PHYLOGENETIC SYSTEMATICS OF THE HESPEROCYONINAE (CARNIVORA: CANIDAE)

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This contribution is dedicated to Prof. Zhai Renjie and my parents.

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ABSTRACT

The subfamily Hesperocyoninae includes the oldest and most primitive members of the Canidae. It has a geological range from Late Eocene (Duchesnean) to Middle Miocene (Early Barstovian), lasting more than 20 million years. Representatives of the Hesperocyoninae are known only in North America. Initial diversification of the Hesperocyoninae began in the Orellan, and by the Whitneyan, all of its main lineages were in place. It achieved a maximum diversity of 14 species in the early Arikareean.

The present study describes the extraordinary fossil canids from the Frick Collection. It contains many new taxa that provide new insight into the phylogeny of the hesperocyonines, and also more complete materials of known forms that allow better assessments of morphological variations. Besides the basal canid *Prohesperocyon*, a total of 10 genera and 26 species of hesperocyonines are recognized; among these, 4 genera and 8 species are new.

A phylogenetic analysis is performed using cladistic methodology, with *Miacis* as an outgroup. Four major lineages can be defined on the basis of shared derived characters: the *Mesocyon–Enhydrocyon* clade, the *Osbornodon* clade, the *Paraenhydrocyon* clade, and the *Ectopocynus* clade. The latter three clades are newly recognized, although some of their included species had previously been referred to various other taxa. In addition, a monotypic *Caedocyon* probably forms a distinct clade of its own.

Hesperocyon occupies the central position of possibly being ancestral to many of the lineages. Its lack of shared derived characters, however, precludes it from being closely linked to any particular derived clade, although there is evidence that the *Paraenhydrocyon* clade may be directly descendant from *H. gregarius*. A new, large-sized *Hesperocyon* ("*H.*" *coloradensis*) provides an important link between *H. gregarius* and the *Mesocyon–Enhydrocyon* clade.

The *Mesocyon–Enhydrocyon* clade is the most diverse lineage of hesperocyonines and includes 10 species. *Mesocyon* and *Cynodesmus*, two medium-sized genera with numerous species previously referred to, are now restricted to include two species each. *Sunkahetanka* and *Philotrox* represent two transitional taxa leading to the hypercarnivorous *Enhydrocyon*. Trends within this lineage include elongation of the posterior portion of the skull so that the rostrum appears to be short, enlargement of carnassials, and increasingly robust premolars.

Materials of a large species from mostly the Frick Collection lead to the recognition of a new genus and species *Osbornodon fricki*. Four additional species are referred to the genus, three of them having been previously described (*O. sesnoni, O. iamonensis,* and *O. brachypus*) and one new species (*O. renjiei*) being the most primitive of the genus. *Osbornodon* is the only genus of the Hesperocyoninae that developed a basined talonid in the lower molars and long upper molars, features paralleling those of the Borophaginae and Caninae. In addition, *Osbornodon* has an elongated rostrum and an extensive frontal sinus (in derived species), a combination of characteristics also seen in the Caninae. A sister-group relationship between the *Osbornodon* clade and the *Mesocyon–Enhydrocyon* clade is suggested by their common possession of a ventrally directed paroccipital process.

The three species presently referred to *Paraenhydrocyon* (a new genus) were previously included in *Mesocyon*, and now form a clade of their own. In addition to its retention of several primitive cranial characters, *Paraenhydrocyon*, with its unique slender, sharp-tipped premolars, clearly contrasts with the robust premolars of the *Mesocyon–Enhydrocyon* clade. *Paraenhydrocyon* does, however, parallel the *Mesocyon–Enhydrocyon* clade in having a reduced metaconid of the lower molars.

Represented by a single partial cranium, *Caedocyon* is a highly apomorphic form, with enlarged, caniniform upper third incisors, shortened upper premolars, and reduced upper molars. Its phylogenetic position is not clear, although its simple, high premolars and the precision of its occlusion suggest affinity with *Paraenhydrocyon*.

Ectopocynus (new genus with three species, all from the Frick Collection) is mainly characterized by its simple, robust, and blunt premolars, and approaches many of the characteristics of *Enhydrocyon*, such as massive premolars and reduced or lost metaconid on lower molars. Materials of *Ectopocynus* are limited to mandibles and teeth only. Its unknown cranial anatomy does not permit a firm answer about its phylogenetic affinity, although a primitive member of this lineage (*Ec. antiquus*) suggests affinity with the *Hesperocyon*-like forms of the Whitneyan.

Hesperocyoninae, as presently defined, is likely a paraphyletic taxon. The subfamily may be characterized by possession of a trenchant talonid of lower first molars, in contrast to basined talonids in the Borophaginae and Caninae. The trenchant talonid, however, is clearly primitive for the Hesperocyoninae (and also for the family Canidae), and no synapomorphy is found to support a monophyletic Hesperocyoninae. The paraphyly of the

Hesperocyoninae is also suggested by its primitive genus *Hesperocyon*, which is probably ancestral to both borophagines and canines.

Evolutionary trends in hesperocyonines include repeated tendencies toward hypercarnivory, involving large body size, strong cranial construction, robust premolars, and increasing length of carnassials. Such tendencies can be observed in nearly all of the clades, although each has a different combination of these tendencies and achieves different degrees of hypercarnivory. Truly hypocarnivorous taxa, on the other hand, did not develop as in Borophaginae and Caninae.

INTRODUCTION

The subfamily Hesperocyoninae is the most primitive group of the family Canidae. It has a diverse fossil record from the Tertiary of North America. These primitive canids began to diversify shortly after first appearing in the Late Eocene, and soon became dominant small- to medium-sized predators until the more advanced subfamily Borophaginae replaced them in the Middle Miocene. Early hesperocyonines are abundantly represented by *Hesperocyon* in the White River Group of the northern Great Plains. Nearly complete skeletons of *Hesperocyon* can be found in many museums and more fragmentary materials in every White River collection. It is therefore no accident that *Hesperocyon* was the first documented hesperocyonine in the study of primitive canids.

Despite their high specific diversity, however, canids display a limited range of morphological patterns throughout their history. Similar dental structures appear independently time and again. Analyses of canid phylogeny thus often proved frustrating, as observed by Simpson (1945: 222): "Fossil canids are very abundant, and this richness is embarrassing since it suffices to complicate rather than elucidate the subdivision of the family. The whole group is extremely polyphyletic, and few of the phyla are yet positively and clearly worked out." One of the primary limiting factors in various attempts of phylogenetic synthesis of fossil canids was the isolated, often fragmentary, materials scattered in many museums. This limitation was greatly obviated when the Frick Collection became available to the larger scientific community.

Mainly in the first half of the present century, the late Dr. Childs Frick developed a keen interest in the evolution of fossil Carnivora. Using his immense personal resources, Frick established the Frick Laboratory, which launched numerous expeditions into the rich terrestrial deposits of Tertiary North America. With the help of a large staff of dedicated individuals, the Laboratory amassed a magnificent collection of Tertiary mammals, known as the Frick Collection, now housed in the American Museum of Natural History (Galusha, 1975a). Among the fossil carnivorans in this extraordinary assemblage, canids make up a significant portion. The Frick Collection includes a large number of undescribed taxa, including entirely new lineages, as well as more complete materials of known taxa. Along with the E. D. Cope Collection and other smaller collections, the American Museum has the largest single collection of Tertiary carnivorans under one roof.

Although Childs Frick invested a significant part of his life in an ambitious study of fossil carnivorans of the world, the project remained incomplete at the time of his death in 1965. Since then, Richard H. Tedford and Beryl E. Taylor (a long-time collaborator of Frick) have initiated a comprehensive study of the systematics and phylogeny of fossil canids, and concluded that canids could be divided into three subfamilies: Hesperocyoninae, Borophaginae, and Caninae (the latter subfamily includes all extant canids). An outline of this idea was published in Tedford (1978). The two more derived subfamilies, Borophaginae and Caninae, are currently undergoing revision (Tedford and Taylor, MS). The third, Hesperocyoninae, is the focus of the present study.

The subfamily Hesperocyoninae, as informally proposed by Tedford (1978), has not been rigorously defined. It was conceived to include a group of most primitive canids, such as *Hesperocyon*, *Mesocyon*, and *Enhydro-*

cyon, which are mainly united by characters that, for the most part, are primitive for all canids. Difficulties in the definition of Hesperocyoninae further arise when the two more derived subfamilies, Borophaginae and Caninae, are assumed to be derived from *Hesperocyon* (Tedford, 1978). Despite all of these practical difficulties, Tedford's (1978) concept of a tripartite radiation in the geological history of canids is of important heuristic value and provides a cohesive program for the present study of hesperocyonine canids.

This study grew out of my Ph.D. dissertation (Wang, 1990) on the phylogeny of primitive canids and was conceived as a post-doctoral project in the Department of Vertebrate Paleontology, American Museum of Natural History. The purpose of this paper is to bring together hesperocyonine materials from the Frick Collection as well as recent and historical collections in museums throughout the United States and Canada, and to present a study of comparative anatomy and phylogenetic systematics of this primitive ancestral stock of canids.

Few of the characters in this phylogenetic analysis are original. The present contribution lies in the synthesis of the large quantity of materials that allows a better appreciation of morphological variations, in the descriptions of many new taxa that provide new insight of possible phylogenetic arrangements, and in the cladistic treatment of the character distributions, which reduces ad hoc hypotheses to a minimum.

INSTITUTIONAL ABBREVIATIONS

ACM Amherst College Museum (Pratt Museum), Amherst

AM:MA Department of Mammalogy, American Museum of Natural History, New York

AMNH Department of Vertebrate Paleontology, American Museum of Natural History, New York

ANSP Academy of Natural Science of Philadelphia, Philadelphia

BHI Black Hills Institute of Geological Research, Inc., Hill City

CMNH Carnegie Museum of Natural History, Pittsburgh

F:AM Frick Collection, Department of Vertebrate Paleontology, American Museum of Natural History, New York

FGS Florida Geological Survey, Tallahassee, now part of the University of Florida collection

FMNH Field Museum of Natural History, Chicago

JODA John Day Fossil Beds National Monument, John Day

KUVP Division of Vertebrate Paleontology, Museum of Natural History, University of Kansas, Lawrence

LACM Natural History Museum of Los Angeles County, Los Angeles

MCZ Museum of Comparative Zoology, Harvard University, Cambridge

NMC Canadian Museum of Nature, Ottawa, Canada

ROM Royal Ontario Museum, Toronto, Canada

SDMNH San Diego Natural History Museum, San Diego

SDSM Museum of Geology, South Dakota School of Mines and Technology, Rapid City

SMNH Saskatchewan Museum of Natural History, Regina, Canada

TMM Texas Memorial Museum, University of Texas, Austin

UCMP Museum of Paleontology, University of California at Berkeley, Berkeley

UNSM Nebraska State Museum, University of Nebraska, Lincoln

UM University of Michigan, Ann Arbor

USNM United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

UW University of Wyoming, Laramie

YPM Yale Peabody Museum of Natural History, Yale University, New Haven

YPM-PU Princeton University Natural History Museum (now in the collection of the Yale Peabody Museum of Natural History)

HISTORY OF STUDY

In 1856, Joseph Leidy described a fragmentary left ramus of a small carnivoran with p4 and m1 discovered during the F. V. Hayden expeditions to the Nebraska Territory. Leidy named it *Amphicyon? gracilis*. Although *A. gracilis* was soon recognized as a previously occupied name (*A. gracilis* Pomel, 1847), the small fossil mandible became the first documented hesperocyonine canid of North America and was later known as *Hesperocyon gregarius*. It was E. D. Cope, however, who truly brought to the world's attention some of best hesperocyonine materials from the Tertiary of North America, particularly the beautifully preserved specimens from the John Day Formation, central Oregon. During the 1870 and 1880s, Cope (1873a, b, 1879a, b, 1881a, b) described a series of primitive canids that are now included in *Hesperocyon, Mesocyon, Enhydrocyon, Osbornodon,* and *Paraenhydrocyon*. Cope was also the first to summarize the systematic relationships of then known fossil canids of North America (1879b, 1881a, b, 1883, 1884; table 1).

A number of new canid taxa were subsequently described around the turn of the century (Scott, 1890, 1893, 1895; Wortman and Matthew, 1899; Merriam, 1906; Matthew, 1907, 1924; Thorpe, 1922b). Some of these authors attempted various themes of classifications or phylogenies of fossil canids (e.g., Scott, 1895; Wortman and Matthew, 1899; table 1), but no apparent consensus emerged. Matthew (1924, 1930) was the first to recognize two major canid lineages with fundamentally different talonid structures of the lower first molars: those with trenchant talonids made up of a predominant hypoconid and those with basined talonids enclosed by a hypoconid and an entoconid (fig. 1; table 1). As a result, the living Asian dhole *Cuon*, which has a trenchant talonid, was linked with such Arikareean hesperocyonine genera as *Mesocyon* and *Enhydrocyon*. Matthew's influential phylogenetic framework was followed with some variations for the next 50 years (Loomis, 1936; Scott and Jepsen, 1936; Simpson, 1945; Macdonald, 1963).

The above traditional phylogenies, based almost exclusively on dental characters, were challenged by Tedford (1978, and more substantially in Tedford and Taylor, MS), who proposed a division of Canidae into three subfamilies: Hesperocyoninae, Borophaginae, and Caninae (fig. 2). Tedford and Taylor (MS) demonstrated that canid talonid configuration was highly homoplastic and that a trenchant talonid had evolved independently a number of times. These convergent developments of a trenchant talonid were further supported by Berta (1987, 1988) in her study of fossil canids of South America. Despite the gradual acceptance of Tedford's tripartite division of canids (e.g., Martin, 1989; Van Valkenburgh, 1991), the traditional view of talonid evolution is so entrenched in published descriptions of fossil canids that popular conceptions of the origins of living canids are still influenced by it (e.g., McLoughlin, 1983; Sylvester, 1989).

At a more fundamental level of carnivoran phylogeny, early studies of canids were intimately linked to amphicyonids, an extinct group of arctoid carnivorans that primitively share many aspects of canid dental morphology. Through their entire geologic history, hesperocyonines coexisted with the amphicyonids. Members of the family Amphicyonidae were almost invariably regarded as aberrant canids (e.g., Romer, 1966; table 1). The fundamental distinction between canids and amphicyonids became increasingly clear as the basicranial anatomy of these groups became better understood (Hunt, 1971, 1977; Flynn et al., 1988).
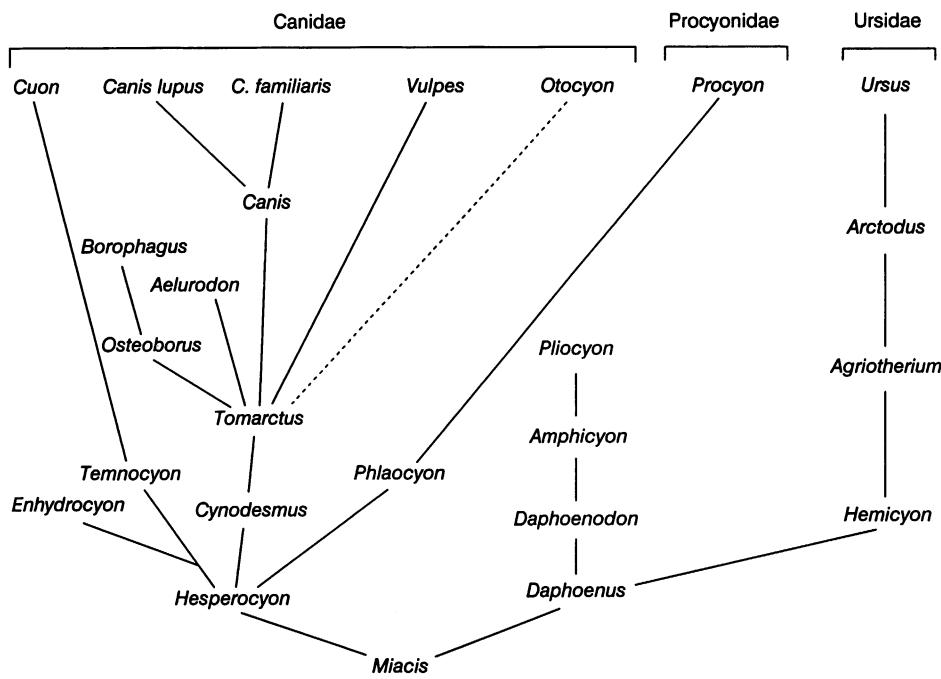
Fig. 1. Phylogeny of Canidae, Procyonidae, and Ursidae by W. D. Matthew, redrawn from Matthew (1930). Some taxa are substituted with current usages (e.g., *Tomarctus* for *Tephrocyon*, *Borophagus* for *Hyaenognathus*).
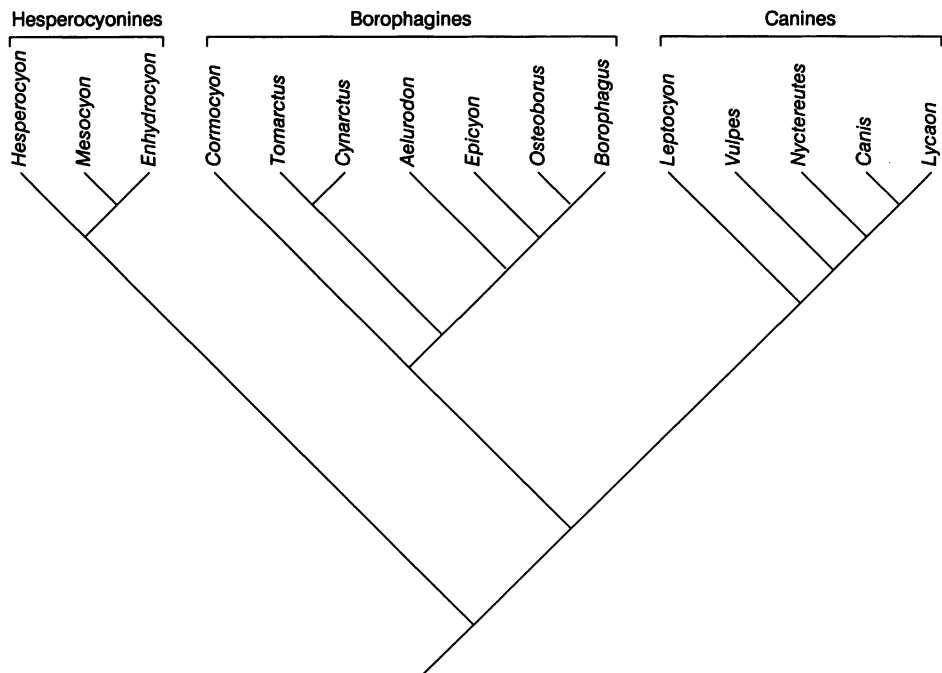
Fig. 2. Phylogeny of Canidae proposed by R. H. Tedford (redrawn from Tedford, 1978). Some taxa are substituted with current usages (e.g., *Cormocyon* for *Nothocyon*, *Aelurodon* for *Prohyaena*, *Epicyon* for *Aelurodon*).

TABLE 1
Previous Classifications (or Phylogenies Modified into Classifications) of Hesperocyonine Canids

1. Cope (1883: 247)
   Family Canidae
   Basal lineage
   Megalotis
   Amphicyon
   Galecynus (= *Cormocyon*)
   Galecynus–Hyaenocyon lineage
   Temnocyon (including *Mesocyon*)
   Enhydrocyon
   Hyaenocyon (= *Enhydrocyon*)
   Galecynus–Aelurodon lineage
   Canis
   Aelurodon
   Oligobunis and others

2. Scott (1895: 75, modified from phylogeny)
   Cynoids
   Miacis–Cynodictis lineage
   Cynodictis (= *Hesperocyon*)
   Miacis–Canis lineage
   Daphoenus
   Temnocyon
   Cynodesmus
   Aelurodon
   Canis

3. Wortman and Matthew (1899: 139, modified from phylogeny)
   Family Canidae
   Uintacyon–Cuon lineage
   Daphoenus
   Enhydrocyon
   Hyaenocyon
   Temnocyon
   Cuon
   Procynodictis–Canis lineage
   Cynodictis (= *Hesperocyon*) *lippincottianus*
   Cynodesmus
   Hypotemnodon = *Mesocyon*
   Canis
   Vulpavus–Nothocyon lineage
   Cynodictis (= *Hesperocyon*) *gregarius*
   Nothocyon (= *Cormocyon*)

4. Matthew (1930: 132, summary from his phylogeny [fig. 1], canid part only)
   Family Canidae
   Miacis–Cuon lineage (trenchant talonid)
   Temnocyon
   Enhydrocyon
   Cuon
   Miacis–Canis lineage (basined talonid)
   Cynodictis
   Cynodesmus (*C.* (= *Tomarctus*) *thomsoni*)

TABLE 1—(*Continued*)

Tephrocyon (= *Tomarctus*)
Vulpes
Canis
Aelurodon
Osteoborus
Borophagus

5. Loomis (1936: 50, modified from phylogeny)
   Canids with trenchant talonid
   Daphoenus–Amphicyon group (amphicyonids)
   Temnocyon group
   Temnocyon (*T. altigens* and *T. precussor*)
   Cuon
   Icticyon
   Lycaon
   Mesocyon group
   Mesocyon coryphaeus
   Mesocyon josephi
   Mesocyon brachyops
   Mesocyon robustus
   Enhydrocyon group
   Brachyrhynchocyon (= *Brachycyon*)
   Enhydrocyon
   "*Temnocyon*" *wallovianus*
   "*Temnocyon*" *venator*
   Canids with basined talonid
   Nothocyon group
   Cynodictis (= *Hesperocyon*)
   Nothocyon (= *Cormocyon*)
   Cynodesmus (sensu stricto *Cynodesmus* (*Tomarctus*) *thomsoni*)
   Tomarctus
   Canis
   Tephrocyon group (primitive borophagines)
   Aelurodon–Borophagus group (advanced borophagines)
   Allocyon–Hemicyon group (ursids)

6. Simpson (1945: 108–111, in part)
   Superfamily Canoidea
   Family Canidae
   Subfamily Caninae
   Cynodictis
   Pseudocynodictis (= *Hesperocyon*)
   Nothocyon (= *Cormocyon*)
   Cynodesmus
   Mesocyon
   Tomarctus
   Leptocyon
   Subfamily Simocyoninae
   Brachyrhynchocyon
   Enhydrocyon
   Philotrox
   Euoplocyon
   Subfamily Borophaginae
   Aelurodon, and more

TABLE 1—(*Continued*)

7. Macdonald (1963: 201, modified from phylogeny)
   Basined talonid group
     Nothocyon
     Neocynodesmus
     Tomarctus (including "*Cynodesmus*")
   Trenchant talonid group
     Hesperocyon
     Mesocyon
     Enhydrocyon (including "*Sunkahetanka*")

Basicranial morphology has long been recognized for its importance in delimiting higher-level relationships among carnivorans (Turner, 1848; Flower, 1869; Van der Klaauw, 1930, 1931). Hough (1944, 1948a, 1952) began to systematically apply basicranial characteristics to the study of North American fossil carnivorans. Amphicyonids, however, remained in the Canidae (Hough, 1948b; Romer, 1966) until a doctoral study of North American amphicyonids by Hunt (1971) demonstrated that amphicyonids are a distinct lineage of carnivorans. The most striking basicranial structure of the amphicyonids is a large pocket formed in the lateral border of basioccipital, which, in living ursids, houses the "ursid loop" of the internal carotid artery (Hunt, 1977: fig. 2). Basicranial studies of a broader phylogenetic spectrum further bring the uniqueness of canids into sharper focus (Mitchell and Tedford, 1973; Hunt, 1974; Tedford, 1976; Flynn et al., 1988; Wang and Tedford, 1994).

MATERIALS AND METHODS

The scope of this study is designed to include all primitive canids (see Wang and Tedford [1994] for the characterization of the Canidae) that are not members of the Borophaginae or Caninae. The latter two subfamilies, presumably constituting a sister-group, share a synapomorphy of a trenchant talonid on m1 and associated development of a metacone on M1. Except for the most primitive taxa, the borophagines have further acquired synapomorphies such as a strong posterior process of premaxillary and developments of accessory cusps on incisors and premolars. The canines, on the other hand, can be characterized by their narrow premolars and slender mandibles. These derived characters of the borophagines and canines are used for preliminary selection of taxa for the present consideration.

The materials from the Frick Collection of the AMNH form the main basis of this study. Efforts were also made to incorporate all historically important specimens as well as most major collections of hesperocyonine canids in North America. Variations among living canids were explored in the collections of the Department of Mammalogy at the AMNH.

Because the primary purpose of this study is to explore the species-level phylogenetic relationships of the Hesperocyoninae, attention is focused on anatomical parts that are most readily available in fossil records—teeth, mandibles, and, to a lesser extent, skulls. Postcranial materials are rarely available for the majority of species and cannot readily be used to elucidate their phylogeny.

The computer program HENNIG86 (version 1.5; James S. Farris, 1988) is used to test phylogenetic hypotheses. Analyses are performed at the species level, and each species is assigned a numerical character state for a particular character. Each character is treated as independent evidence of phylogenetic relationship, and all characters are given equal weight and are unordered. Whenever possible, *Miacis parvivorus*, the genotypic species, is used as an outgroup to determine character polarities. Where the character is not known in *M. parvivorus*, the presumably more primitive *Vulpavus* is used (see Wang and Tedford [1994] for phylogeny of these miacids). Trees found by HENNIG86 are explored and character optimizations are performed through the program CLADOS (version 1.2; Kevin C. Nixon, 1992).

Taxonomic decisions in this study closely follow the phylogeny. However, monophyly of each genus is not always possible unless a
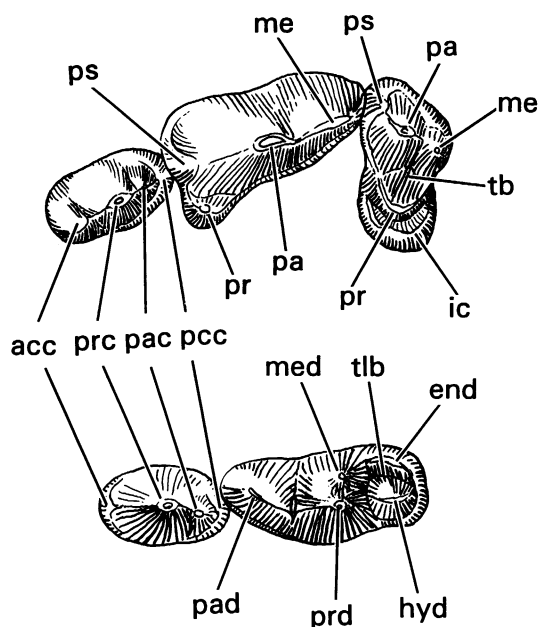
Fig. 3. Dental nomenclature for P3–M1 (upper) and p4–m1 (lower) used in the present study. Abbreviations: acc, anterior cingular cusp; end, entoconid; hyd, hypoconid; ic, internal cingulum; me, metacone; med, metaconid; pa, paracone; pad, paraconid; pac, posterior accessory cusp; pcc, posterior cingular cusp; prc, principal cusp; prd, protoconid; ps, parastyle; tb, trigon basin; tlb, talonid basin.

number of new, monotypic genera were erected for the sole purpose of accommodating the pectinated species. Paraphyletic genera, enclosed by quotation marks, are allowed in cases where the genus is too primitive to be well-resolved phylogenetically and thus is likely to contain species ancestral to more than one lineage.

FORMAT AND DEFINITION

In systematic descriptions, species are organized according to their phylogenetic positions proposed herein; however, the genotypic species is always described first. The present species diagnoses are intended for the purpose of practical taxonomic identification instead of an exact reflection of the phylogeny. Therefore, both derived and primitive characters (and sometimes more subtle mor-

phological tendencies) are usually listed for species delineation; apomorphic characters in the phylogenetic analysis (fig. 64) are listed inside parentheses following the description. Descriptions of each species are divided into three sections: skull, mandible, and dentition (and others when appropriate). Within each section, descriptions are grouped by topographic regions and follow the general direction from anterior to posterior and from dorsal to ventral. The same convention also applies to the character descriptions in the Phylogeny chapter.

Unless otherwise stated, anatomical terminologies, particularly the soft anatomy, follow those of Evans and Christensen (1979). Tooth nomenclature follows Van Valen (1966; see fig. 3). The notation for dental formula is as follows: I1 I2 I3 C1 P1 P2 P3 P4 M1 M2 M3 i1 i2 i3 c1 p1 p2 p3 p4 m1 m2 m3. The term hypercarnivory was originally proposed by Crusafont-Pairó and Truyols-Santonja (1956) on the basis of two angles on the upper and lower carnassial teeth. Present use of this term refers to the teeth that emphasize shearing dentition as opposed to grinding dentition, and is more broadly defined to take into consideration dental features correlated to the angles: robust premolars, elongation of shearing blades, trenchant talonid, etc. Biostratigraphic terminology and correlations follow those of Emry et al. (1987) and Tedford et al. (1987). Names for higher-level taxonomic groupings of carnivorans follow Flynn et al. (1988).

CRANIAL MEASUREMENTS
Figures 4, 5, Appendix II

A modified system of cranial measurements used by Nowak (1979) is adopted in the present study. Because of the fragmentary nature of fossil materials, some of Nowak's 15 measurements are rarely preserved in fossils. Additional measurements therefore are supplemented to allow some sense of dimensions. The numbers of the following measurements correspond to those in figures 4 and 5. Measurements of all hesperocyonines are presented in Appendix II to facilitate comparisons.
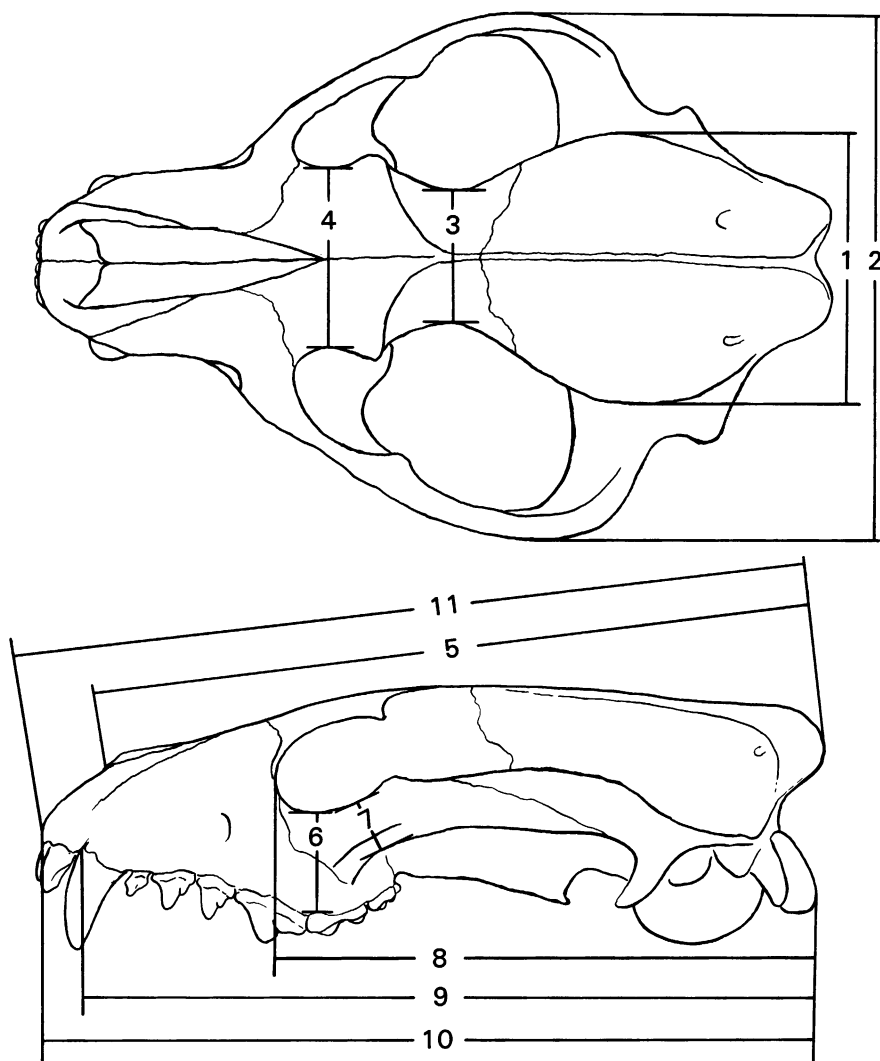
Fig. 4.   Definition of cranial measurements, dorsal and lateral aspects of skull. See text for explanation.

1. WBR (width of braincase)—Greatest width of cranium at the base of the braincase.

2. WZA (width of zygomatic arch)—Greatest distance across zygomatic arches.

3. WPC (width of postorbital constriction)—Least width across frontals at constriction behind postorbital process.

4. WFS (width of frontal shield)—Least width across frontals anterior of postorbital process.

5. LNI (length of nasal tip to inion)—Greatest distance between anterior tip (on the lateral border) of nasal and posterior tip of inion.

6. HTO (height of maxillary toothrow to orbit)—Minimum distance from outer alveolar margin of M1 to most ventral point of orbit.

