *Cormocyon pavidus* remains mostly primitive in its posteriorly oriented paroccipital process, its unexpanded braincase, and its possession of a shallow supraneatal fossa.

The present reference of the Great Plains materials to *C. pavidus* greatly increases its geological and geographical distribution away from its formerly isolated occurrence in California. Our recognition of *C. pavidus* in the Plains establishes it as the earliest and most primitive borophagine, and thus provides an ideal model for the primitive morphotype of the Borophagininae (Wang, 1990, 1994). From this basal position, a number of primitive borophagines are derivable through slight dental modification and size increase, such as *C. leptodus* from the Arikareean of the Great Plains, and *C. oregonensis* and *C. copei* from the ?Whitneyan/ Arikareean of John Day, Oregon. Also derivable from *C. pavidus*, is a small clade of hypocarnivorous taxa represented by *Oxetocyon* described below.

*Oxetocyon cuspidatus* Green, 1954

*Figure 8*

**Holotype** — SDSM 2980, left maxillary fragment with M1 and alveola of P4.

**Type Locality** — “Protoceras channels, 7 miles east of Rockyford, Shannon County, South Dakota” (Green, 1954).

**Diagnosis** — *Oxetocyon cuspidatus* is highly apomorphic among White River canids. It is characterized by a hypocarnivorous dentition with prominent developments of a metacone and a “hypocone” created by a transverse notch on the internal cingulum of M1. The M2 is enlarged and similarly constructed as the M1. The P4 has a well-developed lingual cingulum although no hypocone is developed. Talonid cusps of the lower molars are conical in contrast to primitives crest-like cusps in *Hesperocyon* and *Cormocyon*. The protoconid and metaconid of the m2 are similarly cuspidate.

**Geologic and Geographic Range** — Whitneyan of South Dakota and Nebraska.

**Comments** — The peculiar M1 in *Oxetocyon* is unique among White River canids. The transverse groove on the internal cingulum is continuous with notches between the paracone/metacone and protocone/metacone pairs so that the upper molars are evenly divided into anterior and posterior halves. Such a divided appearance of M1 allows unambiguous recognition of *Oxetocyon*, even based on the single M1 of the holotype.

Specimens collected subsequent to the first publication of the holotype have greatly increased our knowledge of this rare taxon. The morphology of the P4-M2 and part of the skull has been revealed (UNSM 2665, see Tanner, 1973), and the lower teeth and the horizontal ramus (UNSM 25698, partial right ramus with p4-m3 and alveola of p3, see Fig. 8) are presently referred to *Oxetocyon cuspidatus* based on agreement in size of the ramus with the upper jaws. Its p3 is very similar to that of *Cormocyon pavidus* with a distinct posterior accessory cusp and small anterior and posterior circular cusps. The lower molars have the same proportion as
Figure 8. Skull and teeth of *Oxetocyon cuspidatus*. A–C, UNSM 2665, from Roundhouse Rock, Morrill County, Nebraska, in the Whitney Member of the Brule Formation; D, SDSM 2980, holotype, from 7 miles east of Rockford, Shannon County, South Dakota, in the Poleslide Member of the Brule Formation; E and G, UNSM 25381, from 7 miles southeast of Broadwater, Morrill County, Nebraska, in the Whitney Member of the Brule Formation; F and H, UNSM 25698. The scale in A also applies to D, G, and H, and that in C to B, E, and F.

those of *C. pavidus*. However, the talonid cusps of m1 and all cusps of m2 are conical in form, instead of crest-like as in *Cormocyon* and all hesperocyonines. Such cuspidate (bunodont) cusp morphology is typically found in hypocarnivorous carnivores, and forms the basis of our reference of UNSM 25698 to *Oxetocyon*, which is the only candidate for a hypocarnivorous canid in the right size range. The trigonid of the m1 is still relatively high for a hypocarnivorous taxon.

Subfamily CANINAE Gray, 1821
*Leptocyon* sp.