7. DJG (depth of jugal)—Minimum depth of jugal anterior to postorbital process of jugal.

8. LPS (posterior skull length)—Distance between anterior opening of infraorbital fo-
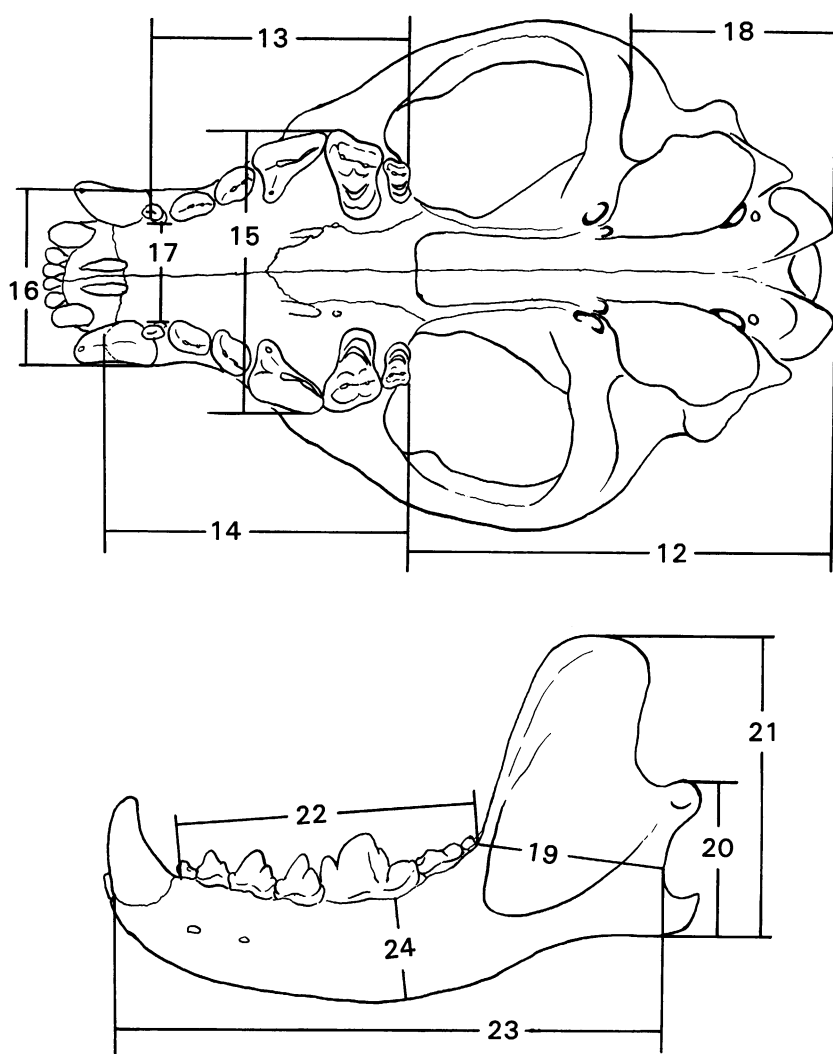
Fig. 5.   Definition of cranial measurements, ventral aspect of skull and lateral aspect of mandible. See text for explanation.

ramen and posterior border of occipital condyle.

9. LCO (length of canine to occipital condyle)—Distance between anterior alveolar margin of C1 and posterior border of occipital condyle.

10. LBS (basal skull length)—Distance from anterior tip of premaxillary to posterior tip of occipital condyle.

11. LDS (dorsal length of skull)—Distance from anterior tip of premaxillary to posterior tip of inion.

12. LMO (length from M2 to occipital condyle)—Distance between posterior alveolar margin of M2 and posterior border of occipital condyle.

13. LMT (alveolar length of maxillary toothrow)—Distance between anterior alveolar margin of P1 (or P2) to posterior alveolar margin of M2 (or M1).

14. LCT (alveolar length of canine to maxillary toothrow)—Distance between anterior alveolar margin of C1 to posterior alveolar margin of M2 (or M1).

15. WUT (crown width across upper cheek teeth)—Greatest distance between labial sides of most widely separated upper cheek teeth (P4 or M1).

16. WAC (width across canines)—Greatest width between the labial margins of canines.

17. WPP (palatal width at P1)—Least width between lingual alveolar margins of P1s (or P2s).

18. LBC (length of basicranium)—Minimum distance between mandibular fossa and posterior tip of occipital condyle.

19. LMF (length of masseteric fossa)—Distance between posterior alveolar margin of m3 (or m2) and the posterior notch below condyloid process.

20. DCP (depth of condyloid process)—Distance between the dorsal border of condyloid process and ventral border of angular process.

21. HCP (height of coronoid process)—Distance between the dorsal margin of coronoid crest and ventral border of angular process.

22. LLT (length of lower postcanine toothrow)—Distance between anterior alveolar margin of p1 (or p2) and posterior alveolar margin of m3 (or m2).

23. LHR (length of horizontal ramus)—Distance between anterior alveolar margin of c1 and posterior notch below condyloid process.

24. DHR (depth of horizontal ramus)—Minimum depth between medial (or lateral when medial side is not preserved) alveolar margin of m1 talonid and ventral border of ramus.

DENTAL MEASUREMENTS
Figure 6, Appendix III

Summary statistics of the following measurements are presented in Appendix III.

LP3 (length of P3)—Greatest longitudinal length of upper third premolar. Similarly defined are LP4, Lp1, Lp2, Lp3, Lp4, Lm1, Lm2, and Lm3.

WP3 (width of P3)—Greatest transverse width of upper third premolar. Similarly defined are WP4, Wp1, Wp2, Wp3, Wp4, Wm1, Wm2, and Wm3.
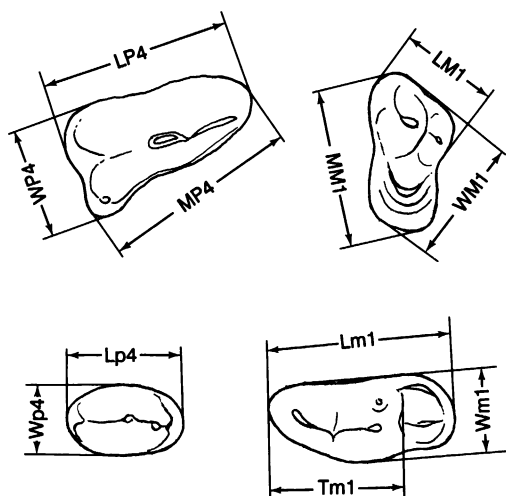
Fig. 6. Definition of dental measurements for P3–M1 (upper) and p4–m1 (lower). See text for explanation.

MP4 (maximum length of P4)—Greatest distance between the anterior border of protocone and posterior border of metacone blade.

LM1 (labial length of M1)—Greatest longitudinal length of upper first molar between anterior border of paracone and posterior border of metacone. LM2 is similarly defined.

WM1 (width of M1)—Shortest transverse width of upper first molar between its labial border and hypocone crest. WM2 is similarly defined.

MM1 (maximum length of M1)—Greatest distance of upper first molar between anterolabial corner of paracone and posterolingual border of internal cingulum. MM2 is similarly defined.

Lc1 (length of c1)—Greatest longitudinal diameter of lower canine at palate plane.

Wc1 (width of c1)—Shortest transverse diameter of lower canine at palate plane.

Tm1 (trigonid length of m1)—Greatest length of lower first molar trigonid between anteriormost tip of paraconid and posterior surface of protoconid–metaconid base that intersects the hypoconid ridge. Tm2 is similarly defined.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1785
Order Carnivora Bowdich, 1821
Suborder Caniformia Kretzoi, 1943
Infraorder Cynoidea Flower, 1869

Family Canidae Gray, 1821

DIAGNOSIS: The family Canidae is derived relative to primitive miacids in a number of basicranial and dental characters: presence of a small suprameatal fossa (in primitive form only, char. 7); presence of an entotympanic bulla (char. 8); medial expansion of petrosal in full contact with the basioccipital and basisphenoid (char. 12); ossification of tegmen tympani; extrabullar position of the internal carotid artery and loss of the stapedial artery (char. 11); presence of posterior accessory cusps on upper and lower third premolars (char. 30); reduction of M1 parastyle (char. 35); and loss of M3 (char. 42) (see further discussion in Wang and Tedford, 1994). Except for Prohesperocyon wilsoni, canids also have an incomplete, low septum at the suture of the ectotympanic and caudal entotympanic. Canids are further distinguished from amphicyonids and ursids in the lack of a large inferior petrosal sinus (Hunt, 1977) and in having a narrower basioccipital between bullae. Canids still primitively possess an alisphenoid canal and a carnassial notch in contrast to living musteloids, which have lost these structures.

DISCUSSION: Tedford (1978) pioneered the tripartite division of canids (i.e., the subfamilies Hesperocyoninae, Borophaginae, and Caninae). Although some of the earliest and most primitive canids may be difficult to place in one group or another, the basic concept of three successive radiations in the history of canids is widely accepted (e.g., Berta, 1988; Martin, 1989; Munthe, 1989); that is, an initial radiation of hesperocyonines in the Eocene to early Miocene, followed by borophagines in the Mio-Pliocene, which was in turn replaced by canines in the Pliocene to Present.

Canidae incertae cedis

Prohesperocyon, new genus

Miacis (Cope) Wilson et al., 1968: 596.
Hesperocyon (Scott) Gustafson, 1986: 52.

TYPE SPECIES: Hesperocyon wilsoni Gustafson, 1986.
INCLUDED SPECIES: Type species only.
DIAGNOSIS: As monotypic species.
ETYMOLOGY: Prohesperocyon, in allusion to its ancestral status to Hesperocyon.
DISTRIBUTION: As monotypic species.
DISCUSSION: The monotypic Prohesperocyon is at the base of the canid phylogeny, as demonstrated in a separate paper on the origin of canids (Wang and Tedford, 1994). The presence of a fully ossified entotympanic bulla in Prohesperocyon along with other basicranial features suggest that it belongs to the canid clade; its dental characters, however, remain primitively similar to some Miacis. A new genus is established herein to recognize Prohesperocyon's paraphyletic relationship with Hesperocyon and its unique combination of characteristics distinct from both more derived or primitive forms in the clade.

Prohesperocyon wilsoni
(Gustafson, 1986)
Figures 7, 8

Miacis gracilis (Clark) Wilson et al., 1968: 596.
Hesperocyon sp. Wilson et al., 1968: 596. Wilson, 1977: 22.
Hesperocyon wilsoni Gustafson, 1986: 52.
"Hesperocyon" wilsoni (Gustafson) Wang and Tedford, 1994: 15.

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: From the Airstrip local fauna, southern Sierra Vieja area, Presidio County, Texas (Wilson et al., 1968: fig. 1). The fauna is mainly restricted within a 5-ft interval of the Capote Mountain Tuff, estimated to be 570 ft (174 m) above the Bracks Rhyolite, which yields a potassium-argon date of 36.5 ± 1.2 m.y. (Wilson et al., 1968: table 3). It is thus equivalent to the ash B of Chadron Formation in Flagstaff Rim, Wyoming

(single-crystal $^{40}Ar/^{39}Ar$ dates around 35.92–35.97 m.y. [Swisher and Prothero, 1990; Prothero and Swisher, 1992]) and has been correlated with the Pipestone Springs local fauna (middle Chadronian) of Montana (Emry et al., 1987: 136, fig. 5.3; Emry, 1992: fig. 5.3), although the authors acknowledged the difficulty in the correlation of the Airstrip local fauna, which has few taxa (13 listed in Wilson, 1977: 22).

REFERRED SPECIMEN: TMM 40504-99, partial mandible with right and left p2–4, from the same locality as the holotype.

EMENDED DIAGNOSIS: *Prohesperocyon wilsoni* possesses a typical canid basicranial and dental pattern distinct from the miacids: presence of a fully ossified and inflated entotympanic bulla (char. 8), laterally positioned internal carotid artery outside the entotympanic bulla (char. 11), medial expansion of petrosal in full contact with the basioccipital and basisphenoid (char. 12), presence of posterior accessory cusps on upper and lower third premolars (char. 30), reduction of anterior segment of internal cingulum on M1, reduction of M1 parastyle and loss of a notch between the parastyle and paracone (char. 35), and absence of a M3 (char. 42) (see diagnosis of Canidae). It can be distinguished from *Hesperocyon* by many primitive characters: lack of a low septum inside the bulla; a large, anteriorly located protocone of P4; a well-developed parastyle of M1; a narrow and poorly developed internal cingulum of M1; a short trigonid shearing blade of m1; a narrow talonid of m1 relative to trigonid; a poorly developed entoconid crest; and a more posteriorly reclined coronoid process. In addition, *P. wilsoni* has autapomorphies that may further differentiate it from *Hesperocyon*: elongated rostrum (char. 1); anteriorly expanded bulla that exceeds, in lateral view, the posterior wall of postglenoid fossa; slender premolars (char. 29); an extremely reduced metacone on M2 (char. 41); and reduced metaconid on m2 (char. 46).

DISTRIBUTION: Capote Mountain Formation, southwestern Texas. Chadronian age.

DESCRIPTION: The original description of *Hesperocyon* (= *Prohesperocyon*) *wilsoni* by Gustafson (1986) still serves as a good reference for its general morphology. In my phylogenetic analysis, I highlight relevant characteristics and point out discrepancies between my observations and those of Gustafson.

Skull: As observed by Gustafson (1986), the rostral part of the skull is elongated. A long rostrum appears to be an autapomorphy for *Prohesperocyon wilsoni* since both its ancestral (*Miacis*) and descendant (*Hesperocyon*) taxa have relatively short snouts. The tip of the premaxillary protrudes anteriorly. Gustafson (1986: 53) remarked that the dorsal (posterior) process of the premaxillary is "distinctly broader and longer" than in *H. gregarius*, contrary to his own illustrations (ibid.: fig. 33B, C), which show slender, short processes like those of *Hesperocyon*. He mistook broken pieces of the maxillary paralleling the posterior process of the premaxillary as the premaxillary, as was illustrated in dashed lines in his figure 33C. Gustafson (1986: fig. 33B) also incorrectly interpreted the maxillary/frontal suture above the orbit and drew a straight line across the forehead (perpendicular to the midline) as if the sutures from the left and right sides met in the midline, a situation not seen in any carnivorans. Instead, the maxillary/frontal suture curves forward to form the lateral border of an anterior process of the frontal rather than truncating the frontal process. Again, he was misled by bone breakage in this region. The posterior half of the skull of TMM 40504-126 has lost a significant amount of bone; however, the endocast, where exposed, is generally well preserved. The temporal crest is lyrate, as correctly inferred from its anterior segment by Gustafson, and the sagittal crest must thus be absent except for the last segment in front of the inion, as is the case in individuals of *Hesperocyon* that have lyrate temporal crests. The postorbital process of the frontal is small, and the postorbital constriction is less deeply incised than in *Hesperocyon* because of the less inflated braincase of *P. wilsoni*.

The bulla is that of a typical hesperocyonine canid. Its degree of inflation exceeds that of *Hesperocyon*; this inflation is presumably mainly caused by the expansion of the caudal entotympanic. The anterior base of the bulla expands forward so that the bulla can be seen

Fig. 7.   Skull of *Prohesperocyon wilsoni*, TMM 40504-126, holotype. **A**, Dorsal and **B**, ventral views. Scale = 20 mm.

to lie in front of the posterior wall of the postglenoid fossa in lateral view. Because of the anterior expansion of the bulla, the external opening of the foramen ovale lies closer to the alisphenoid canal. No bony external auditory meatus is present. The right paroccipital process is partly preserved and is directed posteriorly. The mastoid process is small and about the same size as in *Hesperocyon*. There is a shallow suprameatal fossa in front of the mastoid process on the posterior wall of the external auditory meatus. This fossa is also present in *Hesperocyon*.

There is a diagonal break across the middle part of the right bulla, and disarticulation at this break affords an opportunity to examine the cross section of the bulla wall. No trace of a low septum can be detected on either side of the break, which crosses the region where a low septum is found in *Hesperocyon gregarius*. Further preparation posteriorly did not reveal a septum, although a significant amount of matrix was left intact for fear of damage to the extremely delicate bulla wall. A slender piece of rostral entotympanic can be seen in front of the internal carotid canal near the anterior end of the bulla. No septum, however, is present at the junction between the rostral and caudal entotympanic (see Wang and Tedford, 1994).

The promontorium is medially expanded in contrast to a globular-shaped, isolated promontorium in *Miacis parvivorus* (USNM 214706) and *Vulpavus profectus* (AMNH
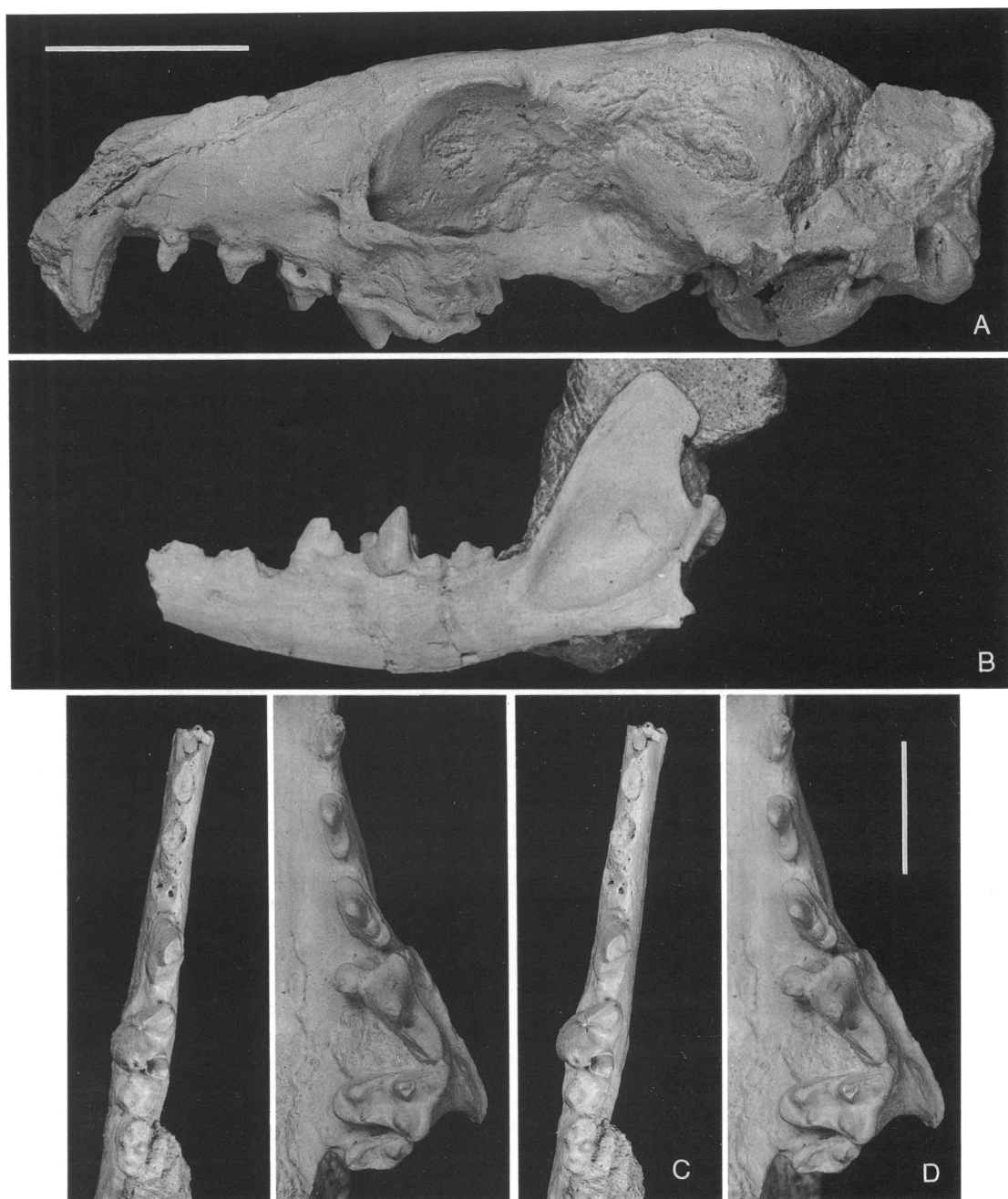
Fig. 8. Skull, mandible, and teeth of *Prohesperocyon wilsoni*, TMM 40504-126, holotype. Lateral views of **A**, skull (reversed from right side) and **B**, mandible; occlusal views (in stereo) of **C**, lower teeth and **D**, upper teeth (reversed from right side). Scale for skull = 20 mm, and that for teeth = 10 mm.

12626). The petrosal touches the lateral border of the basioccipital and basisphenoid, and together with them forms the wall of a narrow canal for the inferior petrosal sinus. The medially expanded petrosal and the dorsal edge of the caudal entotympanic enclose a canal

for internal carotid artery. The artery is thus in an extrabullar position as opposed to an intrabullar condition in primitive caniform carnivorans (e.g., *Miacis* and *Vulpavus*). Overall structure of the *Prohesperocyon wilsoni* basicranium exhibits the configuration of a true canid. A more detailed description and its phylogenetic implication are reported elsewhere (Wang and Tedford, 1994).

Mandible: The horizontal ramus is slender, comparable to that of *Hesperocyon*. The anterior crest of the coronoid process is more posteriorly reclined than in *Hesperocyon*, possibly a primitive condition similar to that of miacids (*Vulpavus* has this condition). The masseteric fossa is shallow. Only the basal part of the angular process on the left ramus is preserved. The remaining cross section of the process suggests the presence of a moderate internal ridge (sensu Gaspard, 1964), which is not expanded to enclose a pocket as in some later hesperocyonines.

Dentition: Corresponding to the long rostrum, the upper premolars are long and slender, and there are rather wide diastemata between the premolars. The P1 is single-rooted. The P1–2 have a single main cusp and only P3 has a very small posterior accessory and cingular cusps, a derived condition over miacids, which mostly lack the accessory cusp. The P4 has a large protocone that protrudes in front of the anterior border of the paracone, a primitive character seen in most miacids. A vague anterior cingulum is present on P4, and a lingual cingulum is seen only toward the posterior end of the tooth at the base of the metastyle. The outline of M1 is more like *Miacis* than *Hesperocyon*; this primitiveness is mainly reflected in its large, transversely oriented parastyle, which displaces the protocone toward the lingual side, and in its narrow, crestlike internal cingulum in contrast to a more swollen cingulum in *Hesperocyon*. The M1 of *Prohesperocyon*, however, is more derived in its relatively reduced parastyle. A notch between the parastyle and paracone is lost in *Prohesperocyon*; this notch is present in most miacids and *Procynodictis*. The anterior segment of the internal cingulum is greatly reduced so that the internal cingulum begins to assume a posterolateral configuration, as in *Hesperocyon*. The M1 thus has a transversely elongated

appearance, leaving room for a larger trigon basin than in *Hesperocyon*. The M1 paraconule (protoconule) and metaconule are also more distinct than in *Hesperocyon*. The M2 is relatively smaller than in *Hesperocyon*. A peculiar dental feature of *P. wilsoni* is its greatly reduced metacone of M2 such that the paracone entirely dominates the metacone. The metacone is no more than an indistinct ridge, lacking a labial cingulum. Such a condition of metacone reduction is shared only with *Procynodictis vulpiceps* Wortman and Matthew (= *Miacis gracilis* Clark) of North American Unitan (see Wang and Tedford, 1994) and is not seen in more derived canids. No M3 is present, although the present sample (one) is obviously too small to exclude the possibility of its presence in some individuals since occasional specimens of *H. gregarius* retain it.

The lower premolars are slightly more slender, or anteroposteriorly elongated, than their upper counterparts. A posterior accessory cusp is present on p3–4, which also have a distinct anterior cingular cusp. Their posterior cingula are low and ridgelike and tend to extend posteriorly. The m1 has a short shearing blade on the trigonid compared to that of *Hesperocyon*. The trigonid is also rather broad because of a labially swollen protoconid, a primitive character present in all *Miacis*. The talonid, in contrast, is much narrower and is relatively low, in lateral view, compared to the high trigonid. The hypoconid is the dominant talonid cusp (i.e., a trenchant talonid), and the entoconid forms a narrow, flat platform at the lingual heel of the hypoconid. Similar to *Procynodictis*, the m2 protoconid is nearly twice the size of the metaconid, as opposed to the nearly equalsized protoconid and metaconid in *Hesperocyon*. The m2 lacks an anterolabial cingulum which is often present in *Hesperocyon*. The talonid of m2 is narrow relative to the trigonid, much like that of the m1. The m3 is small with a single dominant cusp, presumably the protoconid.

DISCUSSION: *Prohesperocyon wilsoni* is by far the most primitive fossil canid, and its overall dental morphology is rather close to the North American Uintan *Procynodictis vulpiceps* Wortman and Matthew, 1899 (= *Miacis gracilis* Clark, 1939), a species that is

near the base of the Cynoidea clade (Wang and Tedford, 1994; it was called "*Miacis*" *gracilis* in that paper). Gustafson (1986) correctly pointed out that *P. wilsoni* is a true canid, as demonstrated mostly by its basicranial structure. Its possession of a fully ossified bulla, not seen in any miacids, serves as a convenient feature for recognition of fossil canids (the lack of a preserved bulla in miacids may have been due to weak attachment rather than poor ossification as reasoned by Flynn et al. [1988] and Wyss and Flynn [1993]). The bulla in *P. wilsoni* is more inflated than in some of the early *Hesperocyon*. The medially expanded petrosal and extrabullar position of the internal carotid artery lend support for its position as a basal taxon of the Canidae. Other than the basicranium, however, most dental features of *P. wilsoni* are more comparable with *Procynodictis* and *Miacis*, especially the P4–M2 and m2. An exception is the presence of posterior accessory cusps on the third upper and fourth lower premolars (also present in *Procynodictis*), a synapomorphy for the Cynoidea (Wang and Tedford, 1994). *Prohesperocyon* is more derived than *Procynodictis* in its loss of a notch between the parastyle and paracone of M1. The remaining features of *P. wilsoni* (e.g., the proportions of m1) are intermediate between *Hesperocyon* and *Procynodictis*.

The primitive morphology of *Prohesperocyon*, that is, close to the cynoid–arctoid dichotomy (see Wang and Tedford, 1994), is not far divergent from such primitive musteloid as *Mustelavus* from the White River Group of the northern Great Plains. In particular, the M1 of *Prohesperocyon* still retains a rather large parastyle (although reduced compared to miacids) and an unenlarged internal cingulum, characters also found in *Mustelavus*. The overall dental morphology and the skull structure are also very similar between the two. While remaining obscure in its phylogenetic position, *Mustelavus* exhibits some basal musteloid features, as suggested by Clark (1937). Some of these features can be used to distinguish *Mustelavus* from primitive canids: poor development of accessory cusps on premolars, presence of a cingulum around the premolars, and low trigonid cusps of m2.

Subfamily Hesperocyoninae
Tedford, 1978

NOMENCLATURE: The name "hesperocyonines" was informally proposed by Tedford (1978). Although no formal diagnosis was made, the contents of this subfamily was indicated by his three included genera: *Hesperocyon*, *Mesocyon*, and *Enhydrocyon*. Martin (1989) was first to adopt the subfamily, including the above genera plus *Oxetocyon*, *Phlaocyon*, and *Sunkahetanka*, and formalized the name as Hesperocyoninae, which he did not diagnose.

INCLUDED GENERA: *Hesperocyon* Scott, 1890; *Mesocyon* Scott, 1890; *Cynodesmus* Scott, 1893; *Sunkahetanka* Macdonald, 1963; *Philotrox* Merriam, 1906; *Enhydrocyon* Cope, 1879a; *Osbornodon*, new genus; *Paraenhydrocyon*, new genus; *Caedocyon*, new genus; and *Ectopocynus*, new genus.

DIAGNOSIS: Hesperocyonines are more derived than the basal canid *Prohesperocyon* and the more primitive miacids in having a low septum in the bullae (char. 10), a medially located P4 protocone (char. 32), an elongated carnassial (char. 34), and a reduced/lost anterior cingulum on M1 (char. 38). Members of Hesperocyoninae have a trenchant talonid of m1 (except in *Osbornodon*) in contrast to the basined talonids in the Borophaginae and the Caninae. Associated with this single-cusped (or hypoconid-dominated) talonid is the absence of a metaconule in M1, which is often present in borophagines and canines. Hesperocyoninae can be distinguished from contemporaneous amphicyonid carnivorans by an ossified entotympanic bulla, lack of an enlarged bony pocket formed by the basioccipital for the inferior petrosal venous sinus, and the absence of M3 in all except some rare individuals of primitive species.

DISTRIBUTION: Duchesnean (Late Eocene) to Early Barstovian (Middle Miocene) of North America.

DISCUSSION: The monophyly of subfamily Hesperocyoninae is not supported in the phylogenetic analysis. A trenchant talonid of lower molars, as in the diagnosis above, is likely a primitive character since it is also seen in the miacids. In fact, the subfamily is mainly defined by its lack of synapomorphies

for the other two subfamilies, Borophaginae and Caninae. Nonetheless, there is some support (see Phylogeny) for monophyly of Tedford's (1978) original series, *Hesperocyon–Mesocyon–Enhydrocyon*. To this clade may be added a sister-clade, *Osbornodon*, members of which tend to be confused with borophagines and canines. *Paraenhydrocyon* is tentatively included in the Hesperocyoninae as it may be directly derived from *Hesperocyon*. Poor preservations of materials of *Caedocyon* and *Ectopocynus* do not allow an adequate evaluation about their phylogenetic position.

Hesperocyon Scott, 1890

Amphicyon (Lartet) Leidy, 1856: 90.
Canis (Linaeus) Cope, 1873a: 3.
Galecynus (Owen) Cope, 1881b: 177.
Cynodictis (Bravard and Pomel) Scott and Osborn, 1887: 152.
Hesperocyon Scott, 1890: 37.
"*Pseudocynodictis*" Schlosser, 1902: 164.
Nothocyon (Matthew) Matthew, 1924: fig. 28.
Hesperocyon (Scott) Green, 1952: 124.
Nanodelphys? (McGrew) Russell, 1972: 7.
Cf. *Hyaenodon*? (Laizer and Parieu) Russell, 1972: 47.

TYPE SPECIES: *Canis gregarius* Cope, 1873.

No type species was designated in the first publication of *Hesperocyon* (Scott, 1890), nor was one subsequently assigned (see Discussion below). Among presently recognized species, *Canis gregarius* Cope is the most common and best known canid in the White River Group of the northern Great Plains, and is here designated as the type species of *Hesperocyon* following the recommendations of the International Code of Zoological Nomenclature (Stoll et al., 1961: recommendation 69B [6] [7]).

INCLUDED SPECIES: *Hesperocyon gregarius* (Cope, 1873a); "*H.*" *pavidus* Stock, 1933; and "*H.*" *coloradensis*, new species.

EMENDED DIAGNOSIS: *Hesperocyon* is more derived with respect to miacids and *Prohesperocyon* in having a low septum inside the bulla (char. 10); a reduced, medially positioned protocone of P4 (char. 32); a posteriorly positioned and enlarged internal cingulum of M1 (char. 38); a more elongated and longitudinally oriented shearing blade of

m1 (char. 34); and a nearly equal width of trigonid and talonid of m1 (see diagnoses of Canidae and Hesperocyoninae). In addition, *Hesperocyon* differs from *Prohesperocyon* in its metacone of M2 nearly the same size as paracone and equal-sized protoconid and metaconid of m2, two characters whose polarity is equivocal (see Phylogenetic Analysis). Besides its larger size, *Hesperocyon* differs from primitive musteloid *Mustelavus* in its better developed accessory cusps on premolars, its broader M1 with a more reduced parastyle, and more cuspidate trigonid on m2.

DISTRIBUTION: Cypress Hills Formation of southwestern Saskatchewan; Renova Formation of western Montana; Chadron, Brule, and correlative formations of the White River Group of the northern Great Plains; Sespe Formation of southern California. Duchesnean to early Arikareean of North America.

DISCUSSION: *Hesperocyon* has undergone a long and rather curious history of nomenclatural changes. Leidy (1856: 90) was first to briefly describe a fragment of a left ramus with p4–m1 from Nebraska (ANSP 11072, fully described and figured in Leidy [1869: 36, pl. I, fig. 7]). He named it *Amphicyon? gracilis*, apparently unaware that the name was preoccupied by the European taxon *A. gracilis* Pomel, 1847. Marsh (1871: 124) erected a second species, *A. angustidens* (type YPM 11762, a fragment of left ramus with c1, p2–4) from "Miocene Shale, at Scott's Bluff, on the North Platte River, Nebraska," although he admitted that it "agrees essentially in size with the corresponding jaw of *Amphicyon gracilis* Leidy." Two years later, Cope (1873a: 3) named another species *Canis gregarius* based on a few ramal fragments from the northeastern Colorado, without mention of the above two taxa. Later, Cope (1874: 507) did acknowledge the similarity between *A. gracilis* and *Canis gregarius*: "This species [*C. gregarius*] is about the size of the *Amphicyon gracilis*, Leidy, from the White River beds of Dakota, and I suspected at one time that I had found that species in Colorado," but decided that there were enough differences between these dogs to maintain distinct species. The fact that *A. gracilis* of Leidy was preoccupied was not acknowledged by Cope until 1884 (p. 916) when he synonymized it under his own species *Gal-*

ecynus gregarius (Cope had earlier [1881b: 177] reassigned the North American small canids to the European genus *Galecynus* Owen, 1847). Cope had, in effect, opted to supersede *Amphicyon gracilis* Leidy with his own taxon (based on different types) instead of giving Leidy's taxon a new name. Cope's specific name has since gained wide usage in the literature (e.g., Scott, 1898; Matthew, 1901; Scott and Jepsen, 1936). Thorpe (1922a: 162; 1922b: 425), however, first raised the issue that *A. angustidens* might be conspecific with *C. gregarius*. He drew the inevitable conclusion that the former clearly had priority. Besides occasional opinions that these two species were distinct (Schlaikjer, 1935: 131; Hough, 1948b), Thorpe's attempt to replace *C. gregarius* was ignored by all subsequent workers.