Figure 9

**Comments**—The earliest known records of the subfamily Caninae are represented by a series of small species of *Leptocyon* in the Arikareean and later deposits (Tedford and Taylor, MS). Although no published record exists for the presence of canines in pre-Arikareean deposits, our preliminary survey suggests potential candidates in the White River deposits. An Orellan specimen (UNSM 25354, left ramus fragment with p3–m1, from Sioux County, Nebraska, Fig. 9) shows such *Leptocyon*-like features as: slender, shallow ramus, slender premolars, complete loss of p3 posterior accessory cusp (that on p4 is still

Figure 9. Mandible fragment of *Leptocyon* sp., UNSM 25354, from Sioux County, Nebraska, in the Orella Member of the Brule Formation. A, lateral view of ramus; B, occlusal view of lower teeth.
well developed), and well-developed entoconid crest on m1 nearly equal in height to that of hypoconid and occupying nearly half of the talonid basin. UNSM 25354 primitively has a short (closed) trigonid of the m1. Such an Orellan occurrence of the Caninae is consistent with a sister-group relationship between the Borophaginae (earliest record Orellan) and Caninae (Tedford, 1978).

PHYLOGENY OF EARLY CANIDS

The phylogeny shown in Figure 10 represents a synthesis of our cladistic analyses of the basal cynoids (Wang and Tedford, 1994), the hesperocyonines (Wang, 1994), the canines (Tedford and Taylor, MS), and our on-going research on primitive borophagines. taxa are included if they have records in the White River Group (only published taxa are presented). Major characters that support this arrangement are listed in Table 1.

Cope (1877, 1883) proposed that the origin of canids was to be found among forms then placed in the Creodonta. More specifically, the "micadids" were postulated as the probable ancestral stock for canids (Cope, 1880, p. 81), and this broad statement has since gained nearly universal acceptance by almost every student of carnivores (e.g., Matthew, 1930; Clark, 1939; Tedford, 1978; Gustafson, 1986), although considerable confusion exists concerning the precise phylogenetic relationships among the "micadids," and how they in turn relate to the living families of Carnivora. Wortman and Matthew (1899) erected the genus Procynodontis in the Uintan and indicated an ancestor-descendant relationship between Procynodontis and Hesperocyon (then known as Cynodontis). Clark (1939) more explicitly allied his late Uintan species Miacin gracilis (here synonymized with Procynodontis vulpiceps) to Hesperocyon. The main evidence cited by Clark was the canine-like postcranial skeleton of P. vulpiceps, e.g., slender and straight limb bones, reduction of deltoid ridge in humerus. However, as acknowledged by Clark (1939), the dentition of P. vulpiceps (Fig. 1A) is little advanced toward canids except its possession of a posterior accessory cusp in the P3 and p3. As in most "micadids," the P4 protocone of P. vulpiceps is still large and isolated from the base of paracone, in contrast to a reduced protocone more appressed to the paracone in H. gregarius and other canids. P. vulpiceps has a primitive M1 with a large parastyle and an internal cingulum surrounding the protocone, unlike that of H. gregarius whose parastyle is reduced to a narrow cingulum and whose internal cingulum is incomplete at the anterior segment. The m1 of P. vulpiceps is equally primitive with a wide trigonid relative to the talonid. Our recent cladistic analysis (Wang and Tedford, 1994) is in essential agreement with the conclusions by Wortman and Matthew (1899) and particularly Clark (1939), and placed P. vulpiceps ("Miacin" gracilis in Wang and Tedford, 1994) as the closest sister-taxon of the Canidae.

The above difference in dental morphology between Procynodontis and Hesperocyon is partially bridged by the recent discovery of Prohesperocyon wilsoni from the Vieja Group of southwestern Texas (Gustafson, 1986). Teeth of P. wilsoni are slightly advanced toward the condition present in Hesperocyon in having a more reduced anterior portion of the internal cingulum of M1, reduction of M1 parastyle and loss of the parastyle notch, absence of M3 (Fig. 1B), and a slightly more elongated shearing blade of m1. The remaining dental morphology of P. wilsoni is still primitive and similar to those of "micad" carnivores: a large protocone on P4, a large parastyle on M1 (relative to that in Hesperocyon), a wide trigonid and a narrow talonid on m1, and an m2 with the protoconid larger than the metaconid. Our study of the basicranium further demonstrates that the middle ear region of P. wilsoni is essentially canid-like except for its lack of a low septum within the well ossified entotympanic bulla (Wang and Tedford, 1994; Table 1, node 1).