There are practical reasons for this resistance to switching to Marsh's name. The type of *Amphicyon angustidens* (YPM 11762) is too poorly preserved to be of any diagnostic value at the species level. The few teeth that are preserved (c1 and p2–4) remain primitive and unchanged at this stage of the evolution in *Hesperocyon*, even though YPM 11762 could be referred to *Canis gregarius* following the usual practice of comparisons of size and stratigraphic occurrence. Resurrection of Marsh's species would only serve to open the question of the uncertainties in the nature of its type, and *Amphicyon angustidens* is here designated as a nomen vanum. This leaves Cope's *Canis gregarius* as the next available name with an adequate type series (see below). That it has been in general usage for the last 100 years further reflects that Cope's taxon is better founded.

The generic status of *Canis gregarius*, however, was also controversial for the first half century of its existence. Scott and Osborn (1887: 152) first adopted the genus *Cynodictis* Bravard et Pomel, 1850, from the late Eocene of Europe for the American species of *Amphicyon* and *Galecynus*, but used Leidy's specific name instead (i.e., *Cynodictis (Amphicyon) gracilis*). Three years later, Scott (1890: 37) proposed a new genus *Hesperocyon* without formal designation of a type species: "The second canine genus of the White River may be called *Hesperocyon*; it has been referred by Leidy to *Amphicyon*, and by Cope to *Gal-*

ecynus, but is really quite distinct from either. . . . Its nearest European allies are *Cynodon* and *Cynodictis*." Subsequently, he (Scott, 1898) seems to have forgotten his generic name and referred to the European *Cynodictis* again (in the same 1890 paper he also proposed the genus *Mesocyon*, which he later did not use; see also Discussion under *Mesocyon*). Schlosser (1902: 164) recognized some dental differences between the North American White River Oligocene species (*Cynodictis gregarius*, *C. lippincottianus*, and *C. temnodon*) and the true *Cynodictis* in Europe. He referred the North American forms as "*Pseudocynodictis*" (his quotation marks); again, no type species was designated. Scott and Jepsen (1936) subsequently followed Schlosser, and *Pseudocynodictis* became widely adopted by North American vertebrate paleontologists. The name *Hesperocyon* was finally resurrected on grounds of seniority by Green (1952: 124) and has since gained wide usage.

Green's attempt to resurrect *Hesperocyon*, however, was also flawed: he did not specify a type species for the genus, which, like *Pseudocynodictis* Schlosser, had been legally empty since its original proposal. *Hesperocyon gregarius* is presently fixed as the type species in recognition of its well-known status in the published literature.

Hesperocyon is paraphyletic not only because of the lack of synapomorphy shared by the three included species, but also because some clades of hesperocyonines may ultimately be derivable from *H. gregarius* (see fig. 65). In addition, borophagines and canines may also have taken their origin from *Hesperocyon* (possibly through "*H.*" *pavidus*). Although the present treatment of *Hesperocyon* is partly based on my dissertation study (Wang, 1990), a number of its conclusions are changed in this paper because of additional materials studied (mainly the Frick Collection) and reanalysis of the type specimens of the various species. I no longer recognize *Hesperocyon paterculus* as a valid species (I had expressed doubts about its validity but tentatively let it stand in my dissertation), and my justifications are given under the discussion of *H. gregarius*. I regard *H. lippincottianus* as a possible daphoenid, and Cope's (1873b) concept of a large-sized *Hesperocyon*

is now replaced by a new species, "*H.*" *coloradensis*. I refer a small-sized species (which I named a new taxon in my dissertation) from the Orellan and Whitneyan of the Great Plains to "*H.*" *pavidus*, which is probably the most primitive member of the Borophaginae.

Hesperocyon gregarius
(Cope, 1873)
Figures 9, 10, 11D–E

Amphicyon? *gracilis* Leidy, 1856: 90, nom. preoc.
Canis gregarius Cope, 1873a: 3.
Canis lippincottianus Cope, 1873b: 9 (referred specimen only).
Galecynus gregarius (Cope) Cope, 1881b: 177.
Cynodictis gracilis (Leidy) Scott and Osborn, 1887: 152.
Hesperocyon gregarius (Cope) Scott, 1890: 37. Green, 1952: 124. Russell, 1972: 53 (in part).
Cynodictis gregarius (Cope) Scott, 1898: 400.
Nothocyon gregarius (Cope) Matthew, 1924: fig. 28.
Pseudocynodictis gregarius (Cope) Schlosser, 1902: 50. Scott and Jepsen, 1936: 101. Galbreath, 1953: 75.
Cynodictis paterculus Matthew, 1903: 209.
Cynodictis lippincottianus (Cope) Lambe, 1908: 61.
Amphicyon angustidens (Marsh) Thorpe, 1922b: 425.
Cynodictis paterculus (Matthew) Thorpe, 1922b: 428.
Pseudocynodictis angustidens (= *lippincottianus*) (Marsh) Hough, 1948b: 590.
Pseudocynodictis nr. *paterculus* (Matthew) Galbreath, 1953: 75.
Hesperocyon paterculus (Matthew) White, 1954: 416.
Pseudocynodictis nr. *paterculus* (Matthew) Hough and Alf, 1956: 136.
Nanodelphys? *mcgrewi* Russell, 1972: 7.
Cf. *Hyaenodon*? *minutus* (Douglass) Russell, 1972: 47 (NMC 9353 only).

LECTOTYPE: AMNH 5297a, fragment of left ramus with p2–m1 and alveolus for p1.

No type was formally designated by Cope (1873a: 3); instead, he stated there were "abundant" specimens of *Canis gregarius* in his collection. Subsequent references to the species by Cope (1873b, 1874, 1881b) shed no light about his intention of a type. In his most comprehensive description of this species, Cope (1884: pl. LXVIIa, fig. 9) figured AMNH 5297a and four additional rami (ibid.: figs. 7, 8, 10, 11, AMNH 5298–5301), again

with no indication of which one was the type. However, he apparently did informally elect AMNH 5297 as the holotype, for this was indicated as such when W. D. Matthew catalogued Cope's collection into the AMNH system. Galbreath (1953: 75) was the first to explicitly list AMNH 5297 as the type of *Pseudocynodictis gregarius*, and thus fixed it as the lectotype.

Problems, however, still remain because AMNH 5297 includes two specimens, here designated as 5297a and 5297b. The latter is represented by a fragment of a right ramus with p4 and broken m1, and its differences in size and wear on the talonid of m1 from AMNH 5297a indicate that AMNH 5297a and 5297b represent different individuals. AMNH 5297a is more likely Cope's holotype not only because of its better preservation, but also because it was illustrated by Cope (1884).

TYPE LOCALITY: In his original description of *Canis gregarius*, Cope (1873a: 3) only commented that it was "abundant in the *Oreodon* beds of the Miocene formation." Galbreath (1953: 75) listed it as "Tertiary of Colorado." AMNH 5297a is thus broadly referable to the White River Formation of northeastern Colorado.

REFERRED SPECIMEN: See Appendix I.

EMENDED DIAGNOSIS: The derived characters listed under the diagnosis of *Hesperocyon* can be used to distinguish between *Prohesperocyon wilsoni* and *H. gregarius*. Among the three referred species of *Hesperocyon*, however, distinctions are more subtle. Being approximately 10–30% larger than "*H.*" *pavidus* in most dental measurements (Appendix III), *H. gregarius* has less pronounced cingular and accessory cusps in premolars, slightly smaller metaconid of m1–2, and a more prominent M1 parastyle and internal cingulum than in the former. Being about 18% smaller than "*H.*" *coloradensis*, *H. gregarius* has a primitively posteriorly directed paroccipital process.

DISTRIBUTION: *Hesperocyon gregarius* is among the most common of carnivorans in Chadronian through Whitneyan strata of most North American localities: Cypress Hills Formation, Saskatchewan, Canada; Renova Formation of western Montana; and Chadron, Brule, and their correlative formations

within the White River Group of Colorado, Nebraska, South Dakota, North Dakota, and Wyoming. Recent studies of carnivorans from the Lac Pelletier Lower Fauna, Cypress Hills Formation, Saskatchewan, by Bryant (1992) referred three isolated teeth to *Hesperocyon* (presently referred to *H. gregarius*; see Discussion below) and thus extended its range downward into the early to mid-Duchesnean (Storer, 1987, 1988).

DESCRIPTION: Among all hesperocyonines, *Hesperocyon gregarius* is the most abundant and also the best known both in its geological and geographical ranges. It is undoubtedly the most common fossil carnivoran in the badlands of the northern Great Plains. A rather detailed description of this species can be found in the extensive treatments of White River faunas by Scott and Jepsen (1936). Their description of *H. gregarius*, however, was mainly a comparison with different genera of living canids, and provided no systematic synthesis of even then-known species of *Hesperocyon*. *Hesperocyon gregarius* is redescribed here because of its important phylogenetic position in relation to other hesperocyonine lineages.

Skull: The overall proportions of a *Hesperocyon gregarius* skull are little different from similar-sized *Miacis*. The rostrum is relatively short as opposed to a long rostrum in *Prohesperocyon wilsoni*. The posterior premaxillary process is slender and short, widely separated from the anterior process of the frontal. The nasal widens slightly toward its anterior end. The postorbital process of the frontal is usually small and forms a sharp tip directed laterally. On skulls with exposed internal surface of the frontal bones (a rectangular piece of the frontal shield is cut off from skulls of F:AM 50278, 50325, and 50345) there is no evidence of a frontal sinus nor is there a sinus in the postorbital process. A frontal sinus is present in all derived members of the three subfamilies of canids and serves as an important character in their phylogeny (Huxley, 1880; see Matthew [1924] for an opposing view). The postorbital constriction is rather anteriorly located (i.e., close to the postorbital process) due to the relatively larger braincase than that of large-sized hesperocyonines. A low sagittal crest is present in some robust individuals and is absent in

others, which tend to have a lyrate double temporal crest instead. The height of the nuchal crest is correlated with that of the sagittal crest.

In the lateral aspect, the lacrimal occupies part of the antorbital rim and is in contact with the anterior process of the jugal. The infraorbital foramen is large and rounded. The zygomatic arch is rather slender, compared to a heavier construction in later hesperocyonines (e.g., *Enhydrocyon*), and the postorbital process of the jugal is similarly lightly constructed.

Ventrally, the posterior border of the palatine slightly protrudes posteriorly at the midline and stops at the level of the posterior border of M2. There is much variation in the size of hamulus of the pterygoid. On one hand, FMNH UC498 possesses a large, backwardly hooked hamulus; on the other hand, USNM 437888 entirely lacks a hamulus. This variation appears to be correlated with a pocket on the angular process of the mandible. In FMNH UC498, the internal ridge of the angular process is medially expanded and forms a pocket, probably for the insertion of the pterygoideus medialis muscle, which in *Canis* originates from either side of the pterygoid wings, including the hamulus (Evans and Christensen, 1979: fig. 6-15). In USNM 437888, however, the internal ridge remains low and inconspicuous.

Major characteristics of the basicranium of *Hesperocyon gregarius* have been outlined by Hough (1948a), Mitchell and Tedford (1973), and Tedford (1976). Wang and Tedford (1994) most recently attempted to trace the basicranial transformation from miacids to primitive canids. One of the most significant characters is the presence of a low septum at the ecto- and entotympanic suture in *H. gregarius*. This septum, presumably composed of the in-bent edge of the caudal entotympanic as in living *Canis* (Hunt, 1974), is different from that in living canids in its position at the ventral edge of the caudal entotympanic instead of the dorsal (caudal/rostral entotympanic) suture in living *Canis*, as emphasized by Hunt (1974). These different positions of the septum in *Hesperocyon* and *Canis* seem to point to a transformation series within the Canidae, that is, shifting positions of the septum (see Wang and Tedford,
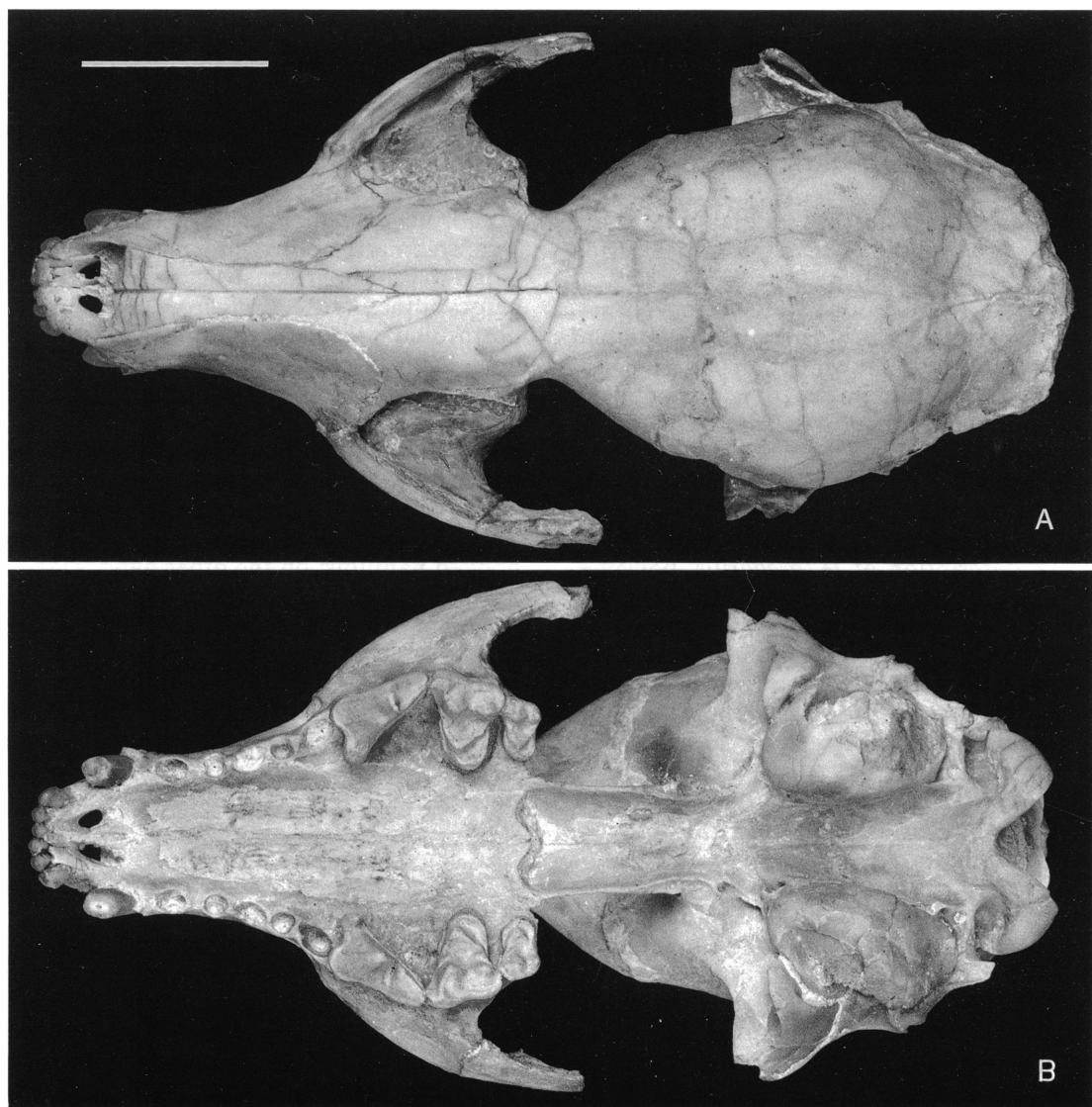
Fig. 9. Skull of *Hesperocyon gregarius*, USNM 437888. **A**, Dorsal and **B**, ventral views. Scale = 15 mm.

1994). The petrosal of *H. gregarius* is medially expanded to fully contact with the basioccipital/basisphenoid, in contrast to globular, isolated petrosals in primitive miacids and arctoids. The internal carotid artery is inside a bony canal formed by the rostral/caudal entotympanic ventrally and by the petrosal dorsally (i.e., a medial position of the internal carotid artery as opposed to a transpromontorial position in miacids). Although all of the above characters have undergone modifications, mostly related to further ossification of the basicranium in more derived canids, the basic canid plan was clearly in place in *Hesperocyon* and has remained unchanged in derived forms: presence of a septum, extrabullar position of the internal carotid artery, and expanded petrosal.

There are, however, several other aspects of basicranial morphology that have undergone extensive modifications in advanced
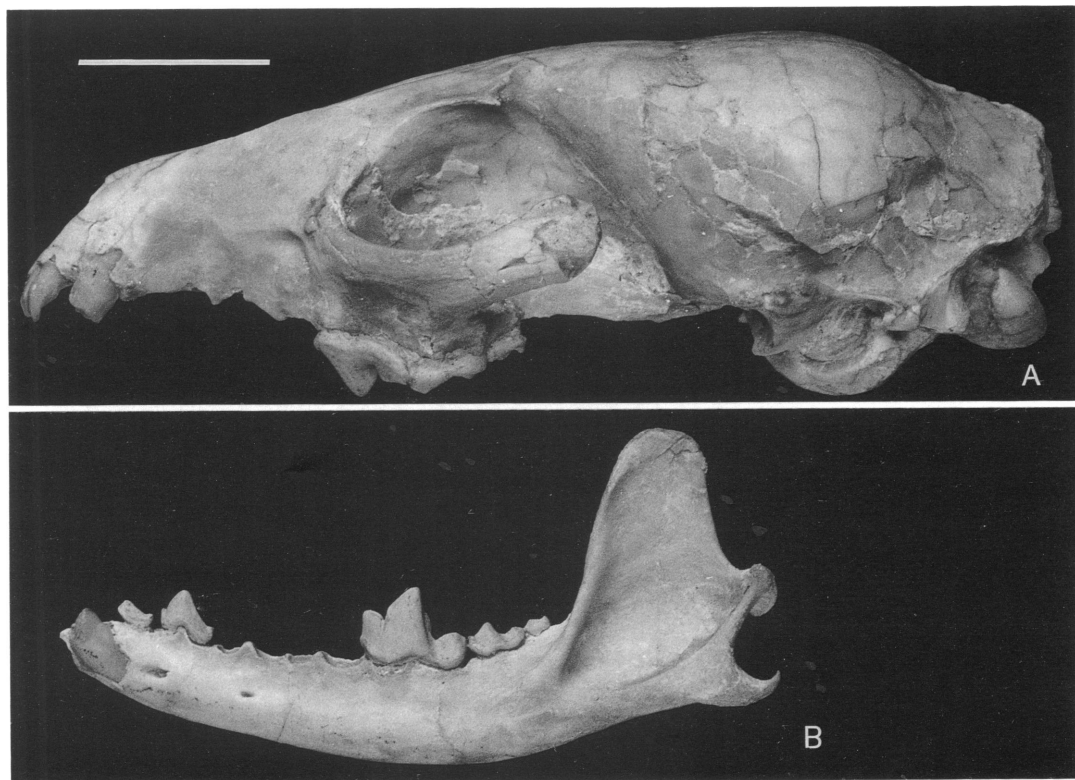
Fig. 10. Skull and mandible of *Hesperocyon gregarius*, USNM 437888. Lateral views of **A**, skull and **B**, ramus (reversed from right side). Scale = 15 mm.

canids of various lineages. Among the most noted is the paroccipital process, which in *Hesperocyon gregarius* is triangular in cross section and is pointed backward, free from fusion with the base of the entotympanic bulla. In all three subfamilies of the Canidae, the paroccipital processes have been independently enlarged and rotated ventrally to be fused with the entotympanic. The osseous external auditory meatus in *H. gregarius* is simply the opening of the ectotympanic and is not laterally extended to form a tube as in many derived canids. The mastoid process is not enlarged as in *Enhydrocyon*, nor has it receded beneath the squamosal shelf as in *Osbornodon*. In front of the mastoid process, on the squamosal portion of the process, there is a small and shallow suprameatal fossa, which is also present in *Prohesperocyon*.

Variations of skulls in *Hesperocyon gregarius* are primarily in robustness; the larger and more robust individuals (presumably males) tend to have broader skulls, more prominently developed postorbital processes, higher and stronger sagittal crests, deeper zygomatic arches, etc. The presumed males also tend to develop rugose surface texture above the occipital condyle, whereas females tend to have thinner skull walls and leave a prominent swelling above the foramen magnum corresponding to the vermis of the cerebellum of the brain. Some of the above variations can also be attributed to ontogeny; on two juveniles (F:AM 50266 and 50377, deciduous teeth still in place), the postorbital process is nearly lacking and there is no trace of a sagittal crest.

Mandible: Mandibles of *Hesperocyon gregarius* are distinguished from those of *Prohesperocyon* mainly in their slightly more upright ascending ramus. The anterior border of the ascending ramus is at a smaller angle with the horizontal ramus than in *Prohesperocyon*. The angular process is usually

lightly built with a low internal ridge (sensu Gaspard, 1964) on the medial side. In some individuals (e.g., AMNH 39096; F:AM 72522, 76518, 128064; FMNH UC498) this internal ridge is more medially expanded and dorsally curved to form a dorsal pocket for attachment of the pterygoideus medialis muscle. In others (e.g., F:AM 50385, 76170; FMNH UC495; UNSM 50787; USNM 437888) the internal ridge remains small. The expansion of this ridge appears to be correlated to the size of the hamulus process of the pterygoid where the pterygoideus medialis originates. This pocket for the pterygoideus medialis is more prominently developed in *Paraenhydrocyon*.

Dentition: The upper incisors are small and, in unworn specimens, have two shallow grooves on the tips to mark the divisions into three cusps. The I3 is larger than the I1–2 and may have only two cusps. All upper canines have a distinct posterior ridge, and some have a less distinct anterolingual ridge. The P1 is always present and single-rooted. There is no anterior cingular cusp on P1–3. Upper premolars of most individuals lack a posterior cingular cusp except P3; some individuals, however, have a posterior cingular cusp on P2. A small posterior accessory cusp is often present on P3. The base of the main cusp of P3 is usually slightly swollen on the lingual side; isolated individuals (e.g., F:AM 76157, 76177, 76520) even have an additional (third) root beneath this enlarged main cusp base (no distinct protocone, however, is present). The protocone of P4 is more reduced and posteriorly located compared to that in *Prohesperocyon*, and it is more appressed toward the base of paracone. There is a small anterior cingulum at the anterior tip of P4, and there may or may not be a labial cingulum, although a lingual cingulum is invariably present. The M1 parastyle is much reduced compared to that of *Prohesperocyon*. Specimens from earlier age (Duchesnean–Chadronian) tend to have larger parastyles, whereas Orellan–Whitneyan samples often have no more than a swollen labial cingulum. The overall shape of the M1 is also less transversely elongated than in *Prohesperocyon*. The most noticeable feature of upper molars of *H. gregarius* is the posteriorly deflected internal cingulum, as opposed to a

more symmetrical internal cingulum in *Miacis*. In many individuals of *H. gregarius*, the anterior cingulum in front of the protocone is lost, leaving the protocone without a surrounding cingulum. The posterior segment of the internal cingulum, on the other hand, is thickened and restricted to the posteromedial corner of the tooth. This swollen internal cingulum has been called a hypocone by some authors. The most prominent difference between the M2s of *H. gregarius* and *Prohesperocyon* is the approximately equal-sized metacones and paracones in the former, in contrast to the much reduced metacone in the latter. Corresponding to the swollen internal cingulum of M1, that of M2 is also better developed in *H. gregarius* than in *Prohesperocyon*. The M3 is suppressed in all but occasional individuals. Five specimens (F: AM 50261, 63934, 63942, 63943, and USNM 18911) possess an M3 (7%) as opposed to 67 that do not (specimens are counted whose maxillary bone behind the M2s is judged to be least disturbed and thus likely indicates natural absence of the M3s). All five specimens are from Chadronian deposits. In most of these cases, the M3s can be said to be practically lost; their size is far too small to be of any functional significance; their length: width ratios (in mm) are: 1.6:2.3 in F:AM 50261, 0.8:2.3 in F:AM 63943, and 0.9:1.1 in USNM 18911 (F:AM 63934 has M3 alveolus only and the M3 on F:AM 63942 is too worn to be measured).

The lower incisors are bicuspid as opposed to the tricuspid upper incisors. The grooves that divide the tips into the two cusps are also deeper and broader than those in the uppers. The lower canine is slightly more backwardly curved than its upper counterpart, and it usually has a posterior ridge. The p1 is single-rooted and tends to have a small posterior cingular cusp, but is otherwise simply single-cusped. An anterior cingular cusp is seen on most p2s, whose posterior ends tend to develop a low cingulum rather than a distinct cusp. The p3 and p4 have a posterior cingular cusp and a posterior accessory cusp of variable size. The shearing blade of the m1 trigonid appears to be more anteroposteriorly oriented than in *Prohesperocyon* because of the less swollen protoconid of *Hesperocyon gregarius*. The metaconid of *H. gre-*
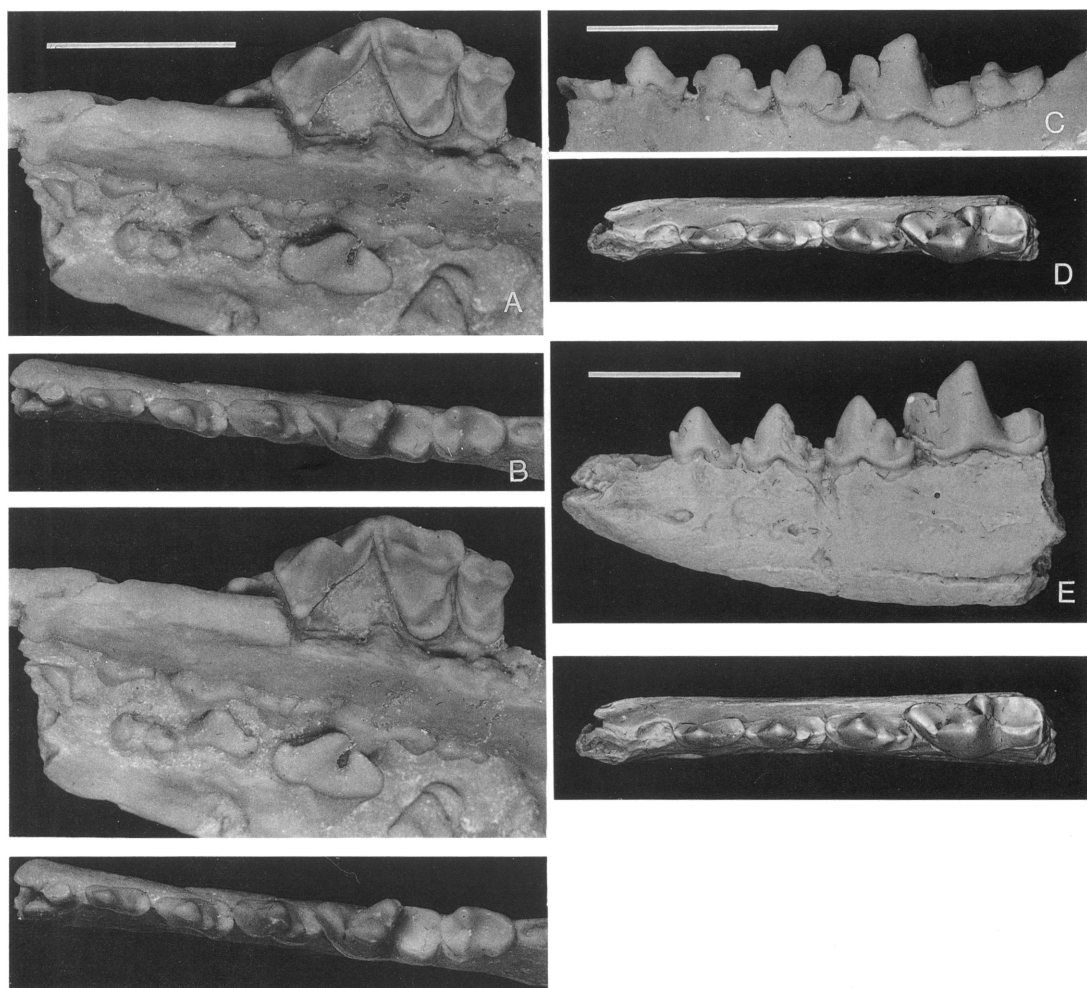
Fig. 11. Teeth of *Hesperocyon*. **A–C**, "*H.*" *pavidus*, LACM466, holotype, scales = 20 mm; **D–E**, *H. gregarius*, AMNH 5297a, holotype, scale = 10 mm. **A**, Occlusal view of upper teeth and articulated mandible (reversed from right side); **B**, occlusal view of lower teeth (reversed); **C**, lateral view of lower teeth (reversed); **D**, occlusal view of lower teeth; and **E**, lateral view of mandible. All are photographs of epoxy casts.

garius is generally smaller than that of *Prohesperocyon*, although earlier samples (e.g., Lac Pelletier) still retain the relatively large metaconid. In addition, the trigonid is low relative to the talonid, as compared to the higher trigonid in *Prohesperocyon*. The relative size of the hypoconid to that of the entoconid varies slightly; however, the hypoconid is always the dominant cusp. The entoconid is usually ridgelike, although in some individuals it may be restricted to the posterolingual corner of the talonid, giving a more cusplike appearance. Enclosed between

the hypoconid and entoconid ridges is an anteroposteriorly oriented valley (an incipient talonid basin), which becomes a low platform when the entoconid ridge is low. Despite the low entoconid ridge, the talonid of *Hesperocyon* is essentially trenchant. The protoconid and metaconid of m2 are subequal in contrast to a much larger protoconid in *Prohesperocyon*. There is no paraconid. In its place there is a flat platform in front of the protoconid and metaconid. At the anterolabial corner, there is a low cingulum, which is absent in *Prohesperocyon*. Similar to the m1,

TABLE 2
Measurements (in mm) of Deciduous Teeth of *Hesperocyon gregarius*

	LDP2	WDP2	LDP3	WDP3	LDP4	WDP4	LDp3	WDp3	LDp4	WDp4	TDp4
AMNH 90307	—	—	—	—	—	—	4.4	1.8	—	—	—
F:AM 50266	—	—	5.7	—	4.5	4.3*	—	—	6.3	—	—
F:AM 50377	3.4	1.4	5.3	3.4	—	—	—	—	—	—	—
F:AM 126898	—	—	—	—	—	—	4.7	1.8	—	—	—
KUVP 8195	—	—	—	—	—	—	4.8	1.8	6.7	2.4	3.8
KUVP 10781	—	—	—	—	—	—	4.8	1.9	6.2	2.5	3.6

* Measurement estimated.

the talonid of m2 is also dominated by a hypoconid, and the entoconid becomes a low ridge that never develops into a cusp. The morphology of the very small m3s varies considerably; most are double-rooted (sometimes fused together) and retain a protoconid and a smaller metaconid.

Deciduous teeth of *Hesperocyon gregarius* are generally extremely rare; an exception occurs in the Calf Creek local fauna of Cypress Hills Formation, Saskatchewan (Bryant, 1991, 1993). They are overall more slender (table 2) and sharp-cusped than their counterparts in the permanent series. The rooted protocone on dP3 is centrally located and medial to the main cusp. The dP4 bears little resemblance to M1, and essentially retains the morphology of a tribosphenic molar of primitive mammals. The outline of dP4 is basically triangular with three cusps (paracone, metacone, and protocone) on each angle and a long metastyle. This superficial resemblance to metatherian molars led Russell (1972, 1984) to assign a dP4 of *H. gregarius* to a new genus and species of marsupial, *Alloeodectes mcgrewi* (Bryant, 1991). The deciduous lower cheek teeth correspond more closely to the morphology of the permanent dentition. Besides sharper anterior and posterior cingular cusps and more slender proportions, dp3 is basically similar to the permanent p4. The dp4 has a well-developed hypoconulid not seen in permanent m1. The talonid cusps on dp4 are also more aligned along the peripheral border of the talonid, creating a deep central basin (see figures in Bryant, 1993).

Postcranial skeleton: One of the striking features of *Hesperocyon* is its large baculum (fig. 12), which is not mentioned in previous literature. The baculum is more than three times as long as that of living foxes of comparable size. The distal end is curved upward as opposed to the relatively straight baculum in living canids (Hildebrand, 1954). A deep dorsal groove along most of the shaft is common in all canids. The overall shape and size of the *Hesperocyon* baculum, among major groups of carnivorans, appear to be more similar to the modern raccoon (*Procyon*) than to any living canids (Scott and Jepsen, 1936: 88; Ewer, 1973: 31). The phylogenetic significance of a large baculum is not clear because it is rarely preserved in the fossil record; Wyss and Flynn (1993), however, postulated that a large baculum was plesiomorphic for the Caniformia clade.

An extensive analysis of the skeletons in primitive canids is presented elsewhere (Wang, 1993). The limb bones of *Hesperocyon* possess a mixture of characteristics that display, on one hand, some advanced cursorial adaptations, such as compressed digits (Tedford, 1978), and on the other hand, primitive limb proportions that were compared to living viverrid carnivorans (Matthew, 1901; Scott and Jepsen, 1936). Although the rarity of associated postcranial materials makes a detailed phylogenetic assessment difficult, it appears that the closed digits may possibly serve as a synapomorphy for Canidae (Clark, 1939), whereas arctoids still have short and sturdy limbs and retained a primitive plantigrade posture.

A significant number of individuals (61%, N = 31) of *Hesperocyon* developed osteochondroma, a genetically controlled bone tumor commonly developed on human distal

limb bones and axial skeletons (Wang and Rothschild, 1992, and references therein). It is unique, however, that all affected individuals of *Hesperocyon* have large tumors on the medial surface of both distal radii. Lesions are occasionally found on sternebrae, vertebral centra, and radial shafts. This multiple occurrence of the tumors are indicative of hereditary multiple exostosis, a pathology that has been identified in living domestic dogs. Similar lesions have been found in North American *Daphoenus* (Romer, 1924) and European *Cynodictis* (Schlosser, 1887).