The advanced status of the White River and more derived canids over Prohesperocyon wilsoni is well supported by a number of basicranial and dental characters: a partial bony septum on the internal surface of the bulla, a reduced protocone of P4, a M1 with a reduced parastyle, an elongated shearing blade (trigonid) of m1, and nearly equal size of metaconid and protoconid on m2 (node 2). Resolutions of phylogenetic relationships among the White River and later canids, however, are poor (multichotomy at node 2) despite well-defined autapomorphies for subsequent clades. Hesperocyon, as presently defined, is clearly paraphyletic. Paraphyly would not be avoidable even for the single type species H. gregarius if the ancestor-descendant relationships between it and other hesperocyonines, as well as the borophagines and canines, are correctly reconstructed (Fig. 10). The Hesperocyoninae is also paraphyletic for lack of a synapomorphy uniting all of its genera.

The clade represented by such familiar genera as Mesocyon and Enhydrocyon has the best documented fossil records (node 6). Indeed, this clade is the most enduring part of canid phylogenies proposed by many authors (Cope, 1883; Matthew, 1930; Macdonald, 1963; Tedford, 1978). It involves a progressive increase in hypercarnivory from a small ancestral "H." colordensis, through median-sized Mesocyon (paraphyletic) and Cynodesmus, to the transitional Sunkahetanka and Philotrox, and ending with the large Enhydrocyon.

The recently recognized clade Osbornodon is characterized by quadrate and enlarged upper molars, basined talonids on lower molars, narrowed premolars, as well as a suite of synapomorphies (e.g., long rostrum,
Figure 10. Phylogeny and geologic distribution of the White River canids and related taxa; phylogenetic analysis follows Tedford and Taylor (MS), Wang (1994), and Wang and Tedford (1994). Numbers beside the nodes (black dots) correspond to those in Table 1. Arrows lead to non-White River canids not reviewed in this paper, and indicate the time of origin (at base of the arrow) of these taxa. In some cases (Paraenhydrocyon and Cynodesmus), ancestral-descendant relationships are suggested by stratigraphic and/or morphologic continuity. Stratigraphic correlations are based on Emry et al. (1987) and Tedford et al. (1987). Calibrations by radiometric dates are based on Swisher and Prothero (1990) and Prothero and Swisher (1992).
Table 1. Shared-derived characters for early canids as identified at major nodes in Fig. 10. Character analysis for hesperocynoynine part of the cladogram is based on Wang (1994).

Node 1, Family Canidae
Ossified entotympanic bulla; extrabullar position of internal carotid artery and loss of stapedial artery; presence of a small suprameatal fossa; reduction of M1 parastyle and loss of a parastyle notch; reduction of anterior segment of internal cingulum of M1; absent or extremely reduced M3; presence of posterior accessory cusps on P3 and p3.

Node 2, Subfamily Hesperocyoninae (minus Node 3, Borophaginae—Caninae clade)
Low septum inside bulla; reduced protocone of P4; further reduction of parastyle of M1; elongated shearing blade of m1; metaconid and protoconid of m2 subequal.

Node 3, Borophaginae—Caninae clade
Bicuspid talonid of m1 with a salient entoconid; reduction of parastyle in upper molars; internal cingulum of M1 expanded anteriorly to surround the protocone.

Node 4, Subfamily Caninae (as defined by primitive Leptocyon)
Narrow premolars with reduced posterior accessory cusps; presence of diastemata between premolars; elongated shearing blade of m1; slender horizontal ramus.