DISCUSSION: Being contemporary with *Hesperocyon*, the extremely rare *Mustelavus priscus* is also found in the White River beds of the northern Great Plains. Their identical dental formula and similar skull and dental proportions can potentially confuse the identification of these two small carnivorans. *Mustelavus* is the size of a weasel and is approximately 25% smaller than *Hesperocyon*. It shows primitive musteloid features that can be used to distinguish it from *Hesperocyon*: simple premolars with weak cingulum and poorly developed accessory cusps, narrow M1 with large parastyle and small internal cingulum, and low trigonid cusps on m2.

With its abundant materials in museum collections, not surprisingly *Hesperocyon gregarius* would seem to be more variable than other species of primitive canids. White (1954: 418) remarked in frustration: "The variety of tooth-cusp arrangement and height of crown exhibited by the small carnivores of the Middle Oligocene which have been referred to *H. gregarius* (Cope), both in the literature and in collections, make any attempt at comparison with that species entirely futile." The shape of M1 is more variable than other teeth, although no consistent pattern was found in the present study to suggest discrete morphotypes. These variations of dental morphology, however, are no more than can be observed within living North American populations of the red fox *Vulpes vulpes* (Gingerich and Winkler, 1979), which has as extensive a geographic distribution as *Hesperocyon*. Furthermore, morphometric analysis of the size of m1 indicates a single species in most strata and localities of northern Great Plains, using a modern an-
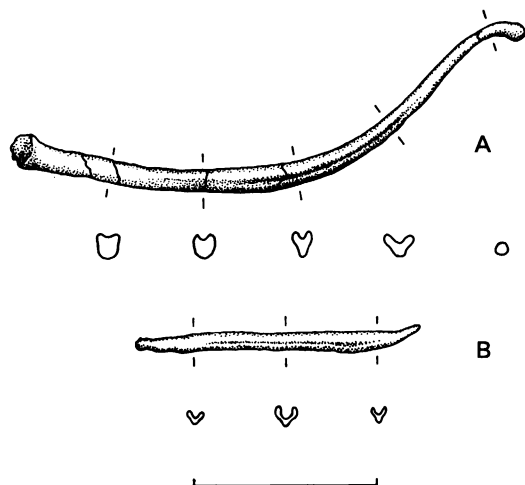
Fig. 12. Lateral view and cross sections of baculum. **A,** *Hesperocyon gregarius* (MCZ 3667), proximal end (left) based on FMNH P12224; **B,** kit fox (*Vulpes velox*, KUMA 121601). Scale = 30 mm.

alog of foxes from the Middle East (see Discussion of "*H.*" *pavidus*).

In addition to the seemingly large variation, the long history of study on *Hesperocyon gregarius* is certainly conducive to the creation of duplicate taxa. This is recognized to be the case in *H. paterculus* (Matthew), 1903, which has been in a state of uncertainty since its first publication. The holotype (AMNH 9616) and referred specimens were from the Pipestone Springs local fauna (Middle Chadronian), Montana. Four authors have since published records of this species from locations other than the type locality: from Colorado and South Dakota (Thorpe, 1922b), from Colorado (Galbreath, 1953), from the Canyon Ferry area of Montana (White, 1954; a nearly complete skull and mandible with partial postcranial skeleton [USNM 18911] was referred to this species), and from Nebraska (Hough and Alf, 1956). Most of the authors (except Thorpe) seem to rely on stratigraphic criteria as a basis of their recognition (i.e., individuals from Chadronian deposits were named *H. paterculus* and those from Orellan, *H. gregarius*).

Matthew's (1903: 210) original description of *Cynodictis paterculus* was brief and is here quoted in its entirety: "Compared with a quite

large series of specimens, including the types of *C. gregarius* and *C. lippincottianus*, these specimens [*C. paterculus*] show certain constant differences, chiefly in the construction of m₂. This tooth is proportionally larger and longer, the heel larger and wider, and the proto- and metaconids are raised above the paraconid, instead of being nearly on a level with it, as they usually are in *C. gregarius*. The shear of m₁ is somewhat more transverse, and m₃ is a little less reduced." Matthew acknowledged the subtle nature of these characters: "the above characters are slight distinctions indeed"; however, he argued that "their constancy in the very considerable series of specimens compared makes them valid specifically." Thorpe (1922b: 428) endorsed Matthew's idea of a distinct species: "The specific characters, as outlined by Matthew, are constant, and thereby afford *strong* evidence for the validity of the species" (emphasis added). Curiously, Thorpe immediately contradicted himself: "I can not help feeling that this form may represent the male of *C. angustidens* [*Hesperocyon gregarius*]." Hough and Alf (1956: 137) also disagreed with Matthew: "the characters described by Matthew are highly variable and that the differences, such as the length of M₂, height of the paraconid, protoconid, and metaconid are so slight that no two people studying the same series of jaws would classify them the same way." Nevertheless, they tentatively retained the species *H. paterculus* pending further study. Mainly based on the three original specimens described by Matthew (1903), I expressed doubt about the distinctness of this species (Wang, 1990). The larger Chadronian samples available in the present study and a more thorough examination of the type series (half of them not mentioned by Matthew) have led me to conclude that *H. paterculus* is morphologically indistinguishable from *H. gregarius* for the following reasons:

First, a total of six rami fragments from the Pipestone Springs (AMNH 9614, 9616, 9617, 9618, 9619, and 9622), which were obtained in the 1902 AMNH expedition, were available to Matthew. Four specimens have complete m2s; half of these (AMNH 9614 and 9618) possess a small (i.e., normal sized) m2, contradicting Matthew's claim of "constancy" of large m2, a key characteristic of

the species. Additional Pipestone Springs specimens (F:AM 50230 and KUVP 88185) examined in the present study further bring the ratio of large-sized m2 to only one-third of the total sample (fig. 13). Second, the high protoconid and metaconid in m2, cited by Matthew (1903) as another diagnosis of *Cynodictis paterculus*, is even more ambiguous. Much of the "raised" protoconid and metaconid (relative to where the paraconid is supposed to be) can be attributed to the larger-sized m2. Furthermore, the size of m1s in the entire Montana sample is well within the range of variation of *H. gregarius* from the northern Great Plains (fig. 14; Appendix III). I therefore agree with the conclusion by Hough and Alf (1956: 137): ". . . *P. [Pseudocynodictis = Hesperocyon] paterculus*, when all characters of the skull and dentition are taken into consideration, grades into *P. gregarius*." A distinct Chadronian species of *Hesperocyon* is not recognized by the present study.

Bryant (1992) referred two right m1s (SMNH P1899.5 and P1899.6) and one left dp4 (SMNH P1899.1428) from the Duchesnean Lac Pelletier Lower Fauna, Cypress Hills Formation, southwestern Saskatchewan, Canada, to *Hesperocyon* sp. The Lac Pelletier materials are assignable to *Hesperocyon* based on their more derived features in the m1s: low trigonid relative to talonid and nearly equal width of trigonid and talonid (as opposed to much wider trigonid in *Prohesperocyon*). However, the m1s still maintain a rather short shearing blade of the trigonid instead of the more "open" trigonid in typical *Hesperocyon*. As noted by Bryant (1992: 852), the size difference between the two m1s is "substantial." SMNH 1899.5 approaches the size of *H. gregarius*, whereas SMNH 1899.6 is closer to the size of "*H.*" *pavidus*. The three teeth from the Lac Pelletier Lower Fauna are here tentatively referred to *H. gregarius* pending more complete materials, and they therefore extend the stratigraphic range of *H. gregarius* downward into the deposits of Duchesnean age.

"*Hesperocyon*" *pavidus*
(Stock, 1933)
Figure 11A–C

Pseudocynodictis(?) *pavidus* Stock, 1933: 31.

Pseudocynodictis sp. (small form) Galbreath, 1953:
  76.

HOLOTYPE: LACM 466, crushed anterior
half of skull and mandible with left P2–M1,
right P3–M2, left and right p2–m2, and al-
veoli for p1 and m3.

TYPE LOCALITY: Kew Quarry local fauna
(all of the Kew Quarry specimens were col-
lected by the California Institute of Tech-
nology expeditions and carry a CIT locality
number 126), Las Posas Hills, Ventura Coun-
ty, California. Sespe Formation, early Early
Arikareean.

REFERRED SPECIMEN: From Whitneyan of
northwestern Nebraska: F:AM 50338, partial
left maxillary with I1–3, P2–M2 and partial
mandible with left and right c1–m3, 1 mi
northeast of Crow Butte, Dawes County, 30
ft above a gray, ashy layer in Whitney Mem-
ber of Brule Formation; F:AM 63976, right
ramus fragment with m2–3, Plunkett-Par-
son's Locality, 8 mi north of Harrison, in E½
of sect. 34, sect. 35, S½ of sect. 36, T. 36 N,
R. 56 W, and N½ sect. 1, T. 32 N, R. 56 W,
Sioux County, below first Whitney ash layer
in a paleo-valley fill that cut through the Or-
ellan clays.

From Whitneyan of southwestern South
Dakota: F:AM 50342, fragment of left ramus
with m1–2, 6 mi southeast of Oelrichs, Fall
River County, 20 ft above first Gray Nodule
Zone in Poleslide Member of Brule Forma-
tion; F:AM 63360, right ramus fragment with
m1, 0.25 mi west of Cedar Pass, Jackson
County, in basal Leptauchenian beds.

From Cedar Creek Member of northeast-
ern Colorado, Orellan: AMNH 5326, left ra-
mus fragment with p3–4; KUVP 8202, left
ramus fragment with m1, SW¼, sect. 31, T.
12 N, R. 54 W, Logan County; KUVP 8203,
right ramal fragment with broken m1 and
complete m2, E½, sect. 3, T. 11 N, R. 54 W,
Logan County; KUVP 8208, left ramal frag-
ment with broken p4–m1 and complete m2,
Clyde Ward Ranch, W1/2, sect. 7, T. 11 N,
R. 53 W, Logan County; KUVP 68924, par-
tial left ramus with broken p2–m2, north of
Bufo Point, locality KU-CO-018, Yuma
County; KUVP 88364, ramus fragment with
m2, KU-CO-046, W½, sect. 7, T. 11 N, R.
53 W, Logan County.

EMENDED DIAGNOSIS: "*Hesperocyon*" *pav-*
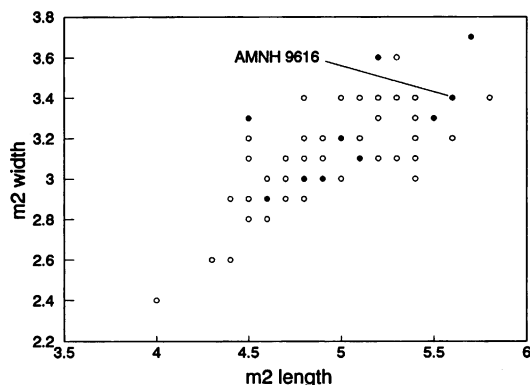
Fig. 13.   Scatter diagram of length versus width
of m2, showing the distribution of individuals from
the Chadronian deposits of Montana (in solid cir-
cles; a composite sample from the Pipestone
Springs local fauna and the Canyon Ferry area in
AMNH, KUVP, and USNM collections) com-
pared to the distribution of an Orellan sample of
Nebraska (in open circles; from UNSM collec-
tion). Despite the large-sized holotype of *Hesper-
ocyon paterculus* (AMNH 9616, noted in the di-
agram), the overall size and proportion of the
Chadronian Montana sample are indistinguish-
able from those of the Orellan Nebraska sample.
The same kind of relationship is found between
the Montana sample and a Chadronian Wyoming
sample from the AMNH (not shown here). Scales
are in mm.

idus is mainly distinguished from *H. gregar-
ius* and "*H.*" *coloradensis* by its significantly
smaller size, its reduced parastyle of M1, its
incipient development of bicuspid talonid of
m1, and its well-developed metaconid of m2.
Additionally, its premolars have more prom-
inently developed accessory and cingular
cusps.

DISTRIBUTION: Cedar Creek Member of
White River Formation, Colorado; Whitney
Member of Brule Formation, Nebraska; Po-
leslide Member of Brule Formation, South
Dakota; and Sespe Formation of California.
Orellan to early Arikareean.

DESCRIPTION: As is the case for most spec-
imens from Kew Quarry, the type of "*Hes-
perocyon*" *pavidus* is badly flattened. Its skull
roof is crushed beyond description. Addi-
tional referred materials from the northern
Great Plains do not fill this void.

Mandible: Being the smallest species of
hesperocyonine, "*Hesperocyon*" *pavidus* also

has the most slender ramus with an average depth of 7.5 mm below the talonid of m1, in contrast to 10.0 mm for that of *H. gregarius* and 13.0 mm for that of "*H.*" *coloradensis.* Accordingly, the lower teeth appear to be broad and anchored on a weak ramus.

Dentition: The I1–2 are well preserved on F:AM 50338. The chisel-shaped tips of the incisors are marked by two shallow grooves to divide the blade into three indistinct cusps. The I3–P1 are absent on all specimens examined. The P2 is double-rooted with a single main cusp and a small posterior cingular cusp. The P3 has added a small posterior accessory cusp, but has no anterior cingular cusp. The P4 has a distinct cingulum on the anterior and medial side. Its anterior cingulum is thickened at the anterior base of the paracone and connects to a distinct ridge on the anterior surface of the paracone. The protocone on the P4 is medial to the anterior border of the tooth and is rather closely appressed to the base of paracone. The upper molars of the holotype have the most reduced labial cingulum seen in *Hesperocyon.* This cingulum reduction is especially apparent near the anterolateral corner of the teeth, in contrast to *H. gregarius* and "*H.*" *coloradensis,* which are conspicuously more swollen here than adjacent segments of the cingulum. Individuals from the Great Plains retain a somewhat larger anterolateral cingulum, but still are more reduced than in *H. gregarius.* Another distinction of the holotype is the presence of a thin precingulum in front of the protocone. This precingulum is not seen in F:AM 50338. The internal cingulum of LACM 466 has a less posteriorly deflected appearance than is seen in *H. gregarius* and "*H.*" *coloradensis.* The upper molars of the type are otherwise quite similar to those of *H. gregarius.* The M2 is relatively large (especially in F:AM 50338) with a well-developed metacone.

No lower incisor is preserved. The canine is small and slightly hooked backward. Post-canine teeth are rather closely spaced antero-posteriorly with a slight overlap between p3 and p4. The p1 is single-rooted. The morphology of the premolars is similar to that of *Hesperocyon gregarius* and "*H.*" *coloradensis,* but with relatively better developed accessory and cingular cusps. The anterior and posterior cingular cusps on the premolars are well developed as far forward as the p2. Both the p3 and p4 also have a distinct posterior accessory cusp in addition to the cingular cusps. Corresponding to this tendency of well-differentiated cingular and accessory cusps in premolars, the m1 also tends to have slightly more distinct cusps (e.g., deeper division between protoconid and metaconid, and therefore, a larger metaconid). The m1 is otherwise difficult to distinguish from that of *H. gregarius.* The metaconid of m2 is slightly higher than the protoconid; however, the reverse is usually true in *H. gregarius.* The m3 has two roots, which are often fused together. The metaconid of m3 is thus also more distinct than in *H. gregarius.*

Discussion: Galbreath (1953) listed, as "*Pseudocynodictis* sp. (Small form)," a small sample (five jaw fragments) of *Hesperocyon* from a few localities in northeastern Colorado, but refrained from giving them a formal name. These small individuals from Colorado appear to be well separated from *H. gregarius* (see below), and I (Wang, 1990) attempted to recognize them as a new species (together with more complete materials from Wyoming, USNM 473888, referred to *H. gregarius* in the present study). I now refer these Colorado individuals to "*H.*" *pavidus* for the following reasons:

Recent studies on morphometrics of canid carnassials of three sympatric Middle Eastern foxes (*Vulpes vulpes, V. ruppelli,* and *V. cana*) suggested that the ratios of the lower carnassial length between pairs of these species remained rather constant, around 1.18–1.21, despite fluctuations of body sizes in different regions (Dayan et al., 1989, 1992). The constant differences between lower carnassial lengths of different species were attributed to character displacement as a result of interspecific competition and niche partitioning. The canid carnassial length was argued to be the most intensely selected trophic feature and, as a result, most likely to show size displacement (Dayan et al., 1992).

The lower carnassials of *Hesperocyon* are the most frequently preserved teeth (3.2 times more than P4, 2.8 times more than M1, and 1.6 times more than p4), and similar statistics can be obtained for comparisons with the above studies of the recent foxes. Histograms of *Hesperocyon* m1 lengths indicate a unimodal distribution in most of the states (fig.

14), especially where samples are sufficiently large (e.g., Orellan samples from Nebraska, fig. 14D, and Wyoming, fig. 14G). The distribution of the Orellan Colorado sample, however, has the greatest spread, with a combined (all three taxa in fig. 14A) coefficient of variance of 9.7, as compared to around 6 in most of the remaining fossil samples. A coefficient of variance of 4.2 was calculated for both males and females of living red fox from the Upper Peninsula of Michigan (Gingerich and Winkler, 1979), 4.82 for red fox from New England (present study of AM:MA collection), and 4.04 for grey fox from Georgia (present study of AM:MA collection). The ratio of m1 lengths between *H. gregarius* and "*H.*" *pavidus* within the Orellan Colorado sample is 1.22 (1.29 for the combined sample of *H. gregarius* versus "*H.*" *pavidus*), far greater than what may be accounted for by sexual dimorphism, which is around 3–6% for species of *Vulpes* (Churcher, 1960; Gingerich and Winkler, 1979; Dayan et al., 1989, 1992; and the present study), and is nearly nonexistent in grey foxes (*Urocyon cinereoargenteus*: 0% in the present study, 69 individuals from Georgia). On the other hand, the ratio of 1.22 is comparable to Dayan et al.'s (1989, 1992) model of character displacement in living foxes.

With the present recognition of "*Hesperocyon*" *pavidus* in the Great Plains, its geographic and geologic ranges are considerably expanded, although materials of "*H.*" *pavidus* continue to be rare during its temporal range (Orellan to early Arikareean). There seems to be a trend of size reduction during the span of "*H.*" *pavidus*: mean m1 length equals 7.53 in Orellan, 7.23 in Whitneyan, and 6.7 in early Arikareean. This is opposite to the increase in size seen in the rest of hesperocyonines.

In the absence of well-preserved cranial materials, Stock (1933) was understandably cautious about his assignment of the Kew Quarry material to *Pseudocynodictis* (= *Hesperocyon*). I have indicated earlier (Wang, 1990) that the molar morphology of "*H.*" *pavidus* is reminiscent of a primitive borophagine in its features of m1 (narrow labial cingulum, internal cingulum surrounding the protocone, and wide talonid) and in its large m2. In addition, the slightly more prominent cingular cusps of premolars in "*H.*" *pavidus*
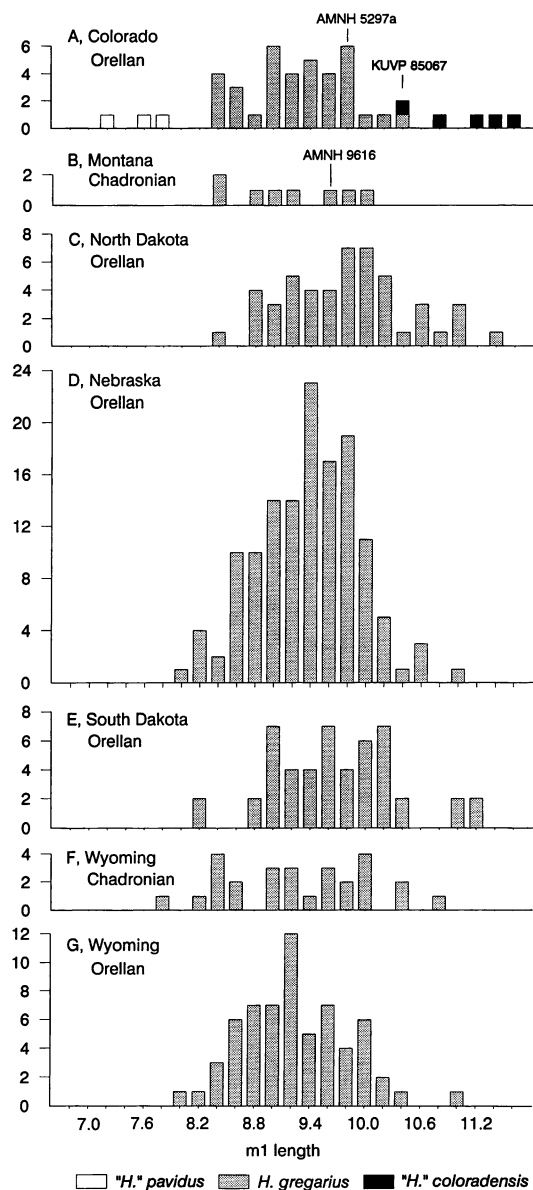
Fig. 14. Histograms of length of m1 in seven samples of *Hesperocyon*: **A**, Colorado, Orellan; **B**, Montana, Chadronian; **C**, North Dakota, Orellan; **D**, Nebraska, Orellan; **E**, South Dakota, Orellan; **F**, Wyoming, Chadronian; **G**, Wyoming, Orellan. Positions of the types of *H. gregarius* (AMNH 5297a), *H. paterculus* (= *gregarius*) (AMNH 9616), and "*H.*" *coloradensis* (KUVP 85067), are indicated within their respective samples (the type of "*H.*" *pavidus*, LACM 466 [m1 length = 7.6], falls outside the present range of distributions). Summary statistics for the three species of *Hesperocyon* are listed in Appendix III. Horizontal scales are in mm.

seems to suggest tendency toward the borophagine premolars.

"Hesperocyon" coloradensis, new species
Figure 15

Pseudocynodictis lippincottianus (Cope) Galbreath, 1953: 75, in part, excluding type.

HOLOTYPE: KUVP 85067, partial skull and mandible with left I3–C1, P2–M1, right I2–C1, P2–M1, left c1–m2, and right i3–m2, partial postcranial skeleton.

TYPE LOCALITY: KU-CO-046, microlocality level 20, Cedar Creek Member of White River Formation, W1½, sect. 7, T. 11 N, R. 53 W, Logan County, Colorado.

REFERRED SPECIMENS: From Cedar Creek Member of White River Formation, Logan and Weld counties, Colorado: F:AM 28305, rostral part of skull with left P2–M2 and right P2–M1, from small hill west of the Butte; KUVP 8191, maxillar fragment with M1–2, below olive band at Beaver Locality, SE¼, sect. 21, T. 11 N, R. 53 W; KUVP 8193, right p4, microlocality, W½, sect. 7, T. 11 N, R. 53 W; KUVP 8196a, fragment of left ramus with m2, Chimney Canyon, Casement Ranch, E½, sect. 3, T. 11 N, R. 54 W; KUVP 8197, fragment of right ramus with m1, NW½, SW¼, sect. 7, T. 11 N, R. 53 W; KUVP 8198, fragment of left ramus with m1, NW¼, SW¼, sect. 7, T. 11 N, R. 53 W; KUVP 8199, partial right ramus with p1–m2, KU-CO-046, see type locality; KUVP 8200, fragment of left ramus with broken m1, Chimney Canyon, 20–40 ft below a white marker, NE¼, sect. 3, T. 11 N, R. 54 W; KUVP 11106, isolated right m2, W½, sect. 7, T. 11 N, R. 53 W; KUVP 14618, fragments of ramus with left m1–2 and right m1, KU-CO-046, see type locality; KUVP 69156, partial left ramus with c1, p3–m2, KU-CO-016, 4 mi east of Chimney Canyon; KUVP 98065, fragment of right ramus with p4, KU-CO-016, same as previous locality.

DIAGNOSIS: Averaging 18% larger than *Hesperocyon gregarius* (measurement of the length of m1), *"H." coloradensis* shows some initial tendencies toward the *Mesocyon–Osbornodon* clade. Its bulla is larger due to further inflation of the entotympanic. The par-

occipital process of *"H." coloradensis* is beginning to be bent ventrally (char. 14), instead of the posteriorly oriented process in *H. gregarius*. The M1 tends to be more transversely elongated and a thin internal cingulum is present anterior to the protocone, although this latter condition is occasionally present in *H. gregarius*. The mandible is deep and robust.

DISTRIBUTION: Cedar Creek Member of White River Formation, northeastern Colorado, Orellan.

ETYMOLOGY: *coloradensis*, from Colorado.

DESCRIPTION: The present description mainly contrasts *"Hesperocyon" coloradensis* and *H. gregarius*. *"H." pavidus* is considerably smaller than *"H." coloradensis* and is easily distinguishable from the latter.

Skull: The type, KUVP 85067, is smaller and less robust than other individuals of this species; however, its morphology is clearly more advanced toward *"Mesocyon" temnodon* than that of *Hesperocyon gregarius*. The size of the skull is intermediate between *H. gregarius* and *"M." temnodon*. The anterior half of the skull of KUVP 85067 is well preserved and shows little difference from that of *H. gregarius* except its larger size. The posterodorsal skull roof of KUVP 85067 is missing, and, judging from the rather rapidly converging temporal crest, it is likely that it has a well-developed sagittal crest.

The tympanic bulla is large and elongated. The external auditory meatus is relatively small and oval in outline. It has no lateral extension into a tube as in most later canids. There is a small suprameatal fossa on the caudal wall of the external auditory meatus just in front of the mastoid process. A low septum between the rostral and caudal entotympanics is better developed than in *Hesperocyon gregarius* and runs the entire length of the bulla instead of tapering off in the middle as in some individuals of the latter. On the posteriorly exposed right bulla, the posterior part of the septum can be seen to turn laterally, forced by the expanding caudal entotympanic; this latter bone covers approximately three-fourths of the bulla as opposed to one-half in *H. gregarius*. On the left bulla, the medial wall of the in-bent edge of the caudal entotympanic can be seen, through a

Fig. 15.   Skull and mandible of "*Hesperocyon*" *coloradensis*, KUVP 85067, holotype. **A**, Lateral view of skull; **B**, lateral view of mandible; **C**, occlusal view (in stereo) of lower teeth (reversed from right side); and **D**, occlusal view (in stereo) of upper teeth (reversed from right side). Scales = 20 mm.

breakage of the basioccipital, to expand dorsally to floor the internal carotid artery. The paroccipital process on KUVP 85067 begins to bend ventrally in contrast to the straight, posteriorly directed process in all *H. gregarius*. In addition, the paroccipital process expands laterally to form a ridge enclosing a fossa which is often seen in advanced canids. There is still no fusion between the base of the paroccipital process and the posterior bulla wall, as one begins to see in "*Mesocyon*" *temnodon*.

Mandible: The ramus is deep and robust. The angular process, preserved on the type, is long, initially hanging down slightly and then curving upward. The internal ridge is low, the anterior end of which, unlike that of *Hesperocyon gregarius*, moves upward about 1.5 mm away from a lower ridge, which is possibly equivalent to the low crest on the inferointernal facet ("crête pointillèe partageant longitudinalement la facette inféro-interne," Gaspard, 1964: 251). The lateral surface of the angular process is smooth and the posterior tubercle is poorly developed.

Dentition: Dental morphologies of "*Hesperocyon*" *coloradensis* are similar to those of *H. gregarius*. The I2 is marked by two indistinct grooves, giving the impression of three cusps at the tip. The I3 has no indication of a basal cusplet and is about twice the size of I2. The stout canines have slight ridges anteriorly and posteriorly. The P1 is single-rooted. The P1–3 are slightly more robust than in *H. gregarius* and none has an anterior cingular cusp. Only P3 has a distinct posterior cingular cusp and a posterior accessory cusp, whereas P2 has only rudimentary development of a posterior cingular cusp. The cingulum around P4 is generally vague and disappears laterally. The P4 protocone is well developed and positioned slightly ahead of the anterior base of the paracone. There is no parastyle on P4; only a low cingulum is present. Initiating a trend in some derived hesperocyonines, M1 is transversely elongated compared to that of *H. gregarius*. The internal cingulum is still posteromedially deflected as in *H. gregarius*. M2 is approximately half the size of M1 and is otherwise similar to the latter. No M3 is present.

Lower incisors are lacking in specimens examined. The canines are robust compared to those of *Hesperocyon gregarius*. The p1 is single-rooted and is of a simple main cusp. The p2 begins to develop an anterior and a posterior cingular cusp. In p3–4, not only are the cingular cusps more distinct, there is also a posterior accessory cusp. Except in size (18% larger than in *H. gregarius*, see fig. 14), the m1 resembles that of *H. gregarius*. The trigonid cusps are relatively low, with a more reduced metaconid than in *H. gregarius*. Both hypoconid and entoconid are crestlike structures running anteroposteriorly. The m2 is similarly large with a slightly higher protoconid than metaconid. Its talonid contains a high ridgelike hypoconid and a low entoconid crest. This is in contrast to a much higher entoconid in the type of "*H.*" *lippincottianus*, AMNH 5327a, whose entoconid is of nearly equal height as the hypoconid. A low entoconid crest in m2, correlated to a trenchant talonid of m1, is consistent in all species of *Hesperocyon*; a high entoconid in AMNH 5327a, however, is seen in primitive *Daphoenus* (e.g., *D. minimus*, Amphicyonidae), and suggests a more basined talonid of lower carnassials typical of amphicyonids (see more discussion below). The m3 is always present and usually double-rooted, although its sizes varies considerably.

DISCUSSION: In 1873, the same year *Canis* (*Hesperocyon*) *gregarius* was described, Cope (1873b) recognized a larger-sized species, *Canis lippincottianus*, from the Tertiary (presumably from the Cedar Creek Member of the White River Formation) of Colorado. Since then, every student of the early Canidae has struggled with the question of its validity (Scott, 1898; Matthew, 1901; Hough, 1948b; Scott and Jepsen, 1936; Galbreath, 1953; Elliot, 1980; Gustafson, 1986).

Confusion seems to partly stem from the status of the holotype. Two specimens were involved in Cope's descriptions of *Canis lippincottianus*: AMNH 5327a, a fragment of right ramus with m2 and the alveolus of m3 (Cope, 1884: pl. LXVIIa, fig. 5), and AMNH 5327b, a fragment of left ramus with p4–m1 and roots of p2–3 (Cope, 1884: pl. LXVIIa, fig. 6). These specimens clearly belonged to different individuals because of their markedly different wear patterns (only slight wear on the cusp tips of AMNH 5327a versus heavy wear on the m1 talonid of AMNH 5327b).

Cope (1873b: 9) clearly indicated that the type of *C. lippincottianus* was to be AMNH 5327a: "Selecting one specimen as type, . . . I find the following peculiarities: The root of the last molar is much compressed. There is only a trace of cingulum on the penultimate [m2], and the tubercles of the inner side of the crown are well developed." Cope (1874: 506) reiterated this statement and also described a "second specimen [AMNH 5327b] from the same locality," which he later (Cope, 1884) figured together with the holotype.

Whereas AMNH 5327b is surely a slightly large-sized individual of *Hesperocyon gregarius*, the holotype of *Canis lippincottianus*, however, is quite differently constructed from any *Hesperocyon*. The most striking feature of AMNH 5327a is its large entoconid, which is an elevated ridge occupying more than one-third of the talonid and forming its conspicuous posterolingual corner, in contrast to that of *Hesperocyon*, whose entoconid is usually no more than a low platform lingual to the hypoconid. An enlarged entoconid can be found, among contemporary carnivorans, in *Daphoenus minimus* Hough, 1948, and to a lesser extent in *Osbornodon renjiei* (see below). AMNH 5327a is indistinguishable, both in size and shape, from some individuals of *D. minimus* (e.g., AMNH 93146, F:AM 63310, F:AM 72514). More significantly, a large entoconid on m2 is invariably correlated with a basined talonid on m1, which is characteristic of primitive daphoenines. It therefore seems likely that *C. lippincottianus* and *D. minimus* are conspecific (contra Wang, 1990), in which case the former name would have priority.

Nevertheless, Cope's concept of a large-sized *Hesperocyon* from the White River Group is confirmed in the present recognition of the new species "*H.*" *coloradensis*. Cope (1873b, 1874, 1884), however, exaggerated the size differences, claiming a 50% larger-sized "*H.*" *lippincottianus* than in *H. gregarius*. Materials from the Orellan of northeastern Colorado appear to best support a trimodal distribution of m1 length (see also discussion of "*H.*" *pavidus*). Galbreath (1953) suggested that, in anticipation of the possibility of sexual dimorphism, *H. gregarius* was "about five times as common" as "*H.*" *coloradensis* (referred to as *Pseudocynodictis*

lippincottianus by Galbreath) in some localities but is completely absent in others. Most living canids are sexually dimorphic, with males being consistently larger than females (Bekoff, 1977; Cohen, 1978; Nowak, 1979). However, there is always considerable overlap in all of the measured dimensions (Nowak, 1979). The size difference between "*H.*" *coloradensis* and *H. gregarius* clearly exceeds sexual variations in living canids as the fossil taxa have little overlap (fig. 14A); the length of m1 in "*H.*" *coloradensis* is, on average, 18% larger than in *H. gregarius*. This carnassial size difference, on the other hand, closely parallels that observed between species of living foxes (Dayan et al., 1989, 1992).

Mesocyon Scott, 1890

Canis (Linnaeus) Cope, 1879a: 58.
Temnocyon (Cope) Cope, 1879b: 180.
Mesocyon Scott, 1890: 38.
Hypotemnodon Eyerman, 1894: 321.
?*Cynodictis* (Bravard and Pomel) Matthew, 1899: 54.
Cynodictis (Bravard and Pomel) Matthew, 1901: 357.
Pseudocynodictis (Schlosser) Matthew, 1918: 189.
Philotrox (Merriam) Thorpe, 1922a: 165.
Nothocyon (Matthew) Matthew, 1924: fig. 28.