Node 5, Subfamily Borophaginae
Primitive borophagines (e.g., Cormocyon pavidus) have no synapomorphies distinct from the Caninae clade, although slightly more derived borophagines progressively acquired characters such as: strong posterior premaxillary process fused with the frontal process, and presence of lateral accessory cusps on upper third incisors.

Node 6, Paraenhydrocyon clade
Dorso-ventrally compressed paroccipital process; deep masseteric fossa which forms a pocket at the ventral border of the fossa; medially pocketed angular process of mandible.

Node 7, "Hesperocyon" coloradensis—Osbornodon clade
Paroccipital process beginning to rotate ventrally and to touch the posterior base entotympanic.

Node 8, "Mesocyon" temnodon—Osbornodon clade
Paroccipital process completely ventrally directed and extensively fused with posterior surface of entotympanic.

Node 9, Mesocyon—Enhydrocyon clade
Fossa on supraoccipital above foramen magnum; paroccipital elongated and robust.

Node 10, Sunkahetanka—Enhydrocyon clade
Massive premolars that tend to be imbricated; reduced metaconid on lower molars.

Node 11, Osbornodon clade
Enlarged entoconid to encircle a basined talonid of m1; quadrate and enlarged upper molars.

Node 12, Osbornodon sesnoni and advanced Osbornodon
Narrowed premolars.

Node 13, Ectopocynus clade
Short, blunt premolars lacking accessory and cingular cusps; reduced metaconid of lower molars; loss of p1.

The relationship between Hesperocyon gregarius and the borophagine clade is bridged by Cormocyon pavidus, one of the smallest and most primitive borophagines recognized in the White River Group. Little different from Hesperocyon, C. pavidus serves as an ideal morphotype for the Borophagines. Its apomorphic characters thus distinguish the borophagine clade: bicuspid talonid of m1, reduced labial cingulum and parastyle of M1, enlarged M2, and m2 metaconid slightly larger than paraconid. Besides Cormocyon pavidus, the Borophagines of the White River Group had evolved a distinct hypocarnivorous clade as represented by Oxtocyon cuspidatus. Teeth of the Oxtocyon are highly derived and suddenly appear in the Whitneyan without primitive precursors.

A sister-group relationship between the Borophagineae and Caninae is supported by basined talonids on the m1, reduced parastyle of upper molars, and enlarged metaconids of m2. The canine clade is further distinguished from the borophagine clade by dental synapomorphies present in primitive Leptocyon: narrow premolars, reduction of posterior accessory cusps in premolars, presence of diastema between premolars, elongated
shearing blade (open trigonid) of lower carnassial, and slender horizontal ramus.

CONCLUSIONS

If the reconstructed pattern of relationship (Fig. 10) is reasonably accurate, the timespan of the White River Group corresponded to a spectacular period of adaptive radiation in the Canidae. Sister-group relationships and the chronological appearance of taxa imply that the major diversification shown in Figure 10 had taken place by the beginning of Oligocene time. The Duchesnean and Chadronian record lacks the predicted diversity, which must have resulted from speciation events peripheral to the mid-continent where the geologic record is preserved. The recorded diversity was assembled in Orellan time corresponding to marked climatic change toward drier and more seasonal climates and presumably greater diversity of habitats. It might be hypothesized that canid cladogenesis took place in locations where such diversity existed in the late Eocene possibly in more northerly or higher elevation sites in habitats that became widespread at lower latitudes and elevations in the early Oligocene.

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Front cover caption: The strata of the Big Badlands of South Dakota preserve one of the best terrestrial
records of terrestrial Eocene-Oligocene transition in North America. This rendition is from Henry
Fairfield Osborn’s 1929 titanothere monograph, showing the upper Eocene Chadron Formation
overlain by the lower Oligocene Brule Formation. Superimposed on this figure are side views of the
skulls of three of the most common oreodonts from the Eocene-Oligocene transition (from bottom to
top): the middle Chadronian *Merycoidodon presidioensis*, the late Chadronian – early Orellan
*Merycoidodon culbertsoni*, and the late Orellan *Merycoidodon bullatus* (from Stevens and Stevens, this
volume, Chapter 25).