TYPE SPECIES: *Mesocyon coryphaeus* (Cope, 1879b).

INCLUDED SPECIES: *Mesocyon coryphaeus* (Cope, 1879b), "*M.*" *temnodon* (Wortman and Matthew, 1899), and *M. brachyops* Merriam, 1906.

EMENDED DIAGNOSIS: As a paraphyletic genus (see Phylogeny), *Mesocyon* has no synapomorphy of its own. *Mesocyon* is distinct from *Hesperocyon* and *Paraenhydrocyon* in its robust and long paroccipital process that is directed ventrally (char. 15). The two derived species, *M. coryphaeus* and *M. brachyops*, have further acquired a pair of round fossae on the supraoccipital above the foramen magnum (char. 6). *Mesocyon* is still primitive in its lack of robust premolars and broadened M2, which are 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*.

DISTRIBUTION: Turtle Cove Member to

Haystack Valley Member of John Day For-
mation, central Oregon; Otay and Sespe For-
mations of southern California; Brule–Ger-
ing (and correlative) formations of the
northern Great Plains. Orellan to Arikareean.

DISCUSSION: In his original description of
Temnocyon coryphaeus, Cope (1879b: 180)
remarked about Temnocyon: "This genus was
characterized by me on evidence furnished
by a mandible of a species which I named *T.
altigenis*, which is of considerably larger size
than the present one [*Mesocyon coryphaeus*],
but which agrees with it in the presence of a
cutting edge instead of a basin in the heel of
the inferior sectorial [m1]." Recognizing the
fundamental differences between the geno-
typic species *Temnocyon altigenis* (which is
an amphicyonid) and *T. coryphaeus*, Scott
(1890) erected a new genus, *Mesocyon*, for
M. coryphaeus. This is based on his belief
that *Mesocyon* had "the basin-heeled lower
sectorial and the tubercular inferior molars
of the dogs," even though *M. coryphaeus* in
fact has a trenchant talonid, as Cope (1879b)
originally described. Scott was probably re-
ferring to the presence of a small, low ento-
conid ridge in m1 of *M. coryphaeus* as op-
posed to absence of the entoconid in
Temnocyon. In his description of carnivores
obtained by the Princeton University 1889
expedition, Eyerman (1894, 1896) arrived at
the same conclusion as that of Scott and
erected a new genus, *Hypotemnodon*, for *H.
coryphaeus*. For some reason, Scott appar-
ently failed to inform Eyerman of the exis-
tence of his own genus *Mesocyon*, even though
Eyerman was obviously influenced by Scott,
as evidenced by his repeated acknowledg-
ment of Scott's suggestions and advice, and
by his similar diagnosis for *Hypotemnodon*
as for Scott's *Mesocyon*. Scott later (1897)
seemed to have forgotten about his *Meso-
cyon*, as he also did with *Hesperocyon*, which
was erected in the same paper as *Mesocyon*
(Green, 1952), and he began to use Eyerman's
junior synonym *Hypotemnodon* instead.
However, unlike the name *Hesperocyon*,
which was ignored for more than half a cen-
tury, *Mesocyon* soon regained its legal status
(first referred to by Douglass, 1903) and has
been widely used ever since to represent
primitive mid-sized canids.

A total of 10 species, belonging to many
clades of hesperocyonines, have been re-
ferred to *Mesocyon* (table 3). In the present
study, the usage of *Mesocyon* is restricted to
its initial content (i.e., two species from the
John Day Formation) plus "*M.*" *temnodon*.
Still, these 3 species do not form a mono-
phyletic genus (see Phylogeny), and they are
here grouped together based on their primi-
tive resemblances.

Mesocyon coryphaeus (Cope, 1879b)
Figures 16, 17

Canis hartshornianus Cope, 1879a: 58 (in part).
Temnocyon coryphaeus Cope, 1879b: 180.
Mesocyon coryphaeus (Cope) Scott, 1890: 38.
     Douglass, 1903: 164. Merriam, 1906: 16. Sel-
     lards, 1916: 89. Thorpe, 1922a: 168 (in part).
     Barbour and Schultz, 1935: 408. Schlaikjer,
     1935: 133. Stevens, 1991: 46.
Hypotemnodon coryphaeus (Cope) Eyerman, 1894:
     321.
Hypotemnodon (Temnocyon) coryphaeus (Cope)
     Matthew, 1899: 63.
Mesocyon brachyops (Merriam) Thorpe, 1922a:
     169 (in part).
Philotrox condoni Thorpe, 1922a: 165 (in part).
Mesocyon josephi secundus Thorpe, 1922a: 170.

HOLOTYPE: AMNH 6859, complete skull
with entire dentition, partial left scapula, and
one cervical vertebra (Cope, 1884: pl. LXXI).
Collected by J. L. Wortman.

TYPE LOCALITY: The exact locality of the
holotype is unknown. Among six specimens
of *Mesocyon coryphaeus* collected by J. L.
Wortman in May–June 1879 that were given
a more specific locality than the general term
"John Day beds," three are from the "Cove"
(Turtle Cove) and three from Camp Creek.
In particular, AMNH 6909 was collected from
the Turtle Cove on 13 June 1879 and bore a
field number 55. The holotype of *M. cory-
phaeus* has a field number of 57, suggesting
that it may possibly come from Turtle Cove,
Grant County, Oregon. If correct, AMNH
6859 is probably from Middle John Day For-
mation (i.e., Turtle Cove Member), Early
Arikareean.

REFERRED SPECIMENS: From the John Day
Formation of Oregon (except as noted oth-
erwise, specimens from Turtle Cove are gen-
erally assumed to belong to the Turtle Cove
Member of the John Day Formation, i.e.,
Middle John Day Formation of Thorpe

TABLE 3
Taxonomic Assignment of Species Previously Referred to *Mesocyon* (in Alphabetic Order)
(The species compositions of *Mesocyon* are considerably narrowed, and their synonym under the heading of each species should be consulted for a complete listing. For species with mixed contents, indicated by an asterisk following the author, individual assignment of a particular specimen can be found in the synonym list and the "Referred Specimens" list of the respective species.)

Previous assignment	Author and year	Present assignment
Mesocyon baileyi	Stock, 1933: 32; Barbour and Schultz, 1935: 412; Stevens, 1991: 46	*Mesocyon brachyops*
Mesocyon brachyops	Merriam, 1906: 17; Merriam and Sinclair, 1907: 184; Matthew, 1909: 107; Barbour and Schultz, 1935: 412; Schlaikjer, 1935: 133; Stevens, 1991: 46	*Mesocyon brachyops*
Mesocyon brachyops	Thorpe, 1922a: 169*	*Mesocyon coryphaeus*
Mesocyon coryphaeus	Scott, 1890: 38; Douglass, 1903: 164; Merriam, 1906: 16; Sellards, 1916: 89; Thorpe, 1922a: 168*; Barbour and Schultz, 1935: 408; Schlaikjer, 1935: 133; Stevens, 1991: 46	*Mesocyon coryphaeus*
Mesocyon coryphaeus	Thorpe, 1922a: 168*	*Paraenhydrocyon josephi*
Mesocyon drummondanus	Douglass, 1903: 164; Olsen, 1956: 1; Stevens, 1991: 46	*Cynodesmus thooides*
Mesocyon geringensis	Barbour and Schultz, 1935: 407	*Sunkahetanka geringensis*
Mesocyon hortulirosae	Schlaikjer, 1935: 133; Olsen, 1956: 1; Stevens, 1991: 46	*Paraenhydrocyon josephi*
Mesocyon hortulirosae	Macdonald, 1963: 213	*Paraenhydrocyon robustus*
Mesocyon iamonensis	Sellards, 1916: 88; Simpson, 1930: 160	*Osbornodon iamonensis*
Mesocyon josephi	Schlaikjer, 1935: 133; Barbour and Schultz, 1935: 412; Stevens, 1991: 46	*Paraenhydrocyon josephi*
Mesocyon josephi josephi	Thorpe, 1922a: 169*	*Mesocyon brachyops*
Mesocyon josephi secundus	Thorpe, 1922a: 170	*Mesocyon coryphaeus*
Mesocyon robustus	Matthew, 1907: 185; Thorpe, 1922b: 429; Schlaikjer, 1935: 139; Barbour and Schultz, 1935: 412; Macdonald, 1963: 213*; Stevens, 1991: 46	*Paraenhydrocyon robustus*
Mesocyon robustus	Macdonald, 1963: 212*	*Mesocyon temnodon*
Mesocyon robustus	Macdonald, 1963: 213*	*Paraenhydrocyon josephi*
Mesocyon venator	Stevens, 1991: 45	*Paraenhydrocyon wallovianus*

[1922a]. Caution should be exercised in this inference because some YPM specimens from Turtle Cove are labeled as coming from the Upper John Day Formation): AMNH 6860, partial skull and mandible with badly preserved upper and lower dentitions (missing right M1–2, lower incisors, and left p4), and postcranial fragments (Cope, 1884: pl. LXXIa, figs. 2–6), from Turtle Cove; AMNH 6862, anterior part of skull with left and right P2–M2, no locality data; AMNH 6865, m1 and two partial canines that may not belong to the same individual, no locality data; AMNH 6866, right ramus fragment with m1 and broken c1–p4, no locality data; AMNH 6867, left P3–M1, right P4, no locality data; AMNH 6868, left M1, from Camp Creek; AMNH 6870, isolated left and right M1 and other fragments that may not belong to the same individual, no locality data; AMNH 6873, P4–M1, no locality data; AMNH 6908a, right P3–M1 and right m1–2, no locality data; AMNH 6909, complete skull with nearly entire upper dentition, from Camp Creek; AMNH 6911, rostral part of skull with nearly complete upper dentition, no locality data; AMNH 6920, partial skull with nearly entire upper dentition (mostly broken), a nearly complete endocast (described in Radinsky, 1973: 174), left humerus, partial left

femur, and other postcranial fragments, no locality data; AMNH 6922, posterior half of skull behind the postorbital constriction, from Turtle Cove; AMNH 6923, rostral part of skull with fragmentary left C1, P4–M1 and right I3–C1, P2, and M1, from Camp Creek; AMNH 6928, isolated left and right P4–M1, and other tooth fragments, no locality data; LACM 2738, rostral part of skull and mandible fragments with left P2, right I2–C1, P4–M1, left m1, m3, and right m2, no locality data; YPM 10062, rostral part of skull with left I1–3, P2–M2 and right I2, P3–M2, from Turtle Cove; YPM 10063, nearly complete skull with left P4–M2 and right I2–M2, holotype of *Mesocyon josephi secundus* Thorpe, 1922a, from Turtle Cove; YPM 12703, complete skull and mandible, from Turtle Cove; YPM 12706, right ramus with c1–m3, from Camp Watson, Logan Butte, Crook Creek, in Turtle Cove Member; YPM 12708, partial crushed skull, mandible, and cervical vertebrae with left and right P3–M2, left p3–m2, and right p4–m2, from Turtle Cove; YPM 12709, right ramus with p4–m3, from Bridge Creek, in Turtle Cove Member; YPM 12710, left maxillary fragment with P4–M2, from Bridge Creek; YPM 12718, maxillary fragments with left P4–M2 and right P4, from Turtle Cove; YPM 12719, left maxillary fragment with P3–M1, from Turtle Cove; YPM 12722, left maxillary fragment with P4–M1, from Turtle Cove; YPM 12723-2, right ramus fragment with m1, from Bridge Creek, Turtle Cove Member; YPM 12725, left ramus with i2–c1, p2, m2–3, from Turtle Cove, in Turtle Cove Member; YPM 12727, right ramus fragment with m1, from Turtle Cove Member; YPM 12729, right ramus fragment with p4–m1, from Turtle Cove, in Turtle Cove Member; YPM 12757, left ramus fragment with p4–m1, from Rowe Creek, Turtle Cove Member; UCMP 75500, nearly complete skull with left and right P2–M1, UCMP locality V6630, South Canyon, Deschutes County.

From Eastlake development in Chula Vista, San Diego County, California, Otay Formation, Early Arikareean (Prothero, 1991; Walsh and Deméré, 1991): SDSNH 28210, rostral part of skull with left C1, P2–M2 and right I3–M2; SDSNH 28211, right premaxillary/maxillary fragment with C1–M1;

SDSNH 28595, fragment of left ramus with broken p2–m2; SDSNH 28998, fragment of left ramus of an immature individual, with roots of deciduous p4 and erupting permanent p3–m1; SDSNH 31195, fragment of left maxillary with M1; SDSNH 42851, fragment of left maxillary with P4–M1 and right ramus with p4–m2.

EMENDED DIAGNOSIS: *Mesocyon coryphaeus* is distinguished from "*M.*" *temnodon* by larger size; possession of a pair of fossae above the foramen magnum (char. 6); large inflated bulla; and a long, robust, ventrally oriented paroccipital process (char. 15). Compared to *M. brachyops*, *M. coryphaeus* has a longer skull; a smaller, less pointed postorbital process of frontal; a less laterally expanded zygomatic arch; a larger and more inflated bulla (char. 9); and an M1 that is not anteroposteriorly narrowed. In contrast to *Cynodesmus thooides*, *M. coryphaeus* has a more inflated bulla, less robust premolars, a less distinct protocone of P4, and a smaller M2.

DISTRIBUTION: Mainly based on the University of California (Berkeley) collections, Merriam and Sinclair (1907) identified *Mesocyon coryphaeus* in both middle and upper divisions (Turtle Cove and Kimberly-Haystack Valley Members, respectively, of Fisher and Rensberger, 1972) of the John Day Formation, in central Oregon. It also occurs in the Early Arikareean Otay Formation of California. Early to Late Arikareean.

DESCRIPTION: *Mesocyon coryphaeus* is the most common medium-sized hesperocyonine canid in the John Day Formation. Good cranial materials are available in several institutions (AMNH, JODA, UCMP, YPM), and the morphology of the species has been known for more than 100 years. Cope (1884: 906–912, pls. LXXI, LXXIa, LXXIIa) gave a rather detailed description of the species. The present description of *M. coryphaeus* thus concentrates on its relationships to other species and its individual variation.

Skull: Among the available materials of *Mesocyon coryphaeus*, the holotype, AMNH 6859, is still unquestionably the best skull available; its lack of distortion and exquisitely preserved anatomical detail offer a level of confidence in observation rarely possible in other taxa.

The skull of *Mesocyon coryphaeus* is larger

than *M. brachyops*, and is about the same size as *Cynodesmus thooides* and *Osbornodon sesnoni*. Despite its larger size, the proportions of the skull of *M. coryphaeus* are similar to those of *Hesperocyon* with an overall slender construction, and the skull is much less strongly built than in *Sunkahetanka* and *Enhydrocyon*. The rostrum remains primitively short in contrast to the elongated rostrum in advanced *Osbornodon*. The posterior process of the premaxillary is not thickened as in *Enhydrocyon*. The nasal is slender, measuring 5 mm across the midsection. The lateral profile of the frontal region arches slightly dorsally, compared to a flat forehead in *M. brachyops*. The postorbital process is small in contrast to the enlarged one in *M. brachyops*. No depression is found on top of the postorbital process, as is present in *M. brachyops*. The sagittal crest is low and thin, and the top edge is straight in lateral view. The nuchal crest extends posteriorly to the level of the posterior edge of the occipital condyle. On the posterior surface of the supraoccipital, there is a thin, central ridge, the external occipital crest. Above the dorsal rim of the foramen magnum and on each side of the external occipital crest are a pair of round, shallow pits for the insertion of the rectus capitis dorsalis minor muscle. This pit is consistently present in all species of *Mesocyon* and immediately more derived members of its clade.

In lateral view, the skull is slender as compared to the deep skulls of *Enhydrocyon*. The top edge of the skull raises steadily from the anterior tip of the nasal to the inion so that the skull has a wedge-shaped lateral profile. The infraorbital foramen is nearly round in cross section. The zygomatic arch is still slender, with a maximum depth of 12 mm near the postglenoid fossa.

In ventral view, the palate is transversely narrow. The posterior margin of the palatine has a sharp process along the center line. This posteriorly pointed process is usually less prominent in *Enhydrocyon* and is completely absent in *Sunkahetanka*. The bulla is conspicuously larger and more inflated than in *Cynodesmus thooides*, a character that consistently distinguishes individuals of these two species (except one young individual, YPM 10063; see Discussion below). There is a shallow fossa for the rectus capitis ventralis mus-

cle on the basioccipital, medial to the posterior lacerate foramen. The paroccipital process is rodlike, thickened, and elongated compared to that of "*Mesocyon*" *temnodon*. Fusion between the basal paroccipital process and caudal entotympanic is limited to a small, circular area of 7 mm in diameter in the type. The mastoid process is not enlarged and lies under a shelf of the squamosal. The postglenoid foramen is surrounded posteriorly by a laterally extended process of the ectotympanic.

Cope (1879b: 181) observed that in *Mesocyon coryphaeus* the orbital fissure and the common anterior opening for foramen rotundum and anterior alisphenoid foramen converged into a large, common external orifice, instead of being separated by a thin, vertical bony plate as in living canids. The lateral wall of the orbital fissure is posterior to the common opening referred to above, so that it is not visible in lateral view. This condition of a common opening for orbital fissure and anterior alisphenoid foramen is caused by a relatively long alisphenoid canal. In living canid genera (*Canis* [AM:CA 2944], *Cuon* [AM:CA 88], *Lycaon* [AM:CA 24218], *Nyctereutes* [F:AM 96750 and 96759], *Urocyon* [AM:CA 2939], *Vulpes* [AM:CA 295]), the alisphenoid canal is short so that the opening for the orbital fissure and the combined opening of the foramen rotundum and alisphenoid canal are both visible in lateral view. This condition of a long alisphenoid canal appears to be a retention of a primitive morphology observable in miacids. This long lateral wall of alisphenoid canal persists in hesperocyonine canids, although some large, more derived forms (e.g., *Osbornodon*, *Enhydrocyon*) tend to reveal a separate orbital fissure in lateral view due to their elongation of basicranial region (i.e., the orbital fissure is shifted forward relative to alisphenoid foramen).

Intraspecific variation in *Mesocyon coryphaeus* is less marked than in more derived forms (e.g., *Enhydrocyon*). The main variation is in the width of skull. The type and UCMP 75500 represent slender individuals, whereas more robust individuals (AMNH 6860, 6862, 6909) tend to have a slightly wider rostrum, broader forehead between orbit, thicker postorbital constriction, and

Fig. 16. Skull of *Mesocyon coryphaeus*. **A**, Dorsal and **B**, ventral views of AMNH 6859, holotype. Photographs of epoxy cast. Scale = 30 mm.

thicker sagittal crest, variations that may be attributable to sexual dimorphism as demonstrated in living canids (Nowak, 1979: appendix B).

Mandible: Well-preserved mandibles are not well represented in most collections of *Mesocyon coryphaeus*. The horizontal ramus is still of the slender type; no thickening or deepening is observed. The symphysial area is small and less extensively ankylosed than in *Sunkahetanka* and *Philotrox*. The ascending ramus is also slenderly constructed. The masseteric fossa is deep. In AMNH 6860, there is a shallow pocket along the ventral
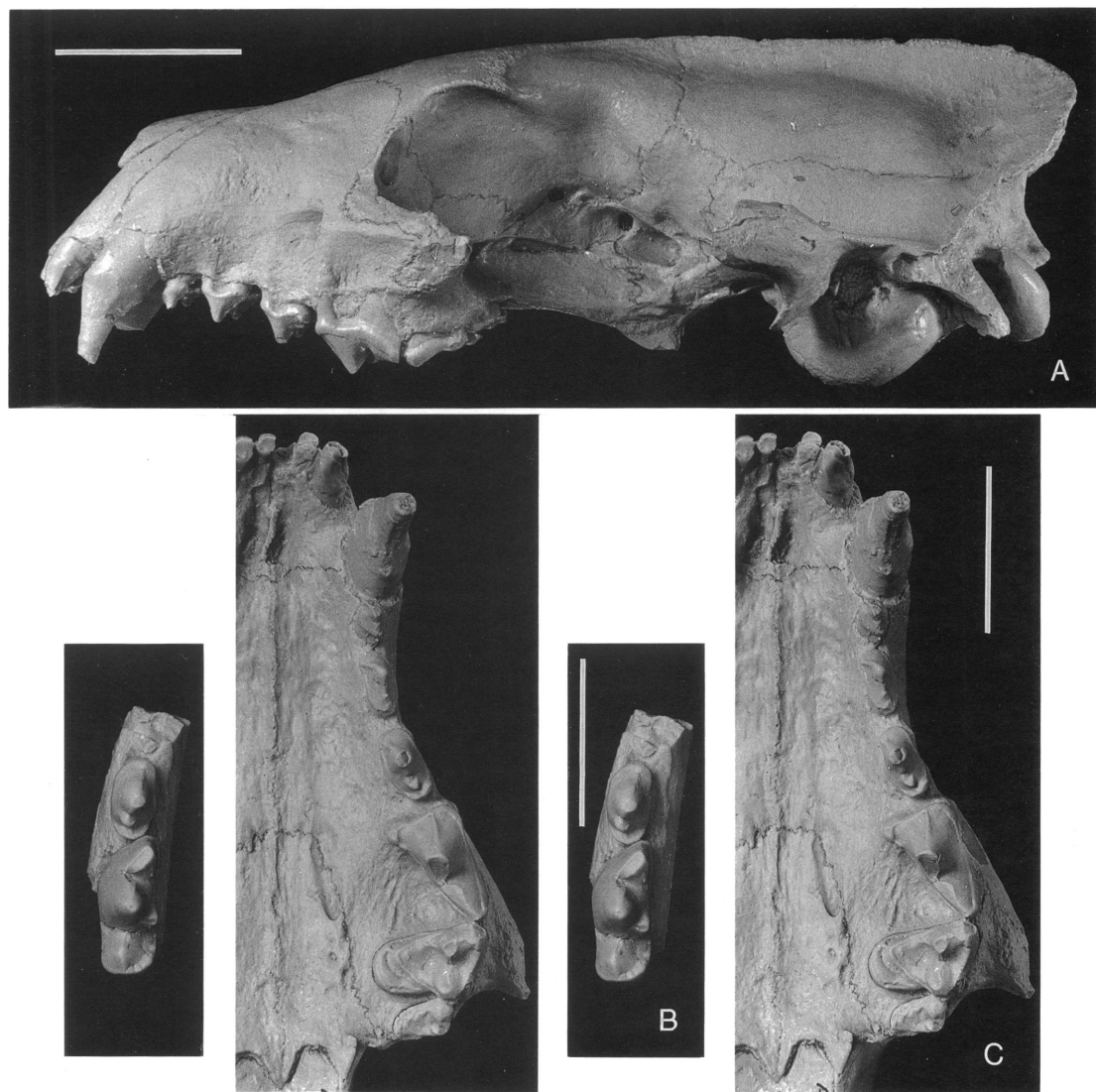
Fig. 17. Skull and teeth of *Mesocyon coryphaeus*. **A**, Lateral view of skull, AMNH 6859, holotype; **B**, occlusal view (in stereo) of p4–m1, YPM 12729, reversed from right side; and **C**, occlusal view of upper teeth, AMNH 6859, holotype. Photographs of epoxy casts. Scales = 20 mm.

border of the masseteric fossa similar to that of *Paraenhydrocyon*.

The angular process is preserved in an immature individual (YPM 12725, permanent teeth still not fully erupted). The tip of the process is short and blunt with a thin, upwardly hooked posterior edge, a condition not seen in any adult forms. There is no apparent pocket on the medial side.

Dentition: Upper incisors are usually too

worn or broken to recognize individual cusps. Increasing in size from I1 to I3, they form a tight row aligned in a transverse plane. The incisors do not seem to differ from related species such as *Cynodesmus thooides*. The upper canine is also similar to that of other primitive hesperocyonines; a posterior ridge is present in the upper canines. The upper premolars are proportionally longer than in "*Mesocyon*" *temnodon* but are slightly nar-

rower than in *Cynodesmus*. The premolars are evenly spaced with small diastemata of 2–3 mm in length. The P1 is single-rooted. The P1–2 have no accessory or cingular cusps, whereas the P3 has a posterior accessory cusp of differing size. No P3 has an anterior cingular cusp. The posterior cingulum of P3 varies from being small to large and cusplike (AMNH 6859). The P4 is proportionally larger than in *M. brachyops*, but is slightly more slender compared to that of *C. thooides*. The anterior cingulum is very weak, in contrast to better development of the cingulum in "*M.*" *temnodon*. Most individuals have a smaller protocone of P4 than in *C. thooides*, and this contrast in protocone size can be rather striking among some individuals. However, this difference is greatly reduced when larger series of both species are considered (see description of *C. thooides*). The M1 is anteroposteriorly wider than in *M. brachyops*. The M1 paracone is larger than its metacone but is not markedly so as in *Enhydrocyon*. The trigon basin is not constricted as in *Enhydrocyon*. The internal cingulum of M1 is not as swollen and variable in thickness as in *C. thooides*. The M2 is consistently smaller than in *C. thooides* and tends to have a more slender outline.

Besides a generally more slender appearance, the lower teeth of *Mesocyon coryphaeus* are difficult to distinguish from *Cynodesmus thooides*. The unworn i3 of YPM 12725 has a faint groove on the lingual side and otherwise has the appearance of a single cusp. The enamel surface of the canine is crenulated. The p2 shows rudimentary anterior and posterior cingular cusps, which are progressively enlarged in p3 and p4. Similarly, a posterior accessory cusp is present in p3–4. The lower molars are little different from those of *C. thooides*; some individuals of *M. coryphaeus* are slightly more slender than in *C. thooides*, but that cannot be reliably used for identification. The metaconid of m1 remains unreduced. The talonid is dominated by a large, conical hypoconid accompanied by a low, shelflike entoconid. The talonid is generally more trenchant than in "*M.*" *temnodon* (i.e., it has larger hypoconid at the expense of entoconid shelf). Corresponding to the small M2, the size of the m2 in *M. coryphaeus* is generally smaller than in *C.*

thooides, although exceptions can be found in both species. The m2 protoconid is slightly larger than its metaconid.

DISCUSSION: Cope (1879a: 58) first referred his sample of *Mesocyon coryphaeus* to *Canis hartshornianus* but quickly realized that he was faced with a different taxon: "This is the most abundant dog of the Truckee beds of the John Day country. I have identified it heretofore as my *Canis hartshornianus*, but I find on examination of the inferior sectorial tooth that it is a species of *Temnocyon*" (Cope, 1879b: 180). The basic composition of *M. coryphaeus* has since remained stable through most of its history (but see discussion below about Thorpe's references), and *M. coryphaeus* becomes the focus of comparison in most later studies of median-sized Arikareean canids.

Thorpe (1922a: 170) recognized a new subspecies *Mesocyon josephi secundus* (type YPM 10063, ibid.: figs. 1, 2) as distinct from "*M.*" *j. josephi* (= *Paraenhydrocyon josephi*). Thorpe cited crowded premolars, lack of diastemata, and obliquely placed P2 as part of the diagnosis for *M. j. secundus*. YPM 10063 is intermediate in size between the type of "*M.*" *j. josephi* and most specimens of *M. coryphaeus*. Although YPM 10063 has an adult dentition, it is still relatively young (and probably is a female judging from its slender canine) for none of its teeth shows appreciable wear. The above three characters (as well as its smaller size) are obviously related to its young age. In another Yale specimen of still earlier ontogenetic stage, YPM 12725 (referred to *Philotrox condoni* by Thorpe [1922a], presently referred to *M. coryphaeus*), the p2 is even more obliquely placed. The rest of Thorpe's diagnosis (presence of a posterior accessory cusp on P3, large-sized P4–M1, and small M2) included the general characteristics of *M. coryphaeus*. In fact, the upper teeth of the type *M. j. secundus* are indistinguishable from those of *M. coryphaeus*. However, one feature (not mentioned by Thorpe) of YPM 10063 that does seem different from the rest of *M. coryphaeus* specimens is its smaller and less inflated bulla, which may again result from its younger age. *Mesocyon josephi secundus* is thus referred to *M. coryphaeus* in the present study based mainly on the dental similarities. Thorpe's

(1922a) other references of YPM specimens to *M. j. josephi* and *M. brachyops* (YPM 12710 and 12719) are also morphologically unsupportable and they are here placed in *M. coryphaeus*.

In addition, Thorpe (1922a: 165) referred "several parts of rami with teeth" to *Philotrox condoni*, although only one specimen (YPM 12725) was explicitly listed in his discussion. Five rami from the Yale Peabody Museum appear to constitute Thorpe's sample (YPM 12706, 12709, 12725, 12727, and 12729); all were identified as *P. condoni* and labeled identically as in YPM 12725. Although all of Thorpe's referred specimens exhibit rather heavy construction of their teeth (fig. 17B), none reaches the robustness and size of the holotypes in *P. condoni*. Instead, these YPM mandibles are closer in their construction to *Mesocyon*. The YPM mandible fragments are here referred to *M. coryphaeus*. In favor of this rearrangement is the ratio of upper and lower jaw materials. In the YPM John Day Collection there are seven isolated maxillary fragments that are directly referable to *M. coryphaeus*, but without corresponding materials of the lower jaw; the opposite is true for the five rami fragments identified as *P. condoni* by Thorpe.

The present reference of fragmentary materials (listed as *Mesocyon* sp. by Demére [1988]) from the Otay Formation to *M. coryphaeus* expands its distribution outside the John Day area. The San Diego materials are of the same size as *M. coryphaeus* and *Cynodesmus thooides*, and have slightly more robust premolars than samples from the John Day *M. coryphaeus*. Their M1 have a rather narrow (anteroposteriorly) lingual half and a slightly more prominent parastyle than are seen in John Day *M. coryphaeus*.

"*Mesocyon*" *temnodon*
(Wortman and Matthew, 1899)
Figures 18, 19

?*Cynodictis* sp. maj. Matthew, 1899: 54 (in part excluding AMNH 1382 and 1386).
?*Cynodictis temnodon* Wortman and Matthew, 1899: 130 (in part excluding AMNH 1382 and 1386).
Cynodictis temnodon (Wortman and Matthew) Matthew, 1901: 357, 370 (in part excluding AMNH 1382 and 1386).

Pseudocynodictis temnodon (Wortman and Matthew) Matthew, 1918: 189 (in part excluding AMNH 1382 and 1386).
Nothocyon temnodon (Wortman and Matthew) Matthew, 1924: fig. 28.
Hesperocyon temnodon (Wortman and Matthew) Green, 1952: 124.
Mesocyon robustus (Matthew) Macdonald, 1963: 212 (referred SDSM specimens from Sharps Formation excluding holotype).

LECTOTYPE: AMNH 8753, partial left ramus with c1, p2–m3. Collected by Barnum Brown in 1898.

In his faunal lists for the "Fresh-water Tertiary of the West" (Article 3 of the Bulletin of the AMNH), Matthew (1899: 54) listed an unnamed species, ?*Cynodictis* sp. maj., under the columns of the "Horizon C" of the Colorado White River deposits and "Protoceras" of the South Dakota Badlands. In the succeeding Article 4 of the same volume, Wortman and Matthew (1899: 130) named this species ?*Cynodictis temnodon* and gave a brief diagnosis without designating a type or mentioning where the species was from. Their diagnosis of ?*C. temnodon* became the only description of this species and is here quoted in its entirety: "Size of *Hypotemnodon josephi*; lower premolars smaller than in that species and trigon wider; p4 (in associated upper jaws) with internal cusp almost obsolete, shear rather more longitudinal than in *Cynodictis lippincottianus*, m1 well extended transversely." Two years later, Matthew (1901: 357, 370) further confirmed the dual-locality listing by stating that *C. temnodon* (note omission of the question mark) occurs in the "Leptauchenia clays" of northeastern Colorado and "Protoceras sandstones" of the South Dakota Badlands.

Six specimens were involved in the original concept of *Cynodictis temnodon*. Four were collected from the Vista Member of the White River Formation of northeastern Colorado during the 1898 American Museum of Natural History Expedition led by W. D. Matthew, Barnum Brown, and H. T. Martin (AMNH 8753, 8765, 8766, 8770; see referred specimens below). The other two were collected from the Poleslide Member of the Brule Formation of South Dakota earlier in 1894 (AMNH 1382 and 1386; both are skulls with

upper teeth and are referred to *Osbornodon renjiei* in this paper).

The original diagnosis of ?*Cynodictis temnodon* by Wortman and Matthew seems to have been based mostly on the Colorado specimens because (1) their first character on the lower teeth can only refer to the mandible fragments from Colorado (there is no ramus from South Dakota); (2) their transversely extended M1 refers to AMNH 8770, not to AMNH 1382 or 1386, because the M1s of the latter two specimens are actually narrowed rather than widened; and (3) no cranial characteristics were mentioned even though there were two skulls present in the sample. The only character derivable from the two South Dakota skulls is the "obsolete" internal cusp of P4, which is not reduced in AMNH 8770. Among the four Colorado specimens, AMNH 8753 has the best series of lower teeth and would be the best choice for a type. The above interpretation is further strengthened by an unpublished manuscript by the junior author (Matthew, MS), in which AMNH 8753 was assigned as the holotype and AMNH 8770 as the paratype.

TYPE LOCALITY: Horizon C (fieldnotes as "D" and changed to C later) at Castle Rock was the only locality information recorded with the holotype in the AMNH archives of the "1898 Colorado Miocene Collection." Commenting on the "Castle Rock" type locality of *Palaeolagus intermedius* Matthew, Galbreath (1953: 50) expressed the opinion that "from the evidence in the 1898 field records, I think Castle Rock is in either R. 53 [W.] or R. 54 [W.], T. 11 N., Logan County," where the type section of Galbreath's Vista Member of the White River Formation is located. Although Matthew (1901: 357) listed *C. temnodon* as occurring in the "Cedar Creek and Martin Cañon Beds" of northeastern Colorado, Galbreath (1953: 18) pointed out that Matthew's lower part of Martin Canyon (where the holotype of *Palaeolagus intermedius* comes from) belongs to the Vista Member of the White River Formation, hence being Whitneyan in age.

REFERRED SPECIMENS: From Logan County, Colorado, Vista Member of the White River Formation, in Horizon C (of B. Brown fieldnotes, 1898), Whitneyan: AMNH 8765, right ramus fragment with p4–m3 (plus three other fragments probably not associated with the ramus), from Castle Rock (see Type Locality above); AMNH 8766, left ramus fragment with broken p4–m1 and roots of m2–3, from Castle Rock; AMNH 8770, partial palate with right P3–M2 and left P2–M1, from Cedar Creek; AMNH 96548, right ramus fragment with p4, m1–2, from Castle Rock.

From Brule and Sharps Formations of southwestern South Dakota, Orellan to Early Arikareean: F:AM 63338, left ramus fragment with m1, from 5 mi southeast of Oelrichs, Fall River County, in brown clay, Poleslide Member of Brule Formation; F:AM 63366, partial maxillary fragment with left and right P4–M2, postcranial fragments, from 0.25 mi west of Cedar Pass, Jackson County, in Poleslide Member of Brule Formation (top of the Upper Oreodon beds of M. F. Skinner fieldnotes, i.e., lower part of Poleslide Member; Upper Oreodon beds are similarly defined in specimens listed below); F:AM 63367, nearly complete skull and mandible with left C1, P2–M2, right P3–M2, left c1, p3–m2, and right m1–2, from westcentral side of the Red Shirt Table in Pine Ridge Indian Reservation, in center of sect. 3, T. 41 N, R. 47 W, Shannon County, Poleslide Member of Brule Formation (Upper Oreodon beds); F:AM 63368, right ramus fragment with p4–m3, from east end of Cedar Butte, SW¼, sect. 15, T. 41 N, R. 44 W, Shannon County, in talus but from higher than Upper Oreodon beds, Poleslide Member of Brule Formation; F:AM 63369, fragments of right basicranium and weathered endocast, right maxillary fragment with P3–M2, ramal fragments with left p4–m1 and right c1–m1, and an isolated astragalus, near the top of Cedar Pass, Jackson County, near the top of Upper Oreodon beds, Poleslide Member of Brule Formation; F:AM 63370, anterior part of skull fragments with left P2, M1, right P4–M1, and right ramus with p2–4, m3, from northeast of Indian Stronghold, on the divide between west Big Corral Draw and Cottonwood Creek, in top of Upper Oreodon beds, Poleslide Member of Brule Formation; F:AM 63372, left ramus fragment with p4–m1 and roots of the rest of the teeth, from head of Battle Creek Draw, near base of Leptauchenia beds, Poleslide Member of Brule Formation; F:AM 63374, rostral portion of skull with left and right C1–

M2, from northeast of Indian Stronghold, on head of western Big Corral Draw, in Protoceras channel, Poleslide Member of Brule Formation; F:AM 63375, left ramus fragment with p2, m1–2, from between the heads of the west fork of Big Corral Draw and Cottonwood Creek, in clay between basal and middle Protoceras channels, in top of Upper Oreodon beds, Poleslide Member of Brule Formation; F:AM 63377, maxillary and ramal fragments with left P3–M2, right M1–2, and left p4–m2, from the same locality as F:AM 63375; F:AM 63379, left ramus with p3–m1, from 3 mi west of Cedar Pass, Jackson County, in base of Upper Oreodon beds, Poleslide Member of Brule Formation; KUVP 46767, partial right ramus with c1–m2 and alveolus of m3, from KUVP Blue Ash locality (KU-SD-016), Poleslide Member of Brule Formation; SDSM 2653, partial skull with left P4–M2, from 2 mi southwest of Swallow's, Cuny Table, lower Oreodon beds, Scenic Member of Brule Formation; SDSM 54126, right ramus fragment with m1–2, from SDSM V545, Grass Creek in sect. 23, T. 39 N, R. 45 W, Shannon County, in Leptauchenia nodules just below the Rockyford ash (Macdonald [1963: 161] regarded this locality as basal Sharps Formation); SDSM 54249, left ramus with p2, p4–m2, referred to *Mesocyon robustus* (Macdonald, 1963: 213), from SDSM V5354, around the common corners of sects. 13, 14, 23, and 24, T. 39 N, R. 42 W, Shannon County, near the top of Sharps Formation; SDSM 69107, left ramus fragment with p4–m1, SE1¼, sect. 4, T. 41 N, R. 42 W, Shannon County, Poleslide Member of Brule Formation.

From Whitneyan and early Arikareean of western Nebraska: F:AM 25435, left maxillary fragment with C1–M2, from Tunnel Hill Locality, on the Ledingham Ranch, NW¼, sect. 29, T. 25 N, R. 55 W, Sioux County, 5 ft above a marly zone, Lower Arikaree Group; F:AM 63961, rostral part of skull fragment with left and right P3–M2, left and right ramal fragments with right m1–3, and a proximal ulna, in the vicinity of Chimney Rock, south of Bayard, NW¼, SW¼, sect. 17, T. 20 N, R. 52 W, Morrill County, 80 ft above base of the first ash in Whitney Member of Brule Formation (80 ft below Gering/Brule contact in M. F. Skinner fieldnotes); F:AM 63962,

partial left and right rami with left p3–m2 and right c1–m2, a few isolated postcranial fragments, from 0.75 mi southeast of Redington Gap, N½, NW¼, sect. 24, T. 19 N, R. 52 W, Morrill County, 7 ft below the base of first ash in Whitney Member of Brule Formation; F:AM 63965, left ramus fragment with p2–m1, near Grace & Son Ranch gate, from 3 mi southwest of Lewellen, on south side of North Platte River, in sect. 31, T. 16 N, R. 42 W, Garden County, in a pink siltstone 40 ft above a double brown layer (M. F. Skinner fieldnotes), probably Whitney Member of Brule Formation; UNSM 25690, partial left ramus with c1–m3, from Morrill County.

From early Arikareean of Niobrara County, Wyoming: F:AM 54116, partial left ramus with p4–m2, from 1 mi east of Tremain, in middle brown sands (M.B.S. of N. J. Vaughan fieldnotes, 1942), which is above a white layer, Lower Arikaree Group; F:AM 129028, fragment of left maxillary with dP3–dP4, C1–P1, P4–M1, and fragment of right ramus with c1, dp2–dp4, m1, from 3.5 mi east of Tremain, 4 ft below a white layer in Lower Arikaree Group.

From Goshen County, Whitneyan of Wyoming: F:AM 102381, partial skull and mandible with nearly entire upper dentition, left i1–c1, p2–m1, and right i3–c1, p2–m3, isolated vertebrae, scapula, and right forelimbs, from Hall Ranch ("Phinney Butte" of M. F. Skinner fieldnotes) on north side of 66 Mountain, below upper ash.

EMENDED DIAGNOSIS: Close to the size of *Paraenhydrocyon josephi* and *Osbornodon renjiei*, "*Mesocyon*" *temnodon* is quite primitive and difficult to diagnose. "*Mesocyon*" *temnodon* (and more derived taxa in the *Mesocyon–Enhydrocyon* clade) has lost the small suprameatal fossa (char. 7, reversal). Compared to more primitive species of *Hesperocyon* and primitive *Paraenhydrocyon*, its paroccipital process is downward so that its base touches and fuses with the posterior surface of the bulla (char. 14). In addition, "*M.*" *temnodon* can be distinguished from *P. josephi* by its slightly wider talonid of m1, its lack of a ventrally pocketed masseteric fossa, and its lack of a medially inflected internal ridge of the angular process to enclose a pocket. In contrast to *M. brachyops*, "*M.*" *tem-*

Fig. 18.   Skull of "*Mesocyon*" *temnodon*. **A**, Dorsal and **B**, ventral views of F:AM 63367. Scale = 20 mm.
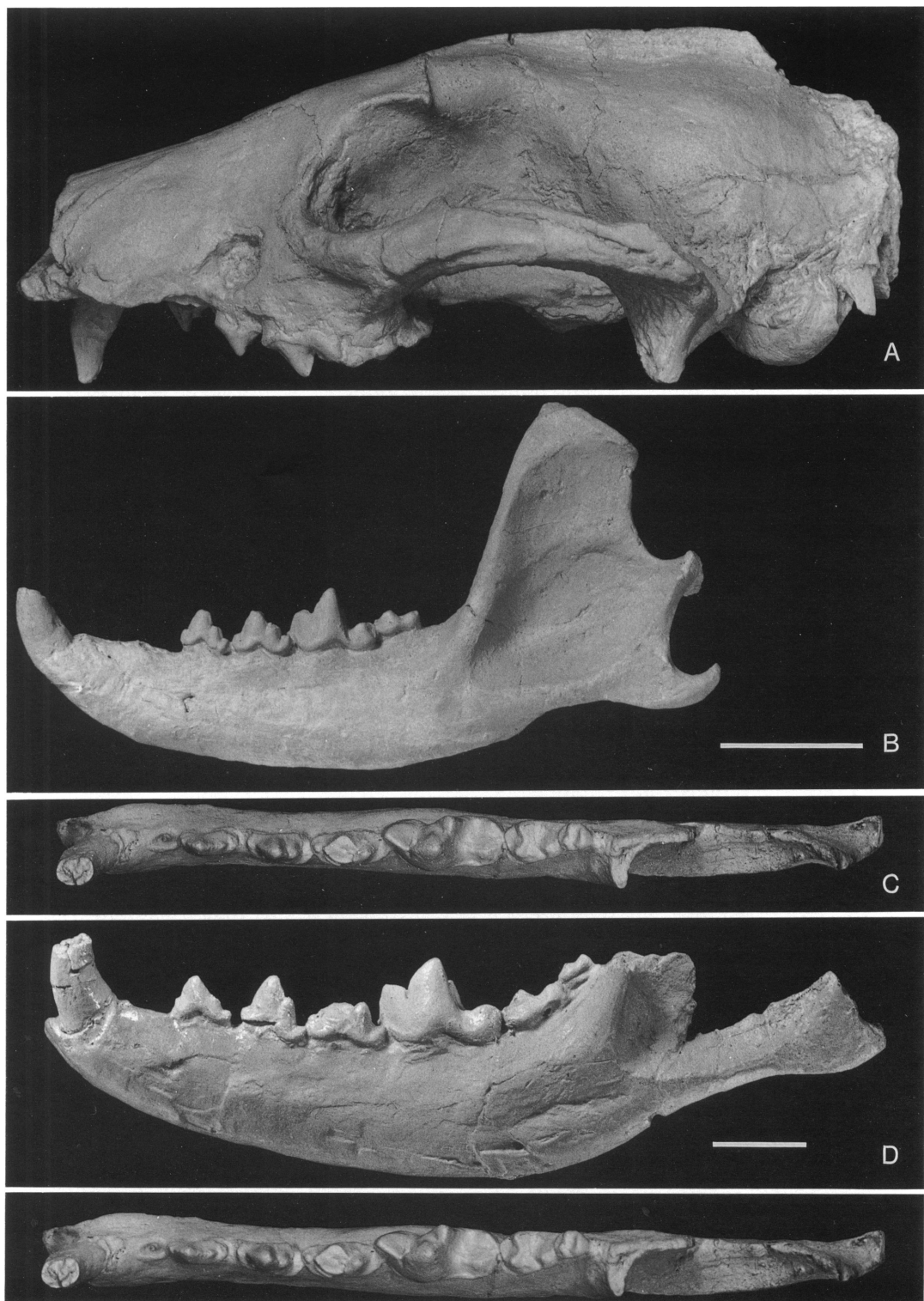
Fig. 19. Skull and rami of "*Mesocyon*" *temnodon*. Lateral views of **A**, skull (reversed from right side) and **B**, ramus of F:AM 63367; **C**, occlusal (in stereo) and **D**, lateral views of AMNH 8753, holotype. Scales = 20 mm.

nodon primitively possesses a well-developed anterior cingulum of P4, lacks a pair of round fossae above the foramen magnum, and lacks a strong, elongated paroccipital process.

DISTRIBUTION: Whitneyan of northeastern Colorado; Whitneyan to Early Arikareean of western Nebraska; Orellan to Early Arikareean of southwestern South Dakota; Whitneyan to Early Arikareean of eastern Wyoming.

DESCRIPTION: "*Mesocyon*" *temnodon* is now known from more numerous and complete materials than when it was first described. The reassignment of two South Dakota specimens (AMNH 1382 and 1386) from Wortman and Matthew's original sample to *Osbornodon renjiei* also changes the original hypodigm of "*M.*" *temnodon*. A detailed description is thus needed.

Skull: Two specimens, F:AM 63367 and SDSM 2653, constitute the main basis of the present description of the cranial morphology of "*Mesocyon*" *temnodon*.

The overall proportions of F:AM 63367 are little different from those of more primitive *Hesperocyon gregarius* and "*H.*" *coloradensis* (SDSM 2653 is of a more slender construction). The skull is approximately the same size as *Paraenhydrocyon josephi* and *Osbornodon renjiei*; all have relatively short rostra. On F:AM 63367, the nasal widens near the anterior end, leaving little room for a thin strip of posterior premaxillary process to be inserted between the nasal and maxillary. On SDSM 2653, however, the premaxillary process is longer. The anterior process of the frontal stops anteriorly at the level of P3 principal cusp. The forehead region above the orbit is slightly domed, similar to that of *P. josephi*, but in contrast to the flat forehead of John Day *Mesocyon brachyops*. There is a rather sharp postorbital process of the frontal on F:AM 63367. The dorsal surface medial to the postorbital process has a small depression, suggesting lacking or a low degree of inflation of a frontal sinus beneath the frontal plate. One unique feature of F:AM 63367 is the strongly convergent temporal crests. Beginning from the tip of the postorbital process, the initial segment of the temporal crest is exactly perpendicular to the sagittal plane, instead of pointing at an angle

with the transverse plane (as in SDSM 2653). Midway through this medially directed segment, the temporal crests turn sharply backward and quickly converge into a single sagittal crest, in contrast to a more gradual convergence of the temporal crests common in most canids. It is not clear whether these contrasting patterns of temporal crests between F:AM 63367 and SDSM 2653 represent any taxonomic significance since the peculiarity of F:AM 63367 is not seen in any other hesperocyonines. The postorbital constriction is 13–15 mm behind the postorbital process. The sagittal crest is a thin bony blade reaching a height of 5 mm in F:AM 63367, although its posterior half is broken off. The posterior supraoccipital shield is mostly broken off on F:AM 63367 and SDSM 2653.

In lateral view, the lacrimal occupies the anterior rim of the orbit and is touched by the tip of anterior process of the jugal. The anterior segment of the zygomatic arch is preserved on both sides of F:AM 63367, and seems to suggest slightly deeper arches than in *Osbornodon renjiei* (seen in AMNH 1386). The infraorbital foramen is round.

In ventral view, the posterior border of the palate is slightly behind that of M2. The tympanic bulla is slightly elongated and inflated (more so in SDSM 2653), similar to that of *Paraenhydrocyon josephi*. The paroccipital process is well preserved in SDSM 2653. It is a short, rodlike structure that has begun to turn downward so that its anterior surface hugs the posterior bulla wall. The paroccipital process on SDSM 2653 is so short that there is barely a free tip left beyond the part that is fused to the bulla, in contrast to a much more robust and long process in *M. coryphaeus* and other more derived forms. The right paroccipital process on F:AM 63367 is broken at the base and is pushed forward and downward. It exhibits the same shortness and slenderness as in SDSM 2653, and only a small disk of bone, 3 mm in diameter, is attached to the posterior bulla wall. The cross-sectional shape of the paroccipital process also serves as an important distinction between the *Mesocyon–Enhydrocyon* and the *Paraenhydrocyon* clades. In "*M.*" *temnodon*, the lateral edge is not sharpened and flattened in contrast to the laterally extended edge and relatively flattened appearance in *P. josephi*

(there are some parallel developments of this feature in *Enhydrocyon*). The mastoid process is small; its lateral articulation surface faces somewhat ventrally instead of laterally as in most primitive hesperocyonines.

Mandible: Mandibles are abundantly represented in the present study, all exhibiting primitive proportions that are of limited use in distinguishing them from other taxa. The horizontal ramus of the holotype is arched ventrally below m1–2. Rami from the referred specimens tend to have less convex lower borders. On F:AM 63367, there is a triangular extension on top of the coronoid process. The extended part of the coronoid is inflected toward the medial side and has a small tubercle on the tip. F:AM 63367 is the only specimen that has a completely preserved angular process. The process is modestly long with a dorsally hooked tip. In the medial side, the facet above the internal ridge (aréte interne; Gaspard, 1964: 251, for attachment of the superior ramus of the medial pterygoideus muscle) is not excavated as opposed to a deeply excavated facet in *Paraenhydrocyon josephi*. This unpocketed angular process is found in most individuals of *Mesocyon* through *Enhydrocyon*. On the type, the angular process is broken in half; the remaining basal segment of the process indicates a slightly more medially extended internal ridge that may have enclosed a shallow pocket, but would certainly be shallower than in *P. josephi*.

Dentition: Abundant teeth are available, although most of them are fragmentary. The teeth of "*Mesocyon*" *temnodon* are little different, other than their larger size, from species of *Hesperocyon* and other primitive hesperocyonines (e.g., *Mesocyon brachyops*, *Paraenhydrocyon josephi*). The few subtle features described below that may be used as distinguishing features are certainly not infallible.

No upper or lower incisors are preserved. The P1 is single-rooted and differs little from that of "*Hesperocyon*" *coloradensis*. A posterior accessory cusp begins to develop on most P2s (well developed on F:AM 102381, see comments in Discussion) and becomes enlarged on P3. A posterior cingular cusp is only present on P3, as is usually the case in most primitive hesperocyonines. The pro-

tocone of P4 is large, distinct, and anteriorly positioned (i.e., protruding forward beyond the anterior border of the paracone), another primitive feature also found in *Cynodesmus thooides*. The anterior cingulum at the base of the paracone is usually well developed in contrast to the reduced conditions in larger, more derived taxa such as *Mesocyon coryphaeus* and *C. thooides*. The M1 of AMNH 8770 has a posteriorly deflected internal cingulum that is disconnected from the anterior segment of the cingulum, a primitive condition prevalent in most *Hesperocyon*; others (e.g., F:AM 63367 and SDSM 2653), however, have a slightly more anteriorly extended internal cingulum narrowly encircling the protocone. The M1 parastyle, if present, is low. The posterior border of M1 is more deeply concave on F:AM 63367 than in other specimens. The M1 of F:AM 63377 is somewhat differently proportioned with a longer labial border and a cusplike internal cingulum. The relative size of M2 is slightly enlarged in some individuals (SDSM 2653, F:AM 63366, and 63961).

Most of the p2s have an incipient posterior accessory and anterior and posterior cingular cusps (F:AM 63965 has no posterior accessory cusp, whereas F:AM 102381 has a well-developed one; see also comments in Discussion). These cusps become more conspicuous on the p3 and p4. Like *Hesperocyon gregarius*, there is still a large metaconid on the m1. The talonid of m1 is slightly wider than in *Paraenhydrocyon josephi* but about the same as in *Osbornodon renjiei*. In most individuals, the entoconid of m1 is reduced to a low platform about one-fourth of the talonid width. The remainder of the talonid is occupied by a large hypoconid. The m2 is almost identical to that of *H. gregarius* and other primitive hesperocyonines (e.g., *Mesocyon brachyops*, *P. josephi*); the protoconid and metaconid on m2 are nearly equal in size. The type has a slightly wider anterolateral cingulum than most specimens. A small, oval-outlined m3 is present in all individuals; all are double-rooted.

DISCUSSION: Since its establishment by Wortman and Matthew in 1899, "*Mesocyon*" *temnodon* has largely remained in obscurity, even though specimens of this species are not particularly rare. The lack of a des-

ignated type and detailed descriptions (see discussion under Lectotype) are probably partly responsible for this situation. The only recent reference of this species was by Setoguchi (1978: 56), who tentatively assigned one "m1" (CMNH 21678) from the Badwater Creek, Wyoming, to *Hesperocyon temnodon*; the Carnegie specimen is a deciduous p4 of probably an amphicyonid carnivoran and is under study by H. Bryant (personal commun. 1991).

Although *"Mesocyon" temnodon* and *Paraenhydrocyon josephi* (both primitive members of two diverging lineages) may be differentiated on a few nondental characters, these two species are difficult to distinguish on the basis of dental morphology alone. Besides a very slight slenderness of m1 in *P. josephi* that may be used as a general (often unreliable) guide, teeth of both these species remain primitive and have not acquired features that later are to become readily diagnosable characters. This difficulty is further compounded by their stratigraphic overlap and their similar size; measurements of the two do not readily aid taxonomic identification. Therefore, the inclusion in one taxon or another of fragmentary specimens with only teeth remaining are, regrettably, subjective.

Macdonald (1963: 212) referred five specimens from Sharps Formation to *Mesocyon robustus* Matthew: SDSM 53327, 54131, 54242, 54249, 55145. Except SDSM 54249, which has left p2, p4–m2, all are ramal fragments with mostly broken m1s. Most of these Sharps specimens clearly do not belong to *Paraenhydrocyon robustus* (some are too poorly preserved to be adequately determined) because they possess one or more of the following five features: (1) presence of a distinct posterior accessory cusp on lower premolars, (2) low and less sharp principal cusps of premolars, (3) relatively large metaconids on m1 and m2, (4) relatively wide entoconid shelf on the talonid of m1, and (5) lack of a ventrally pocketed masseteric fossa. Features 4 and 5 further suggest that the SDSM specimens are probably not *P. josephi*. The SDSM specimens are here tentatively placed in *"Mesocyon" temnodon*.

An interesting variation is seen in F:AM 102381 from the Whitneyan of Wyoming. It

has perfectly well-developed posterior accessory and cingular cusps on all upper and lower premolars (P1 and p1 not preserved), a phenomenon not seen in any primitive hesperocyonine and paralleled only in some borophagines. Its teeth and skull proportions are otherwise quite similar to most individuals of *"Mesocyon" temnodon*. In absence of any lineage that possesses this peculiar character, F:AM 102381 is presently left in *"M." temnodon* and is assumed to be an individual variation without leading to a new taxon.

Mesocyon brachyops
Merriam, 1906
Figure 20

Hypotemnodon josephi (Cope) Wortman and Matthew, 1899: 130 (AMNH 6921 only).
Mesocyon brachyops Merriam, 1906: 17. Merriam and Sinclair, 1907: 184. Matthew, 1909: 107. Barbour and Schultz, 1935: 412. Schlaikjer, 1935: 133. Stevens, 1991: 46.
Mesocyon josephi josephi (Cope) Thorpe, 1922a: 169 (YPM 12705).
Mesocyon baileyi Stock, 1933: 32. Barbour and Schultz, 1935: 412. Stevens, 1991: 46.

HOLOTYPE: UCMP 1692, almost complete cranium with left P1–M1 and right P2–M2, and partial pelvis.

TYPE LOCALITY: The holotype was found in UCMP Loc. 898 from the "upper portion of the John Day series at Logan Butte, Crook County, Oregon" (Merriam, 1906: 17). In the same paper, however, Merriam (1906: 4) seemed uncertain about its stratigraphic position and listed *Mesocyon brachyops* under "Upper John Day" followed by a question mark. Subsequently, Merriam and Sinclair (1907: 191) positively listed *M. brachyops* as one of the "typical forms" of the Upper John Day, that is, Kimberly or Haystack Valley Members of Fisher and Rensberger (1972). In a footnote, however, Matthew (1909: 106) once again cast doubt about Merriam's determinations of stratigraphy: "the level of many species (marked "?") is doubtful as it is determined only by character of matrix."

REFERRED SPECIMENS: From the John Day Formation of central Oregon, Arikareean: AMNH 6915, left maxillary fragment with C1–P3, from Turtle Cove; AMNH 6921, nearly complete skull with left and right P4–

M1, broken left P2–3, and right P1–2 (referred to *M. josephi* by Wortman and Matthew [1899: 130]), from Camp Creek; AMNH 7239, maxillary fragments with left P4–M1 and right P4–M2, from Turtle Cove; LACM 2740, maxillary fragments with left C1, P3–4 and right P4–M1; YPM 12705, partial skull and mandible, referred to *M. josephi josephi* (Thorpe, 1922a: 169), from "the Fossil Horse beds on Cottonwood Creek," middle John Day Formation (ibid.).

From Kew Quarry local fauna (all of the Kew Quarry specimens were collected by the California Institute of Technology expeditions and therefore carry a CIT locality number 126), Las Posas Hills, Ventura County, California, Sespe Formation, early Early Arikareean: LACM 467, left partial ramus with c1–m3; LACM 468, right maxillary fragment with I3–P4; LACM 469, right maxillary fragment with P4–M1; LACM 471, laterally crushed skull and mandible with left and right C1–M2, left i3–m3, right p1–m3, holotype of *Mesocyon baileyi* Stock (1933: pl. 1, fig. 7, pl. 2); LACM 472, maxillary fragments with left P4–M1 and right P2–3; LACM 1242, maxillary fragments with left P2–4 and right C1–M2; LACM 1346, partial left ramus with c1–m2; LACM 1818, dorsoventrally crushed skull with left C1–M2 and right P2–M1; LACM 1819, mediolaterally crushed skull and mandible with all postcanine teeth; LACM 1820, dorsoventrally crushed skull with left P3–M2 and right P2–M2; LACM 1822, left ramus fragment with p3–m2; LACM 1824, partial right ramus with p2–m3; LACM 5262, partial crushed skull roof with left P4–M1 and right P3–4; LACM 5264, right ramus fragment with p4–m2; LACM 5265, left ramus fragment with p4–m1; LACM 5266, skull fragments with left P4–M1 and right C1, P4; LACM 5268, right ramus fragment with broken c1–m1; LACM 5269, left ramus fragment with p4–m1; LACM 5271, right ramus fragment with p3–m1; LACM 5273, partial mandible with left p3–m3 and right p2–m3; LACM 5274, left ramus fragment with c1–p4; LACM 5289, partial right ramus with c1–m3; LACM 15465, maxillary fragments with left P4–M1 and right P3–M2.

EMENDED DIAGNOSIS: In addition to being larger-sized, *Mesocyon brachyops* can be distinguished from "*M.*" *temnodon* by having two derived characters: a longer and more robust paroccipital process (char. 15) and a pair of small, round pits above the foramen magnum (char. 6). In contrast to *M. coryphaeus*, *M. brachyops* has a relatively short and broad skull, a short infraorbital canal, a prominent postorbital process of frontal and associated broad forehead, a small bulla, a laterally bowed zygomatic arch (char. 19), and an anteroposteriorly shortened M1.

DISTRIBUTION: As in most of the John Day taxa, the stratigraphy of specimens of *Mesocyon brachyops* from the John Day Formation is poorly known. The referred specimens in the AMNH collection have even less field documentation than the type. Specimens collected from the Turtle Cove may indicate origins from the Middle John Day beds (Turtle Cove Member), as has been assumed in other species of AMNH Turtle Cove specimens. The assignment of the Kew Quarry specimens to *M. brachyops* considerably extends the known geographic distribution to the southwestern United States and further supports its Early Arikareean age (Tedford et al., 1987). If the type is correctly assigned to the Upper John Day Formation, *M. brachyops* spans most of the Early to Late Arikareean.

DESCRIPTION: Kew Quarry specimens collected subsequent to the publication of *Mesocyon baileyi* have considerably increased its original sample size. Although specimens from the Kew Quarry are all severely crushed, the Sespe sample is an important addition to the better preserved John Day specimens not only in its value in assessment of variation in the species but also in its representation of a population distant from John Day. Fortunately, teeth from the Kew Quarry are usually undistorted.

Skull: Despite a nearly complete skull of the holotype, Merriam's (1906: 17–19) original description of *Mesocyon brachyops* is rather short. Its cranial morphology is now nearly completely known with the combined knowledge from AMNH 6921 and UCMP 1692.

The size of *Mesocyon brachyops* is intermediate between "*M.*" *temnodon* and *M. coryphaeus*. The most conspicuous feature of *M. brachyops*, as diagnosed by Merriam
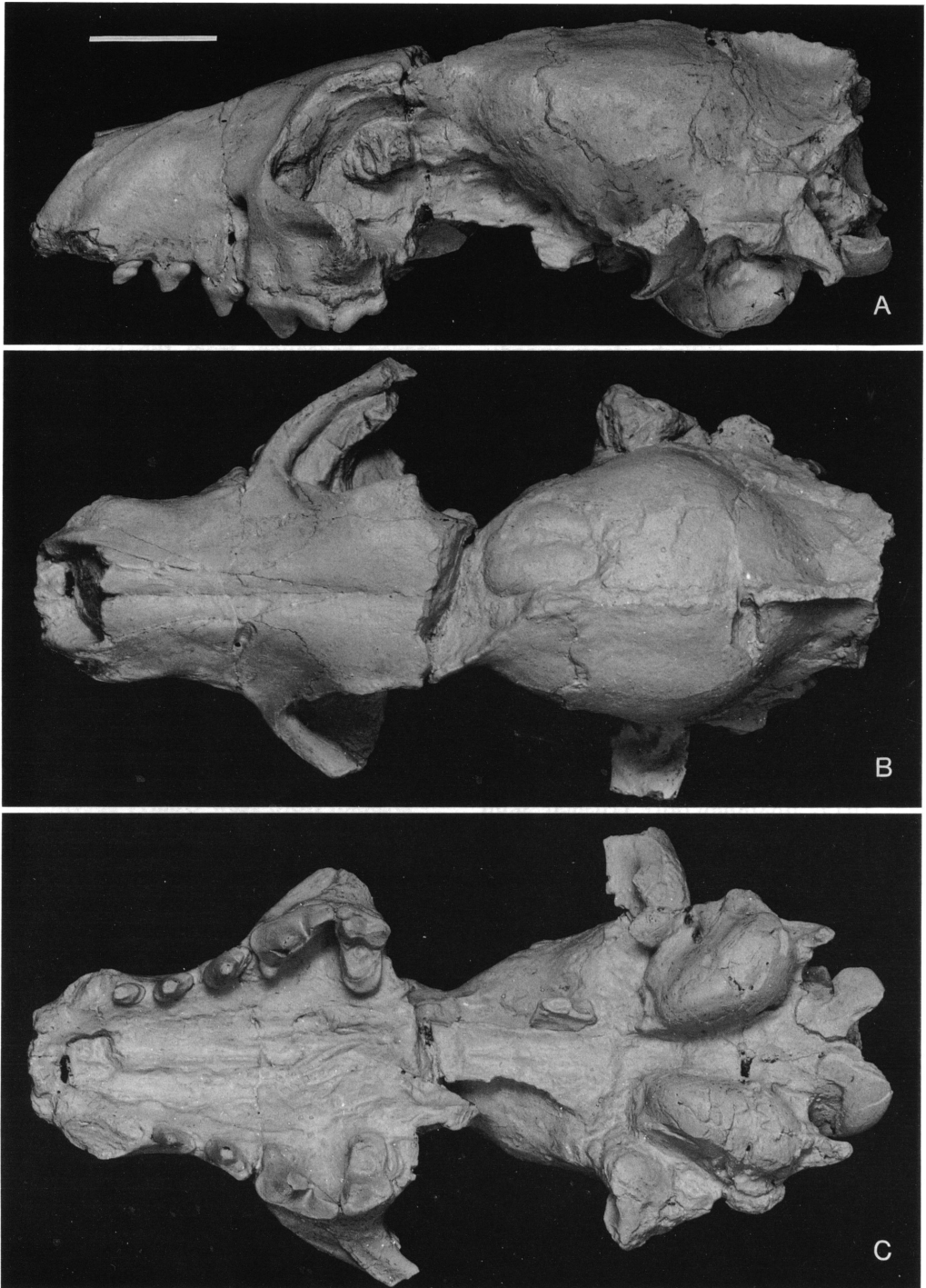
Fig. 20.   Skull of *Mesocyon brachyops*. **A**, Lateral, **B**, dorsal, and **C**, ventral views of UCMP 1692, holotype. Scale = 30 mm.

(1906), is its "short rostrum." Although the anterior premaxillary tips on both of the John Day skulls (AMNH 6921 and UCMP 1692) are broken, comparisons on the remaining parts clearly indicate a snout 19% shorter on average than those in *M. coryphaeus* (measured from the anterior tip of the nasal to the level of anterior infraorbital foramen). This apparent shortness of rostrum is actually the result of an overall shortened skull, because the total skull length (from anterior tip of incisor to posterior tip of occipital condyle) of *M. brachyops* is also 17% shorter than in *M. coryphaeus*. The skull of *M. brachyops* thus is more stout since it has a transversely broad construction in most parts (e.g., the forehead, the zygomatic arch, etc.). Specimens from the Kew Quarry also suggest a short rostrum although their poor preservation does not allow accurate measurements. Associated with the shortened skull, the nasal is wide at its anterior tip and tapers rapidly toward the posterior end. This wedge-shaped appearance is due to a shortened nasal that condenses the primitively longer but gentler inclination of the nasal/premaxillary–maxillary suture into a more steep gradient. The posterior process of premaxillary is long and wide. The transverse distance between the dorsal rims of the orbits is relatively wide, which is associated with a large, laterally extended postorbital process of the frontal. The postorbital constriction, in contrast, is relatively narrow. Specimens from the Kew Quarry appear to have less prominent postorbital processes. The sagittal crests on both AMNH 6921 and UCMP 1692 are mostly broken off and are probably rather low, as in *M. coryphaeus*, judging from the remaining part of the crest. The sagittal crest on LACM 471 is slightly lower than in *M. coryphaeus*. The nuchal crest is broken on John Day specimens and is low on Kew Quarry specimens. The zygomatic arch, shown undistorted in AMNH 6921, is laterally arched, strongly built, and deep in lateral view, in contrast to the relatively straight, slender, parasagittally oriented lateral border in *M. coryphaeus*.

In posterior view, there is a small, oval-shaped dome on the supraoccipital above the foramen magnum, corresponding to the vermis of the cerebellum. This small dome is often seen in canids the same size or smaller

than *Mesocyon brachyops*, and is usually absent in larger canids. Instead, there is usually a central external occipital crest running from the tip of the inion to the foramen magnum in large canids (e.g., *M. coryphaeus*, *Cynodesmus*, and more derived taxa). Above the dorsal border of foramen magnum, there is a pair of small, round pits (also seen on LACM 471). This character is consistently present in the immediately more derived taxa such as *Cynodesmus thooides*.

On the two John Day skulls, the frontal area above the orbit is flat, in lateral view, as opposed to a slightly arched profile in *Mesocyon coryphaeus*, "*M.*" *temnodon*, and *Cynodesmus thooides*. The frontals in the Kew Quarry specimens, however, seem to be slightly arched, although it is difficult to determine the degree of distortion. The length of the infraorbital canal, as measured by the anterior base of zygomatic arch, is short as a result of a shortened palate.

The palate is shorter and wider than in *Mesocyon coryphaeus*. The tympanic bullae on both sides of the type are crushed medioaterally, resulting in a slightly more inflated appearance. The left bulla of AMNH 6921, on the other hand, is undistorted although its posterior surface is broken off. It is less inflated than in *M. coryphaeus*; the ecto-entotympanic suture (as indicated by a cross-hatching texture on the ventral bulla surface) is more medially positioned and the ectotympanic inclines toward the median plane. The paroccipital process is caudoventrally oriented, slightly less downward than in *M. coryphaeus*. The size (both thickness and length) of the paroccipital has considerably increased over that of "*M.*" *temnodon*. Also indicating its advanced stage of paroccipital development, a small basal segment of the process is fused to the caudal entotympanic. The mastoid process on AMNH 6921 is primitive in being small and sheltered beneath a basal lambdoidal crest.

Mandible: No mandible is available from the John Day deposits. Materials from the Kew Quarry, on the other hand, are too poorly preserved to yield more detailed morphology beyond an approximate size. In general, the mandibles from the Kew Quarry sample are proportionally larger than in "*Mesocyon*" *temnodon*.

Dentition: The more abundant dental materials from the Kew Quarry offer a good sense of intraspecific variation. The dentition is, in general, quite slender and primitive. On both of the skulls from John Day, the incisors and canines are lost, and only partial alveoli remain. The incisors, judging from the alveoli, are small and closely spaced. The upper canines of Kew Quarry specimens (e.g., LACM 471 and 1242) have ridges on both their anterior and posterior surfaces. The upper premolars are proportionally smaller than in *Mesocyon coryphaeus*, and are not imbricated (except AMNH 6915, a young individual with unworn, sharp tips on premolars); there are diastemata of 1–2 mm between premolars. The P1 and most P2s have a single main cusp without cingular cusp, although one individual, AMNH 6921, begins to develop a distinct posterior cingulum. The P3 has both a posterior accessory cusp and a posterior cingular cusp. Except in LACM 1818, all P4s are shorter than, but otherwise similar in shape to, those of *M. coryphaeus*. Their anterior cingulum is more reduced than in "*M.*" *temnodon*. The protocone of P4 is smaller than in most *Cynodesmus*. The most distinct feature of the M1 is its slender (anteroposteriorly) outline; this is particularly the case in John Day specimens. The slender shape of M1 is apparently in keeping with the short but broad palate (presumably more so in John Day individuals but the palate width of the Kew Quarry specimens is difficult to determine). The Kew Quarry sample contains individuals with both wide M1s (LACM 471 and 1818) and narrower M1s (LACM 1242). The angle between labial and anterior borders of M1 is small compared to that of *M. coryphaeus*. The M2 is usually slender and follows the proportions of M1, that is, being broad if the M1 is also broad (in Kew Quarry specimens).

The lower dentition is represented by the Kew Quarry materials only. Besides their larger size, the lower teeth of *Mesocyon brachyops* are little different from those of "*M.*" *temnodon*. LACM 471 has a left i3, which is composed of a main cusp and a much smaller lateral accessory cusp. The p2 is devoid of accessory or cingular cusps. A small posterior accessory cusp is present on most p3s, which also have a distinct posterior cin-

gular cusp and may have a smaller anterior cingular cusp. These accessory and cingular cusps are further enlarged on p4. The m1s are proportionally larger than in "*M.*" *temnodon*. The trigonid still retains a relatively large metaconid. The talonid is somewhat less trenchant than in *M. coryphaeus*, because of a relatively wide entoconid shelf that occupies approximately one-fourth of the total talonid width. The hypoconid is still the dominant cusp in the talonid, whereas the entoconid is usually expressed as a low, ridgelike platform slightly raised along the lingual edge. The protoconid and metaconid are nearly equal-sized cusps on m2. The paraconid is indistinct and, in its place, is a low, triangular platform. The talonid of m2 is occupied by a broad hypoconid and a much narrower entoconid shelf. A m3 is always present and double-rooted.

DISCUSSION: Although Stock (1933) recognized the similarity between *Mesocyon brachyops* and *M. baileyi*, he listed two diagnostic features to distinguish these two species. The first is a transversely shorter M1 of *M. baileyi*. This is indeed the case between the types of *M. baileyi* (LACM 471) and *M. brachyops* (UCMP 1692). However, this distinction, very slight even in the extreme forms, is completely blurred when the entire Kew Quarry sample is taken into consideration (many more specimens were collected after Stock's publication of *M. baileyi*). As for Stock's second diagnostic feature, a more prominent "hypocone crest" (i.e., internal cingulum) of M1 in *M. baileyi*, it is obviously due to the heavy wear on the type of *M. brachyops* that its protocone and internal cingulum are nearly worn flat, which contrasts with the "prominent," unworn internal cingulum of LACM 471. Whereas there is no major difficulty in synonymizing *Mesocyon baileyi* with *M. brachyops* in the present study, subtle differences exist between these two distant populations. In addition to the more primitively proportioned M1 (less slender) discussed above, the Kew Quarry skulls seem to be less shortened and laterally expanded even though their crushed skulls do not permit definite conclusions. Because the short and broad skull (and associated characters such as laterally expanded zygomatic arch and anteroposteriorly narrowed M1) in the John

Day specimens of *M. brachyops* are probably derived characters (relative to *M. coryphaeus*), the more primitive appearance of the Kew Quarry specimens may represent a population of an older geological age. If the assignment of the type of *M. brachyops* to the Upper John Day strata (see Type Locality) is correct, the Kew Quarry specimens could be older by one or more million years (sensu Tedford et al., 1987: fig. 6.2).

Cynodesmus Scott, 1893

Cynodesmus Scott, 1893: 660.
Temnocyon (Cope) Douglass, 1901: 2.
Mesocyon (Scott) Douglass, 1903: 164.
Sunkahetanka (Macdonald) Macdonald, 1963: 214.
Brachyrhynchocyon (Loomis) Macdonald, 1970: 60.

TYPE SPECIES: *Cynodesmus thooides* Scott, 1893.

INCLUDED SPECIES: *Cynodesmus thooides* Scott, 1893; and *C. martini*, new species.

EMENDED DIAGNOSIS: *Cynodesmus* is generally distinguishable from other hesperocyonines by its two autapomorphies: a strong paroccipital process that has a posterior keel (char. 15) and a broadened M2 (char. 40). Within the *Mesocyon–Enhydrocyon* clade, *Cynodesmus* has, in addition to the above autapomorphies, a less inflated bulla, more robust and closely spaced premolars, and a larger protocone of P4, as compared to *Mesocyon*. On the other hand, *Cynodesmus* has less robust premolars (except *C. martini*) and a shorter m1 with unreduced metaconid, as compared to *Sunkahetanka*, *Philotrox*, and *Enhydrocyon*.

DISTRIBUTION: Whitneyan to earliest Early Arikareean of western Nebraska and South Dakota; Early Arikareean of western Montana.

DISCUSSION: *Cynodesmus* is one of the most misunderstood and misused genera of hesperocyonines (table 4). The main source of confusion can be traced back to the original concept of the genus. In his discussion of the systematic position of *Cynodesmus*, Scott (1895: 72) emphasized the importance of "Miocene dogs" of North America as the most probable ancestors of the living *Canis*. He proposed a phylogeny of North American

"cynoids" in which *Cynodesmus* was placed as an intermediate taxon between *Daphoenus* (an amphicyonid) and *Canis*. Scott (ibid.) followed Cope's (1881a, 1883) opinion that *Canis brachypus* Cope (= *Osbornodon brachypus* in the present study) played a central role in the origin of living *Canis*. The critical feature in Scott's linkage of the two taxa is the "microdont" dentition in *Cynodesmus* and *Canis brachypus* (i.e., P4 and M1 with similar labial length), a concept first proposed by Huxley (1880: 248) in contrast to "macrodont" teeth (longer P4 versus shorter M1).

In the 10 years following the description of *Cynodesmus*, the genus was still perceived to be closely related to *Mesocyon*, because Douglass (1903) contrasted his new species *Mesocyon? drummondanus* with *M. coryphaeus* and *Cynodesmus thooides*. Matthew (1907), however, drastically altered the concept of *Cynodesmus* by erection of two species under this genus, *C. minor* and *C. thomsoni* (both now belonging to the Borophaginae), and *Cynodesmus* began to take on a borophagine identity. The central concept of the genus had shifted from the type species *C. thooides* with a trenchant talonid to "*C.*" *thomsoni* with a basined talonid. A new species "*C.*" *cuspidatus* was soon named by Thorpe (1922b), which is another borophagine canid. *Mesocyon iamonensis* Sellards (= *Osbornodon iamonensis*) was next referred to *Cynodesmus* (Simpson, 1932; Olsen, 1956) along with two other Thomas Farm canids, "*C.*" *nobilis* Simpson (= *Osbornodon iamonensis*) and "*C.*" *canavus* Simpson (a borophagine) (Simpson, 1932), even though the Florida species do not necessarily have a "microdont" dentition. Matthew (1930), followed by Simpson (1932) and Olsen (1956), placed *Cynodesmus* in a hypothetical lineage *Hesperocyon–Cynodesmus–Tomarctus* leading to the living canids. *Cynodesmus* thus gained increased popularity and more species were either erected under the genus ("*C.*" *casei* Wilson, 1939 and "*C.*" *euthos* McGrew, 1935; both are borophagines) or referred to it ("*C.*" *vulpinus* (Matthew) Macdonald, 1963, a species of *Leptocyon*). The contents of *Cynodesmus* were further stretched to the extreme when Macdonald (1963: 210) named a very small canid (the size of a living fennec), *Cynodesmus cooki*, based on two ramal frag-

ments with p4–m3. Nearly complete skulls in the Frick Collection referable to "*C.*" *cooki* clearly indicate that it belongs to an extremely modified borophagine lineage quite unlike any known canid. Macdonald (1963: 212) also erected a supposedly related genus *Neocynodesmus* (type *N. delicatus* (Loomis), 1932), a small arctoid about the same size as "*C.*" *cooki*, and placed it, together with *Cynodesmus*, in a sidebranch in his phylogeny of North American canids.

Cynodesmus thus included species belonging to all three subfamilies of Canidae, although it was dominated by borophagine forms (table 4). In the complex history of *Cynodesmus*, the type species *C. thooides* was rarely mentioned despite its well-preserved cranial and dental morphology and its detailed description and illustration by Scott (1895). The confusion about the taxonomic status of *Cynodesmus* has been deeply entrenched in the literature (in addition to publications cited above: Peterson, 1910: 209; Hough, 1948a: 103; Wilson, 1960: 986, 991; Olsen and Olsen, 1977: 533; Hemmer, 1978: 105; Honey and Izett, 1988: 22; Stevens, 1991: 46), and the notion of its being ancestral to *Canis* is likely to remain in the semitechnical literature for some time to come.

Radinsky (1973: fig. 3) illustrated an endocast of "*Cynodesmus petersoni*" on the basis of F:AM 61300 (a specimen of *Tomarctus thomsoni*). He clearly did not attempt to establish a new taxon; his reference to an unpublished name was an error. *Cynodesmus petersoni* Radinsky, 1973, is thus a nomen nudum.

Cynodesmus thooides Scott, 1893
Figures 21, 22

Cynodesmus thooides Scott, 1893: 660. Sellards, 1916: 89. Stevens, 1991: 46.
Cynodesmus thoöides (Scott) Scott, 1895: 63. Matthew, 1899: 54. Douglass, 1903: 164. Peterson, 1910: 267. Olsen, 1956: 2.
Temnocyon sp. Douglass, 1901: 2.
Mesocyon? drummondanus Douglass, 1903: 164.
Mesocyon drummondanus (Douglass) Olsen, 1956: 1. Stevens, 1991: 46.
Sunkahetanka geringensis (Barbour and Schultz) Macdonald, 1963: 214 (SDSM 53334 only).
Sunkahetanka sheffleri Macdonald, 1967b: 1.
Brachyrhynchocyon douglasi Macdonald, 1970: 60.

HOLOTYPE: YPM-PU 10412, partial skull with nearly complete upper dentitions except right I1–2, P1 and M2, partial mandible with left i1–m3 and right i1–p3. Collected by O. C. Mortson.

TYPE LOCALITY: Scott (1893, 1895) placed the type of *Cynodesmus thooides* in the "lower strata" of the Deep River Beds that he correlated with John Day deposits of Oregon. The lower strata of the Deep River deposits were later named the Fort Logan Formation by Koerner (1939, 1940) following the usage of Douglass (1903). Scott (1895) commented that fossil mammals of the lower beds of the Deep River came from exposures that are "very limited in extent, a few acres at most." Rensberger (1981: 187, fig. 2) further established that the historical collections by the Princeton expedition were probably from three localities (Crabtree Bluff, Thompson Gulch North, and Spring Creek) "within a radius of about 5.5 km" near the branching point between Smith River and Spring Creek (in NW¼, sect. 9, T. 10 N, R. 5 E [Koerner, 1939: 29]), in Meagher County, Montana. However, the lithological characteristics of all three localities are quite uniform, with reddish to brownish-tan volcanoclastic siltstones (Rensberger, 1981: 187), and precise placement of the holotype of *C. thooides* among the above three localities is difficult. The small and large mammals from Fort Logan Formation can be correlated with those of Gering and Monroe Creek Formations of the northern Great Plains (Tedford et al., 1987: 162–165), indicating an Early Arikareean age.

REFERRED SPECIMENS: From the Whitneyan and Early Arikareean of Wounded Knee area and Big Badlands of South Dakota: AMNH 13801, partial skull with left P2–M2 and right P3–M2, from Oak Creek, southwest of Eagle Nest Butte, Washabaugh County, "Lower Rosebud" (W. K. Gregory field map, 1907); BHI 1965, complete skull and lower jaws with most of the dentition, from Big Corral Draw, Shannon County, in Nodular Zone, Stronghold unit, lower Poleslide Member of Brule Formation; F:AM 63342, right ramus fragment with P2 and M1, from between the heads of Big Corral Draw and Cottonwood Creek, Washington County, from Leptauchenia beds just above Protoceras

TABLE 4
Taxonomic Assignment of Species Previously Referred to _Cynodesmus_
(Because of the shift in the concept of _Cynodesmus_ [see text], most species do not belong to the Hesperocyoninae. The lists of authors for species that are nonhesperocyonine canids are not exhaustive.)

Previous assignment	Author and year	Present assignment
Cynodesmus brachypus	Scott, 1895: 72; Matthew, 1907: 186; 1909: 112; Peterson, 1910: 209, 213; Cope and Matthew, 1915: pl. CXIXa, b, c; Stevens, 1991: 46	_Osbornodon brachypus_
Cynodesmus canavus	Simpson, 1932: 19	"_Tomarctus_" _canavus_
Cynodesmus casei	Wilson, 1939: 315	"_Cynarctus_" _kelloggi_
Cynodesmus cooki	Macdonald, 1963: 210	A new genus of borophagine
Cynodesmus cuspidatus	Thorpe, 1922b: 433	_Carpocyon compressus_
Cynodesmus euthos	McGrew, 1935: 306	"_Tomarctus_" _euthos_
Cynodesmus iamonensis	Simpson, 1932: 14; Olsen, 1956: 5	_Osbornodon iamonensis_
Cynodesmus kelloggi	Stirton, 1939: 628	"_Cynarctus_" _kelloggi_
Cynodesmus minor	Matthew, 1907: 189; Macdonald, 1963: 212	"_Phlaocyon_" _minor_
Cynodesmus nobilis	Simpson, 1932: 17; White, 1941: 91	_Osbornodon iamonensis_
Cynodesmus petersoni	Radinsky, 1973: fig. 3	Nomen nudum
Cynodesmus thomsoni	Matthew, 1907: 186; Peterson, 1910: 267; Hough, 1948a: 103	"_Tomarctus_" _thomsoni_
Cynodesmus thooides	Scott, 1893: 660; 1895: 63; Matthew, 1899: 54; Douglass, 1903: 164; Peterson, 1910: 267; Sellards, 1916: 89; Olsen, 1956: 2; Stevens, 1991: 46	_Cynodesmus thooides_
Cynodesmus vulpinus	Macdonald, 1963: 211	_Leptocyon vulpinus_

channels, Poleslide Member of Brule Formation; F:AM 63371, anterior skull fragment with left P2–M2 and left ramus fragment with broken m1, from 1 mi east of Cedar Pass, Jackson County, in the first white layer of the Leptauchenia beds, base of the Sharps Formation; F:AM 63373, maxillary fragments with left P2–M1 and right P3–M1, ramal fragments with left m1–3 and right p1–m1, from Hay Creek (a tributary of Bear Creek south of White River), going through T. 42 N, R. 38 W, Washabaugh County, in Leptauchenia beds, middle Poleslide Member of Brule Formation; F:AM 63381, fragments of upper and lower jaws with left C1, right P3–M2, left and right p4–m1, from 0.25 mi west of Cedar Pass, Poleslide Member of Brule Formation (in top part of Upper Oreodon Beds in M. F. Skinner fieldnotes); F:AM 63382, complete skull and mandible with all cheek teeth except right p1, from west side of Potato Creek, approximately 3 mi east of Horgan Ranch near the head of the east branch of Redwater Creek, Washabaugh County, in Leptauchenia beds, middle Poleslide Member of Brule Formation; F:AM 63385, left half skull with P2–M2, left and

right rami each with p2–m2, from west of Grass Creek area, in sect. 33, T. 39 N, R. 45 W, Shannon County, 80 ft below Rockyford Ash (M. F. Skinner fieldnotes, 1961), in basal Leptauchenia beds, Poleslide Member of Brule Formation; F:AM 63386, partial skull with left P2, P4–M2 and right P4–M2, from southwest of Indian Stronghold on Cuny Table, Shannon County, upper part of lower Leptauchenia nodules below the Protoceras channels (M. F. Skinner fieldnotes), middle Poleslide Member of Brule Formation; LACM 17003, partial anterior mandible with left p2–m3 and right p1, p3–m2, holotype of _Brachyrhynchocyon douglasi_ Macdonald, 1970, from LACM loc. 1819 (= SDSM V5354), "in the common corner of sects. 13, 14, 23, and 24, T. 39 N., R. 42 W., near the top of the Sharps Formation" (Macdonald, 1963: 159); LACM 17076, partial skull and mandible with left C1–M2, right P2–M2, left p1–m2, holotype of _Sunkahetanka sheffleri_ Macdonald, 1967b, from "LACM no. 2006, Medicine Root Creek, Shannon County, South Dakota. Poleslide member of Brule Formation, from twenty five feet of gray clays whose top is fifty nine feet below the base of

the Sharps formation. These clays are over-lain by *Protoceras* channels and underlain by a red clay" (Macdonald, 1967b: 1); SDSM 53334, rostral part of skull with left P2–M1 and right P2–M2 from SDSM V5354, near corners of sections 13, 14, 23, and 24, T. 39 N, R. 43 W, Shannon County, near top of Sharps Formation.

From Court House Rock, on Pumpkin Seed Creek, south of Bridgeport, NW1/4, NW1/4, sect. 29, T. 19 N, R. 50 W, Morrill County, Nebraska: F:AM 63960, left ramus fragment with m1, from east face of Court House Rock, in basal Gering Channel (M. F. Skinner field-notes, 1957), early Early Arikareean; F:AM 63969, left maxillary fragment with P4–M1 and isolated right M2, from west end of Court House Rock, 85 ft below the Brule–Gering unconformity and 55 ft below the Upper Ash (M. F. Skinner fieldnotes, 1957), in Whitney Member of Brule Formation, Late Whitney-an.

From Cabbage Patch Formation, Granite County, Montana: CMNH 792, nearly com-plete skull with left I1–3 and all cheek teeth except left M1, a scapula and other postcra-nial fragments, holotype of *Mesocyon? drum-mondanus* Douglass (1903: figs. 9, 10). CMNH 792 was found "three or four miles east of Drummond, near the Hellgate River" (Douglass, 1903: 164). Konizeski and Do-nohoe (1958) determined that it probably comes from 1.5 mi southeast of the Cabbage Patch bar, in sect. 10, T. 10 N, R. 12 W, and named the associated fauna Cabbage Patch local fauna. Rasmussen (1989) listed the spe-cies (referred to as "*Mesocyon* (coyote-sized dog)") under the Lower Cabbage Patch For-mation, which was correlated with the Gering and Sharps Formations of the Great Plains (i.e., Early Arikareean).

EMENDED DIAGNOSIS: *Cynodesmus thooides* is easily distinguishable from its sister-spe-cies, *C. martini*, in its smaller size, less robust skull and teeth, slender rostrum, lower sag-ittal crest, and presence of a P1, features mostly primitive for the genus.

DISTRIBUTION: From Whitneyan to earliest Early Arikareean of western Nebraska and South Dakota; Early Arikareean of western Montana.

DESCRIPTION: Scott's (1895) description of

the holotype of *Cynodesmus thooides* is rath-er detailed. A significant increase of sample size in the present study (three complete and two partial skulls), however, allows a better appreciation of its morphological variation. Because of its transitional nature between *Mesocyon* and *Sunkahetanka*, the present sample of *C. thooides* contains individuals with morphological variations that approach these species. On the other hand, there is con-siderable morphological distance between the two species of *Cynodesmus*. The present de-scription of *C. thooides* will thus contrast it more with *Mesocyon* and *Sunkahetanka*, rather than with *C. martini*, because the latter is quite distinct.

Skull: The size and proportions of *Cyno-desmus thooides* are very close to those of *Mesocyon coryphaeus*. The cranial similari-ties are so great that, except for the size of the bulla and paroccipital process, distinc-tions between these two species are quite sub-tle. The frontal is slightly domed like that of *M. coryphaeus* and some specimens have a shallow fossa on the dorsal side of the post-orbital process. The sagittal crest is slender and low compared to a much higher one in *C. martini*. The nuchal crest is not greatly expanded caudally as in *C. martini* and in the more derived *Sunkahetanka* and *Enhydro-cyon*. A distinct, thin-edged external occipital crest is present on the supraoccipital. The fossae for the rectus capitis dorsalis minor muscle are clearly present. In BHI 1965, these fossae are rather deeply excavated as is also shown in *Sunkahetanka geringensis* and *Phil-otrox condoni*. There is a shallow notch on the dorsal edge of the foramen magnum in F:AM 63386 and to a lesser extent in F:AM 63382. The zygomatic arch is relatively slen-der, a primitive condition in contrast to the deep zygoma in *Sunkahetanka* through *En-hydrocyon*.

Scott (1895) described the endocast of YPM-PU 10412 in detail and concluded that brain morphology of *Cynodesmus thooides* is very different from that of living canids, mainly in its simpler surface convolutions. Radinsky (1973: 174) further pointed out that, in addition to the suprasylvian and corono-lateral sulci that are present in *Hesperocyon*, *Cynodesmus* has added the ectosylvian, ec-

tolateral, and presylvian sulci, but still lacks a sylvian sulcus along with a number of other advanced features of living canids.

On the ventral side of skull, the width of the palate is intermediate between *Mesocyon coryphaeus* and *Sunkahetanka*. The posterior border of the palatine has a small posterior protrusion in contrast to a straight posterior border in the holotype of *S. geringensis*. There is a shallow fossa for the rectus capitis ventralis medial to the posterior lacerate foramen. The posterior wall of the postglenoid foramen formed by the ectotympanic varies from incomplete (F:AM 63382, 63386) to complete (F:AM 63385, BHI 1965, PU 10412). The bulla is consistently smaller and less inflated than in *M. coryphaeus*. The paroccipital processes in the Whitneyan South Dakota specimens are indistinguishable from those of *M. coryphaeus*. The type, YPM-PU 10412, on the other hand, has an exceptionally strong paroccipital process with a thick base. Its posterior border slightly arches backward and has a keel on its posterior edge, a key character linking it with *Cynodesmus martini*. The basal segment of the paroccipital process extensively fuses with the caudal end of the bulla. The mastoid process is still primitively small as in *M. coryphaeus*. Its lateral surface is rough and sheltered beneath the basal lambdoidal crest.

Mandible: The mandible of *Cynodesmus thooides* retains a primitively slender construction, despite the onset of the tendency toward more robust dentition beginning in this species. The coronoid crest is relatively low, without the prominent posterior extension seen in *Sunkahetanka geringensis*.

Only the type has a completely preserved angular process. The process remains primitive like that in "*Mesocyon*" *temnodon* (F: AM 63367). The supero-internal facet (Gaspard, 1964) is not excavated into a pocket as in *Paraenhydrocyon*. A distinct longitudinal ridge is present below the internal ridge to mark the ventral extent of the inferior ramus of the medial pterygoideus muscle. This ridge, commonly present in living canids, is often indistinct or completely absent in hesperocyonine canids, except occasional occurrences (e.g., F:AM 54073, *Enhydrocyon crassidens*). The ventral border of the angular

process has a sharp ridge. On lateral side, the angular process is rather smooth-surfaced.

Dentition: The overall construction of the dentition of *Cynodesmus thooides* is more robust than in *Mesocyon coryphaeus* but less so than in *C. martini* and *Sunkahetanka geringensis*. The I3 is nearly twice as large as I2 or I1. The wear on upper incisors of the holotype does not permit identification of cusp patterns. The upper premolars are more robust than in *M. coryphaeus* and are closely spaced. The P1 is small, single-rooted, and has a single main cusp. The P2 either has a very vague posterior cingulum or none at all. All P3s have a well-developed posterior accessory cusp and a distinct posterior cingulum, but none has an anterior cingulum. The P4 is always stout compared to that of *M. coryphaeus*. The labial length of P4 is approximately the same as that of M1 (i.e., a "microdont" dentition) as opposed to a "macrodont" dentition with more differentiated carnassial tooth (long P4 versus short M1) (Huxley, 1880: 248). Scott (1893, 1895) thus used this concept of microdont to diagnose the genus *Cynodesmus*. The size and shape of the protocone of P4 varies in most canids. The large protocone in the holotype represents one end of the spectrum whereas the other end is seen in F:AM 63382 and BHI 1965 in which the protocone is much less distinct and is appressed toward the paracone. The placement of the protocone ranges from far anteriorly positioned to laterally positioned. The ratio of distinctly large protocones to small protocones seems to be large for *C. thooides* (7:3) compared to that in *M. coryphaeus* (7:9). The shape of M1 also varies substantially, especially the size and shape of the internal cingulum. Most individuals have a transversely elongated outline of the M1. Compared to *M. coryphaeus*, the paracone shows greater enlargement over the metacone, thus creating a deeper trigon basin, a modification further amplified in *Sunkahetanka* through *Enhydrocyon*. The internal cingulum of M1 is slightly more elevated than that of *M. coryphaeus*. The M2 is larger than that of *M. coryphaeus* and *S. geringensis*, and resembles more closely the morphology of M1 than in taxa with more reduced M2s.

The lower incisors of *Cynodesmus thooides*

Fig. 21.   Skull of *Cynodesmus thooides*. **A**, Dorsal and **B**, ventral views of YPM-PU 12730, holotype. Scale = 20 mm.

are aligned into one row in contrast to the crowded, imbricated incisors in *Sunkahetanka geringensis*. The i2 and i3, worn flat on the tips on the holotype, show a lingual groove near their base. The lower canine has a weak posterior ridge. The size of lower premolars is intermediate between *Mesocyon* and *Sunkahetanka*. The p1 is small and single-cusped. A small anterior and posterior cingular cusps may or may not be present on p2. These cingular cusps, however, are always present on p3 and p4. Although distinct on p4, a pos-
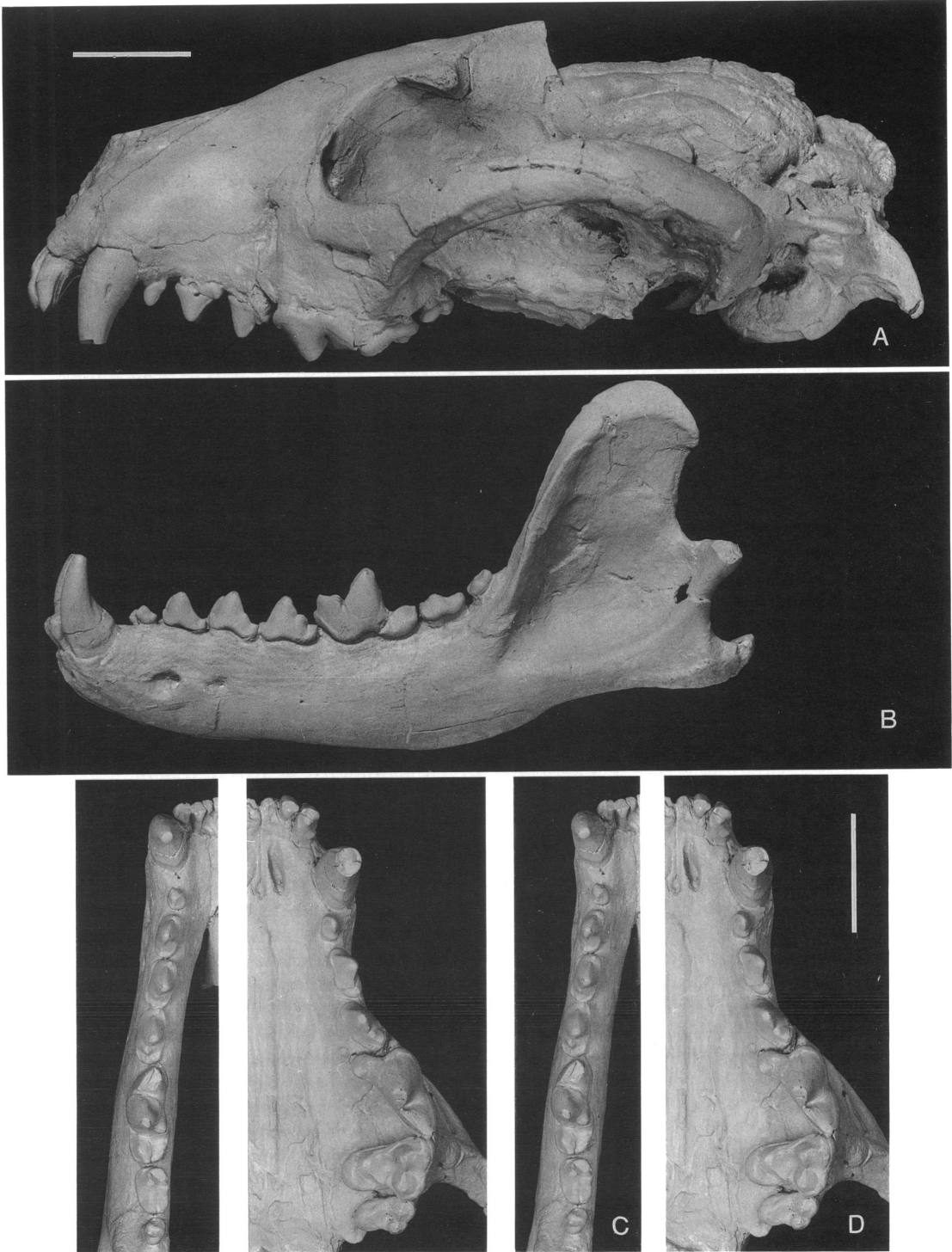
Fig. 22.   Skull and mandible of *Cynodesmus thooides*, YPM-PU 12730, holotype. Lateral views of
A, skull and **B**, left ramus, and occlusal views of **C**, lower and **D**, upper teeth. Scales = 20 mm.

terior accessory cusp is variably developed on p3. The size of m1 is nearly identical to that of *M. coryphaeus* but is smaller than in *S. geringensis*. It is not transversely widened as in *S. geringensis*. As in *M. coryphaeus*, the m1 metaconid is not reduced, in contrast to the small metaconid in *S. geringensis*. The trenchant talonid on m1 is dominated by a large hypoconid on the labial side. The entoconid is reduced from the condition in "*M.*" *temnodon* to a low ridge in PU 10412 and BHI 1965 or a narrow, flat shelf in F:AM 63373 and 63386. Despite the large M2, the m2 is not always correspondingly large. The slightly more anterior protoconid is enlarged at the expense of the metaconid, a derived condition compared to "*M.*" *temnodon*. The paraconid is absent and in its place is a flat platform. Except for F:AM 63386, which has a peculiarly short talonid on m2, the length of the m2 talonid is the same as that in *Mesocyon*. The hypoconid forms a low, longitudinal ridge, limited anteriorly by the base of the protoconid but not connected to a posterior ridge of the protocone as in *S. geringensis*. The m3 is double-rooted, oval in outline, and has nearly equal-sized protoconid and metaconid.

DISCUSSION: Scott (1895: 75) emphasized the "microdont" dentition of the Deep River species and placed it in a phylogenetically intermediate position between *Daphoenus* and *Canis* (see Discussion under genus *Cynodesmus*), even though he was clearly aware of the primitiveness of *Cynodesmus* and of the difficulties in separating *Cynodesmus* from *Hesperocyon* except by size (ibid.: 63). Huxley's (1880) concept of microdont teeth (similar labial length of P4 and M1, as opposed to much longer P4 in macrodont teeth) is not useful in the present comparisons of species closely related to *Cynodesmus*—from *Mesocyon* to *Sunkahetanka*, the P4–M1 are all more or less microdont. Only in *Enhydrocyon* and *Osbornodon* does the P4 begin to elongate relative to M1.

The discovery of the skull of *Mesocyon?* *drummondanus* was first mentioned in Douglass (1901: 2): "on the north side of the Hell Gate River, in gray sandy bluffs, the skulls of a dog much like *Temnocyon*, a *Leptomeryx*, and an Oreodont were discovered." His subsequent (1903: 164–167) formal descrip-

tion of this dog included comparisons mainly with *M. coryphaeus* and *Cynodesmus thooides*. Although Douglass tentatively placed the Drummond specimen under *Mesocyon*, the present study indicates that the type *M. drummondanus*, CMNH 792, is an individual of *C. thooides* because of two characters: a much smaller auditory bulla and an overall more robust dentition than in *Mesocyon*. However, CMNH 792 does possess some dental peculiarities (e.g., reduced accessory cusp on upper premolars, small protocone of P4, and more quadrate M1) distinct from the type of *C. thooides*. The taxonomic value of these dental distinctions tend to disappear when compared with the entire sample of *C. thooides* (in particular, BHI 1965 is perhaps the closest in dental proportions to CMNH 792). Although the time equivalence between the associated faunas of the types of *M. drummondanus* and *C. thooides* is still somewhat unsettled, they are certainly in close geographic proximity—within 100 mi of each other. If the conspecific status of these two individuals is correct, this Early Arikareean occurrence of *C. thooides* on each side of the continental divide represents an exception to the usually observed geographic differentiations of taxa across the continental divide (see Distribution at end of the paper).

Macdonald (1967b) compared his new species *Sunkahetanka sheffleri* (holotype LACM 17076) with the genotypic species *S. geringensis* only, and concluded: "The Whitneyan specimens [*S. sheffleri*] were found 310 feet stratigraphically below and 14 miles geographically from the nearest record of *S. geringensis*. This occurrence is a unique example of a species to species evolution in a restricted area, the younger species replacing the older one in place during a relatively short span of geologic time, perhaps on the order of 2 to 3,000,000 years." The badly preserved skull of LACM 17076 provides little more than an overall proportion of *S. sheffleri*. It has a short rostrum, which is also reflected in its imbricated upper premolars. Aside from this single feature, LACM 17076 is almost identical to *C. thooides* in all respects. The present inclusion of *S. sheffleri* in *C. thooides* does not necessarily negate Macdonald's assertion that LACM 17076 represents a population that is ancestral to *S. geringensis*.

In his subsequent revision of Wounded Knee South Dakota fauna, Macdonald (1970: 60) named another new species *Brachyrhynchocyon douglasi* from the Sharps Formation. The holotype, LACM 17003, consists of a partial mandible with most of the left and right lower cheek teeth. *Brachyrhynchocyon douglasi* has elongated premolars and an enlarged posterior accessory cusp on the p4, characters suggesting some similarity to *Osbornodon*. However, the unreduced width of its premolars and its trenchant m1 talonid seem to exclude it from *Osbornodon*. In most other respects, LACM 17003 is quite similar to *C. thooides*, except for a slightly smaller m1.

Cynodesmus martini, new species
Figure 23

HOLOTYPE: UNSM 25796, nearly complete skull and mandible with left I2–3 and P2–M2, right I3 and P2–M2, and left c1 and p4–m3.

TYPE LOCALITY: One mi west of Redington Gap, north of an abandoned concrete house, Morrill County, Nebraska. Thirty to 40 ft above the Brule/Gering Formations contact, in the Gering Formation, Early Arikareean.

REFERRED SPECIMENS: Known from holotype only.

DIAGNOSIS: *Cynodesmus martini* has many advanced features distinct from its primitive sister-species *C. thooides*: a much larger and more robust skull, a broader rostrum, a more elongated postorbital area (char. 3), a higher sagittal crest, a posteriorly overhung nuchal crest, loss of the P1 (char. 28), and stronger premolars (char. 29).

DISTRIBUTION: From the type locality only.

ETYMOLOGY: In honor of Dr. Larry D. Martin, professor and curator of the Museum of Natural History, University of Kansas.

DESCRIPTION: *Cynodesmus martini* has a massive skull that superficially resembles many aspects of *Enhydrocyon*. Where appropriate, the description below will emphasize the distinctions between the two.

Skull: The skull of *Cynodesmus martini* is much more robustly built than, and thus easily distinguishable from, that of *C. thooides*. In contrast to *C. thooides*, it approaches the cranial proportions of an *Enhydrocyon* with a short and broad rostrum, wide nasals, a large postorbital process of frontal, an elongated postorbital region, and a high sagittal crest. It lacks, however, a laterally pinched anterior process of the frontal, which is a unique characteristic of *Enhydrocyon* (see descriptions of *Enhydrocyon* spp.). Although the sagittal crest is mostly broken off, it is judged to be very high because the frontal region posterior to the postorbital process is elevated and the temporal ridges quickly converge to form an anterior segment of the sagittal crest. The nuchal crest extends posteriorly to overhang the occipital condyle by more than 10 mm. Only the anterior and posterior bases of the right zygomatic arch are preserved, which indicate a deep and strong zygoma.

The palate is broad and its posterior edge is 7 mm behind the posterior border of the M2. The auditory bulla is elongated and not well inflated as in *Enhydrocyon stenocephalus*. There is no hypertrophy of the anterior horn of the ectotympanic to be fused with the postglenoid process as seen in derived *Enhydrocyon*. The mastoid process remains primitively small and sheltered beneath the lateral segment of the lambdoidal crest, in contrast to the hypertrophied processes in *Enhydrocyon*. The paroccipital process displays the typical *Cynodesmus* configuration. It is oriented ventrally and has a massive fusion with the bulla. There is a keel on the posterior surface of the process in contrast to the smooth surface in that of *Enhydrocyon*.

Mandible: The overall contruction of the mandible parallels some aspects of hypercarnivorous forms, such as *Enhydrocyon* and *Ectopocynus*. It has a robust horizontal ramus with a rather uniform depth along much of the tooth-bearing portion of the ramus. The anterior end of the ramus tapers quickly, leaving a tight curve on the anteroventral border. The ascending ramus is broad and similar to that of *Enhydrocyon*.

Dentition: The I3 is large relative to the I2, but is not as conspicuously enlarged as in *Enhydrocyon*. Although heavily worn, the upper incisors do not seem to have cingular cusps, which characterize those of *Enhydrocyon*. Both upper canines are missing, and their alveoli indicate the presence of a large canine. The P1 is absent, although the root of p1 still exists. The P2–3 are strongly con-
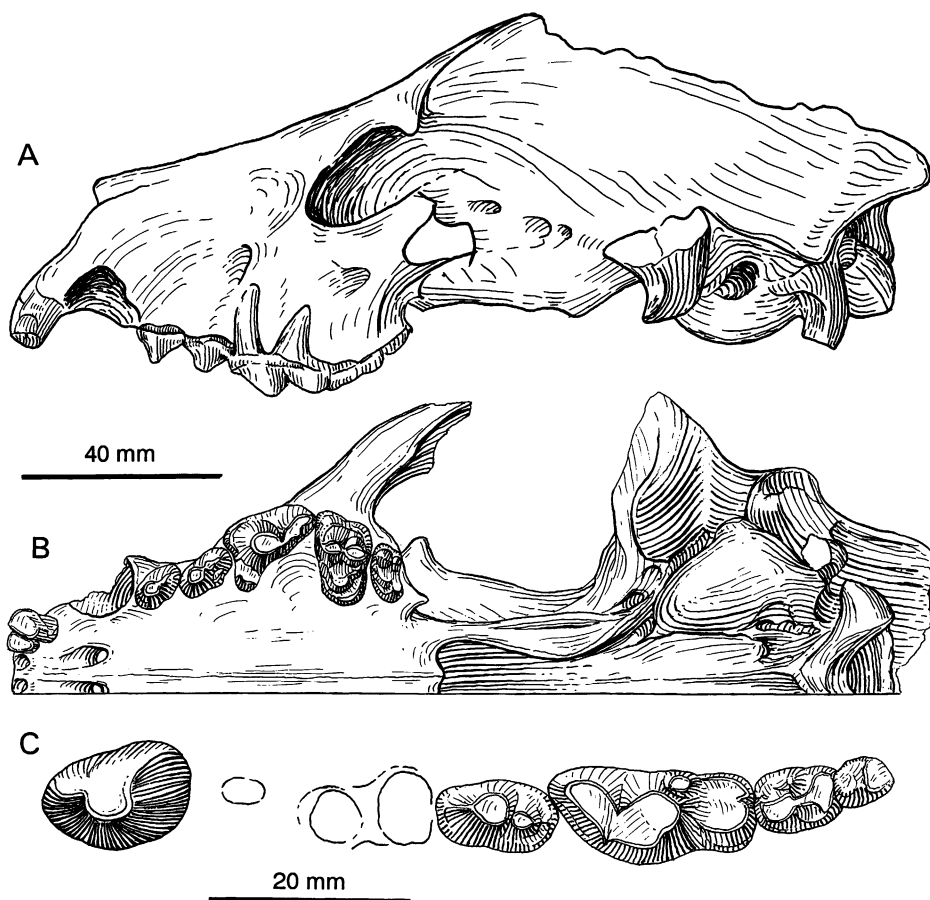
Fig. 23. Skull and lower dentition of *Cynodesmus martini*, new species, UNSM 25796, holotype. **A**, Lateral and **B**, ventral views of skull, and **C**, occlusal view of lower teeth. The partial zygomatic arch and part of the basicranial area are drawn from those of the right side. Illustrated by Raymond J. Gooris.

structed and imbricated. The P3 has a posterior accessory and cingular cusps, whereas the P2 has none. The P4 is broad and its protocone is anteriorly positioned; the protocones in *Enhydrocyon*, however, tend to be medially positioned. The M1 is almost an enlarged version of *Cynodesmus thooides*; it lacks such advanced features as enlarged parastyle, constricted waist, and encircling internal cingulum that are typically seen in *Enhydrocyon*. The M2 is mediolaterally broad and has rather laterally located paracone and metacone.

Lower incisors are not preserved. The c1 is robustly built; the wear on the medial side does not allow determination of the presence of ridges. Like its counterpart of P3, the p4 has a well-developed posterior accessory cusp

and a raised posterior cingulum. The m1 still has a distinct metaconid, as opposed to reduced metaconids in *Enhydrocyon*. The m1 talonid is worn flat, but seems to indicate the presence of an entoconid ridge approximately 1 mm wide lingual to the dominant hypoconid. The m2 also has a large protoconid and a small metaconid. Its talonid is mainly composed of a large hypoconid. A relatively large m3 is present.

DISCUSSION: *Cynodesmus martini* displays an interesting array of primitive and derived characters. It reaches to the size and proportion of an *Enhydrocyon*, and has derived cranial and dental structures such as short and broad rostrum, elongated postorbital region, high sagittal crest, robust premolars, etc. Indeed, if these structures were all coded as

independent characters, *C. martini* could easily have been placed within *Enhydrocyon* in the phylogenetic analysis by HENNIG86. Instead, most of the similarities between *C. martini* and *Enhydrocyon* are here treated as independent attempts by *C. martini* to evolve hypercarnivorous adaptations. Two key synapomorphies shared by *C. thooides* and *C. martini* support such a contention: a thick paroccipital process with a posterior keel and a transversely broadened M2, both characters of which are not seen in other hesperocyonines. In addition, *C. martini* has a fundamentally primitive dentition (except its robust premolars) in contrast to *Enhydrocyon*: lack of cingular cusps on upper incisors; distinct, anteriorly located P4 protocone; unconstricted waist on M1; internal cingulum not circling the anterior segment of the protocone on M1; still well-developed metaconid and entoconid on m1; and large m3. Taken singly, most of above dental characteristics may be dismissed as homoplasies or variations, but collectively, these features suggest a taxon best fitted as a sister-species of *C. thooides*. In fact, the dentition of *C. martini* best matches the holotype of *C. thooides*.

Sunkahetanka Macdonald, 1963

Mesocyon (Scott) Barbour and Schultz, 1935: 407.
Sunkahetanka Macdonald, 1963: 214.
Enhydrocyon (Cope) Tedford et al., 1985: 342.

TYPE SPECIES: *Sunkahetanka geringensis* (Barbour and Schultz) Macdonald, 1963.

INCLUDED SPECIES: Type species only.

EMENDED DIAGNOSIS: As its monotypic species.

DISTRIBUTION: As its monotypic species.

DISCUSSION: Macdonald (1963: 214) proposed the new genus *Sunkahetanka* for *Mesocyon geringensis* that was "a derivative of the *Mesocyon* line" and named a second species *S. pahinsintewakpa*. The many derived characters of *S. pahinsintewakpa* demonstrated in the present study suggest that it belongs to *Enhydrocyon*. A third species, *S. sheffleri* Macdonald, 1967, is now synonymized with *Cynodesmus thooides*. The genotypic species is thus all that remains in the genus.

Sunkahetanka geringensis (Barbour and Schultz, 1935)
Figures 24, 25

Mesocyon geringensis Barbour and Schultz, 1935: 407.
Sunkahetanka geringensis (Barbour and Schultz) Macdonald, 1963: 214 (in part excluding SDSM 53334). Macdonald, 1967b: 1. Macdonald, 1970: 58 (holotype only).
Enhydrocyon geringensis (Barbour and Schultz) Tedford et al., 1985: 342.

HOLOTYPE: UNSM 1092, complete skull (slightly crushed) and mandible with almost entire dentition and postcranial skeleton.

TYPE LOCALITY: "Gering Formation (lower Miocene), fifteen feet above the Brule, 400 feet west of the road in Redington Gap, near the center of the S.½, sect. 14, T.19 N., R.52 W., west of Bridgeport, Morrill County, Nebraska" (Barbour and Schultz, 1935). The basal "Gering" rocks in the vicinity of Redington Gap, which contains the small hypsodont leptauchenine *Sespia* (typical of the Gering Fauna), were placed in the Gering Formation by Vondra (1963), Vondra et al. (1969), and Martin (1973, 1974). These strata, now informally referred to as the Brown Siltstone beds, represent a gradual upward shift in grain size from siltstone to sandstone that are lithologically continuous with the underlying Brule Formation (Tedford et al., 1985) and are thus regarded as a unit of the White River Group. *Sespia* also occurs in the Brown Siltstone beds in the White River valley outcrops of northwestern Nebraska. Tedford et al. (1985, 1987) thus assigned the rocks containing *Sunkahetanka geringensis* at Redington Gap to the uppermost Brule Formation. The age of the holotype of *S. geringensis* is earliest Early Arikareean.

REFERRED SPECIMENS: From the Wounded Knee area and Big Badlands of South Dakota: SDSM 5667, partial left ramus with p3–m1, from SDSM V5360, Sharps Cutoff road in N½ of sect. 17, T. 39 N, R. 43 W, Shannon County, in middle of Sharps Formation, Early Arikareean; SDSM 53324, left ramus fragment with broken m1, from SDSM V5358, west side of Tibbets Ranch road in SE¼ of sect. 31, T. 40 N, R. 43 W and NE¼ of sect. 6, T. 39 N, R. 43 W, Shannon County, in middle of Sharps Formation, Early Arika-

reean; SDSM 54331, fragments of immature mandible with left c1–p1, m1–2, dp1–dp3, right c1, p2, p4, from SDSM V541, in NW¼, sect. 8, T. 39 N, R. 43 W, Shannon County, in middle Sharps Formation, Early Arikareean; YPM-PU 13602, complete right ramus with c1–m3, from Cedar Pass, near Interior, Jackson County, in a channel about 40–50 ft above a prominent white ash, Sharps Formation, Early Arikareean.

From the Arikareean of western Nebraska: CMNH 1275, fragments of mandible with left p4–m2 and right m1–3, from head of Warbonnet Creek, Sioux County, stratigraphy unclear.

EMENDED DIAGNOSIS: *Sunkahetanka geringensis* has two synapomorphies that distinguish it from *Cynodesmus*: more massive premolars that tend to be imbricated (char. 29) and reduced metaconid on lower molars (char. 43). In addition, *S. geringensis* possesses some subtle features that, collectively, can be used to differentiate it from *Cynodesmus* and *Mesocyon*: larger postorbital process; posteriorly extended nuchal crest, but not overhanging the occipital condyle; deep and laterally arched zygomatic arch; bulla narrowed anteriorly; slightly anteroposteriorly constricted M1 trigon; crowded lower incisors; and wider m1. In contrast to *Philotrox condoni*, *S. geringensis* has a smaller auditory bulla and a shallower ramus.

DISTRIBUTION: Following the scheme of Tedford et al. (1985), *Sunkahetanka geringensis* is now restricted to the topmost part of the Brule Formation in western Nebraska and the Sharps Formation of western South Dakota. Early Arikareean.

DESCRIPTION: The holotype, UNSM 1092, is still the best and certainly most complete material for the species. Barbour and Schultz's (1935) original description of *Mesocyon geringensis* consisted of a list of 13 characters that were used to contrast it with *M. coryphaeus*. A more detailed description is needed here to demonstrate its transitional nature between the more primitive *Mesocyon–Cynodesmus* and the derived *Philotrox–Enhydrocyon* clade.

Skull: Except for its more robust construction, the skull of *Sunkahetanka geringensis* is similar in size and proportions to *Cynodesmus* and *Mesocyon*. The relative length of the rostrum remains primitively short. The posterior process of the premaxillary is thick and long, stopping at the level of the anterior opening of the infraorbital foramen. The frontal portion of skull is slightly raised upward and the postorbital process of the frontal is strongly developed. The sagittal crest is slightly higher than in *C. thooides* but much lower than in *Philotrox* and *Enhydrocyon*. The nuchal crest is caudally extended but is less so than in *Philotrox* and *Cynodesmus martini* (i.e., the posterior tip of the nuchal crest does not overhang the occipital condyle). In posterior view, the lateral edge of the lambdoidal crest is slightly constricted in the middle as opposed to a more straight lateral edge in *Mesocyon* and *Cynodesmus*. The occipital condyle appears to be tilted upward partly as a result of the dorsoventral crushing of the skull. The fossa for rectus capitis dorsalis minor is present.

In lateral view, the upper incisors are recumbent. Barbour and Schultz (1935: 410) distinguished the robust zygomatic arches in "*Mesocyon*" *geringensis* from the slender ones in *M. coryphaeus*. The zygomatic arch in the type is deep, heavily constructed, and laterally expanded, a tendency continued in the *Philotrox–Enhydrocyon* clade. The relative length of the skull (behind the infraorbital foramen) to the length of rostrum remains primitively short in contrast to an elongated posterior part of the skull in *Enhydrocyon*.

In ventral view, the palate is slightly wider than in *Mesocyon coryphaeus* and *Cynodesmus thooides*. The posterior border of the palatine is straight without a small posterior process along the midline seen in *M. brachyops*, *M. coryphaeus*, and *C. thooides*. The auditory bulla is slightly longer than most individuals of *C. thooides* but is not as inflated as in *M. coryphaeus*. The anterior end of the bulla is slightly narrowed and begins to take the pear-shaped appearance of *Enhydrocyon*. A slender bony plate formed by the lateral extension of ectotympanic surrounds the posterior wall of the postglenoid foramen. Much of the paroccipital process was broken off from UNSM 1092. The mastoid process is ventrally expanded but not laterally inflated as in *Enhydrocyon*.

Mandible: The mandibles of the holotype and YPM-PU 13602 are similar to but with

a more robust construction than in *Cynodesmus*. The symphysis is more extensively ankylosed than in *Cynodesmus* but less so than in *Philotrox* (especially UCMP 76712). The coronoid crest is high and has a posterior deflection not seen in *Cynodesmus*. Corresponding to its nonelongated skull, the anteroposterior dimension of the masseteric fossa is not elongated as it is in *Enhydrocyon*. The internal ridge of the angular process in the type is more medially expanded than in YPM-PU 13602 and encloses a shallow, longitudinal pocket (the supero-internal facet of Gaspard, 1964: fig. 2) as the site of insertion of the superior medial pterygoideus muscle. The internal ridge of YPM-PU 13602, on the other hand, is not medially expanded and therefore does not have a pocketed supero-internal facet.

Dentition: Descriptions of the upper teeth are based on the holotype only. The overall appearance of the upper dentition in *Sunkahetanka geringensis* is rather robust, particularly the premolars. The upper incisors are aligned in a single row in contrast to the lower incisors that are staggered (see below). Individual cusps are difficult to recognize because of wear. The I1 and I2 are nearly equalsized, whereas I3 is twice as large. There are two low ridges on the upper canine: one on the posterior surface and one on the anteromedial surface. As observed by Barbour and Schultz (1935: 410), the premolars are stronger and more imbricated than in *Mesocyon coryphaeus* and *Cynodesmus thooides*. The P1 is a simple cone (single-rooted) and is considerably smaller than P2. The P2 and P3 are much larger than those of *C. thooides*. There is a small posterior accessory cusp on P2. The anterior ridge on the P2 principal cusp is delineated at the base into an incipient anterior cingular cusp. On the P3, however, the anterior ridge is not interrupted, reversing the general rule that posterior premolars tend to have more distinct cingular cusps. The P3 has a distinct, cusplike posterior cingulum. The P4 is also larger and more massive than that of *M. coryphaeus* and *C. thooides*. It has a small protocone closely appressed toward the base of the paracone in contrast to a more distinct protocone of P4 in many *C. thooides*. The cingulum anterior to the paracone is very weakly developed. The M1 has an enlarged

paracone and an elevated parastyle. The paracone–metacone ridge is slightly lengthened compared to that of *M. coryphaeus* and is raised high above the protocone. This lengthened paracone–metacone ridge thus contrasts with a narrow trigon basin—indication of *Enhydrocyon*-like upper molars. The internal cingulum primitively still forms the posteromedial corner of the protocone instead of encircling the protocone as in most *Enhydrocyon*. The M2 is relatively small and narrow as compared to that of *Cynodesmus*. Its slender outline follows less closely the M1 morphology, as it does in *Cynodesmus*.

In addition to the holotype, the lower dentition is supplemented by YPM-PU 13602 and more fragmentary specimens. As noted by Barbour and Schultz (1935: 410), the lower incisors on the holotype are mediolaterally compressed so that the i1 and i2 are staggered, a condition not seen in any other hesperocyonine. The lower canine is stout, short, and curves slightly backward. It has an indistinct posterior ridge and a more distinct anteromedial ridge. The lower premolars are strong and similarly imbricated as their upper counterparts. The p1 is single-rooted and has a faint posterior ridge. A shallow cingulum is present on p2–4 on both anterior and posterior sides. Although small, these anterior cingula on p2–4 are distinct and cusplike. The posterior cingula on p2–4, on the other hand, are not cusplike. Those on CMNH 1275 and YPM-PU 13602 have wider shelves. Posterior accessory cusps are generally distinct on p3–4. The m1 is slightly wider than that of *Cynodesmus thooides*. The metaconid is small but not as extremely reduced as in derived species of *Enhydrocyon*. The talonid is dominated by a hypoconid. The entoconid is reduced into a narrow, low ridge in SDSM 5667, 54331, and the type, and disappears in CMNH 1275. On YPM-PU 13602, however, the entoconid shelf is slightly wider and encloses a tiny basin. The m2 of the type is larger than any individual of *C. thooides*; however, this distinction does not hold when referred specimens of *Sunkahetanka geringensis* are taken into consideration. The m2 paracone is indistinct. Correlated with the reduced metaconid in m1, the base of the m2 protoconid is enlarged at the expense of the metaconid. The protoconid in the type has a

50 mm
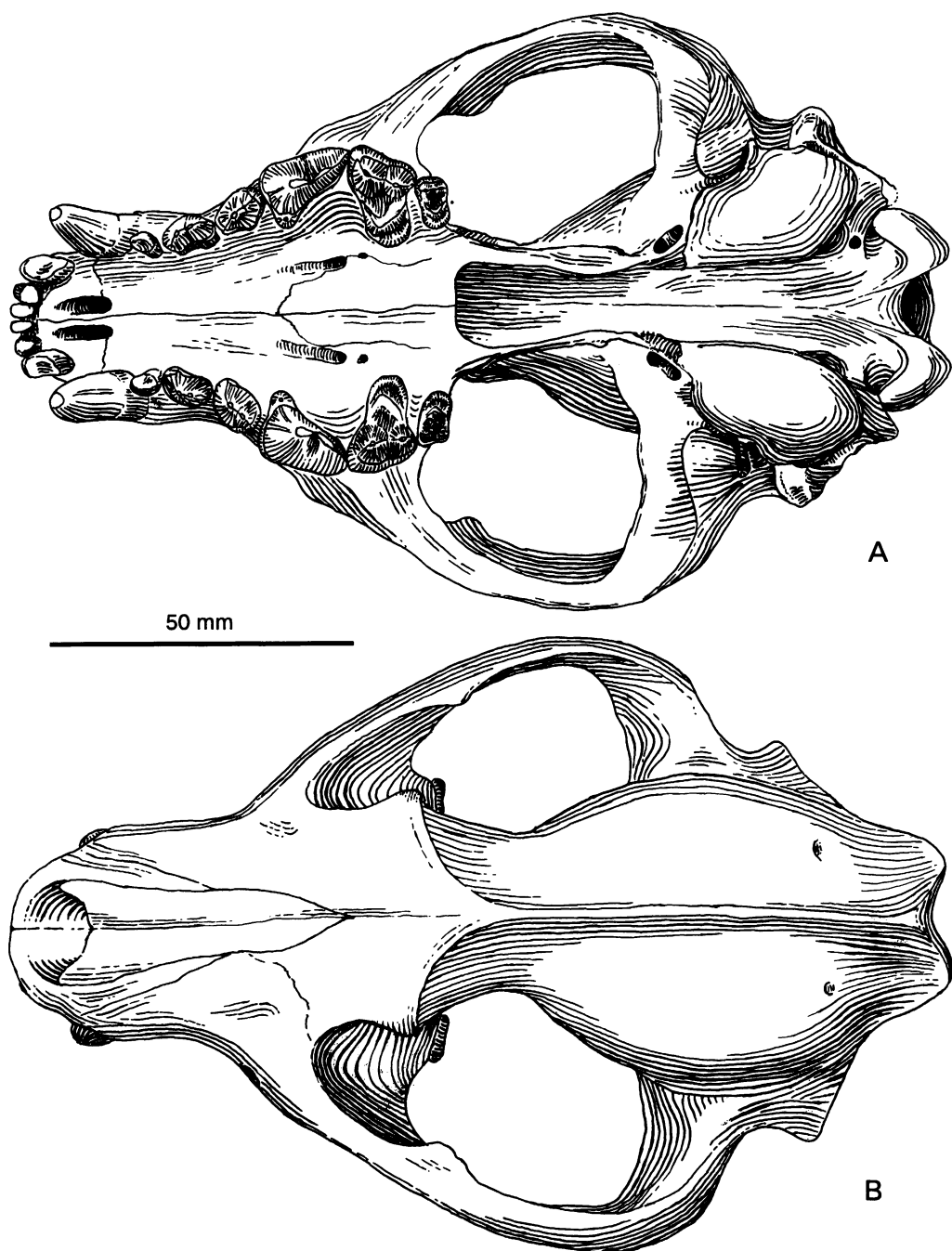
Fig. 24.   Skull of *Sunkahetanka geringensis*, UNSM 1092, holotype. **A**, Ventral view of skull; **B**, dorsal view of skull.

posterior ridge connecting posteriorly with the hypoconid. The m3 is oval or round-shaped and double- or single-rooted. On the type, the protoconid and metaconid are approximately equal in size and are connected by a transverse ridge. On CMNH 1275, however, there is a single large protoconid without a trace of metaconid, followed behind by a small hypoconid.

DISCUSSION: Barbour and Schultz (1935)
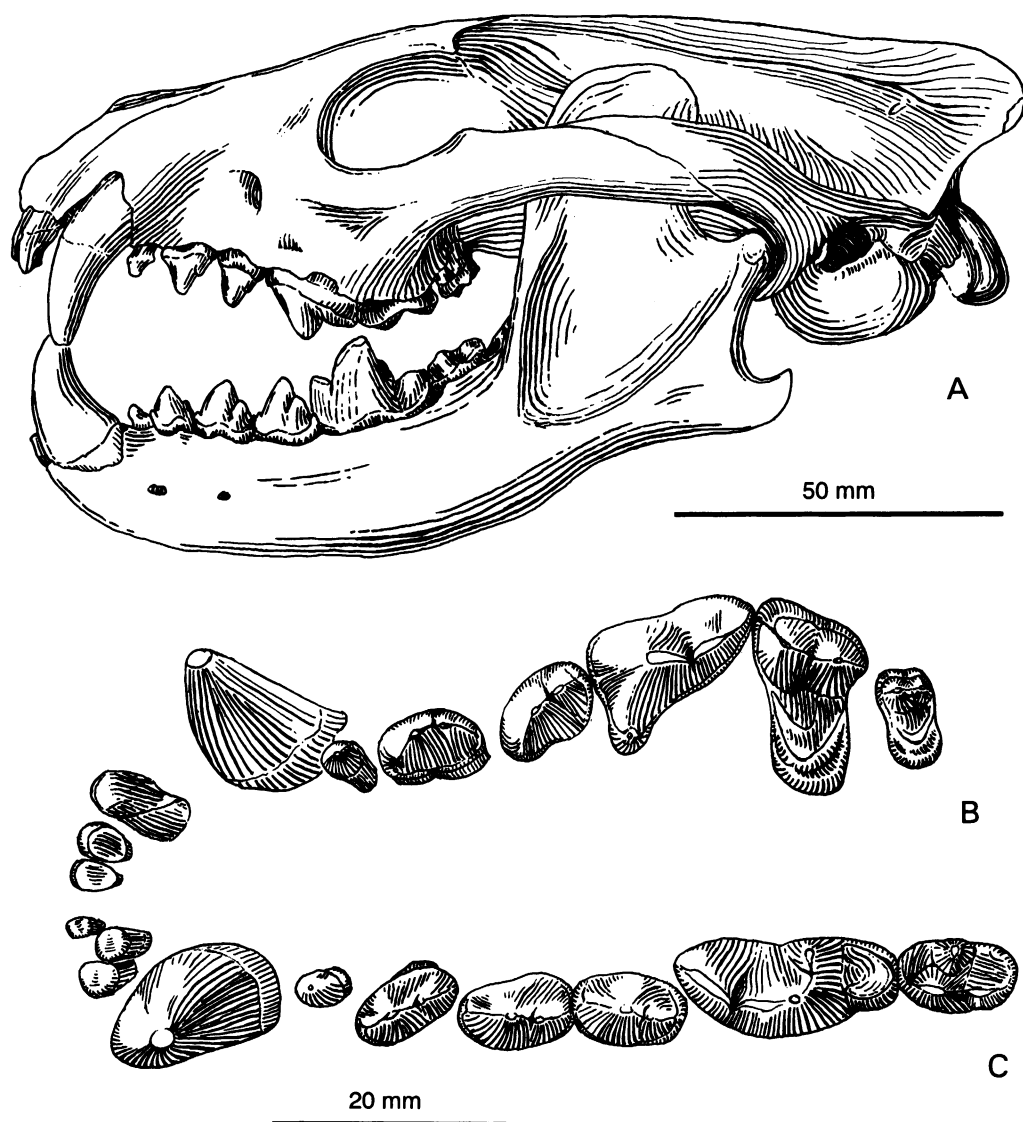
Fig. 25. Skull and details of dentition of *Sunkahetanka geringensis*, UNSM 1092, holotype. **A**, Lateral view of skull and mandible; **B**, occlusal view of upper dentition; and **C**, occlusal view of lower dentition (i1–2 drawn from those of right side).

listed 13 significant characters of *Mesocyon geringensis*, all in contrast to the type species *M. coryphaeus*. The majority of these characters represent a general tendency in *Sunkahetanka geringensis* toward a heavily constructed skull and robust dentition as compared to those of *Mesocyon* and *Cynodesmus*. *Sunkahetanka geringensis* shows definite signs toward the development of the massive dentition of *Enhydrocyon* and, to a lesser extent, *Philotrox*. Isolated teeth are difficult to distinguish between *S. geringensis* and *P. condoni*. However, its short posterior section of skull (relative to rostrum length), low sagittal crest, and shallow mandible indicate that *S. geringensis* is still a few short steps away from being a true *Enhydrocyon* (as has been suggested by Tedford et al., 1985: 342).

Macdonald (1963: 214) referred four SDSM specimens from the Wounded Knee South Dakota to *Sunkahetanka geringensis*. Later,

he (Macdonald, 1970: 58) included an additional six LACM specimens, also from Wounded Knee. The LACM specimens are far more complete and some can be clearly referred to *Philotrox* based on their skull characteristics. The fragmentary SDSM materials, however, are problematic, except for SDSM 53334, which is referable to *Cynodesmus thooides*. They are left in *S. geringensis* for lack of evidence to suggest otherwise.

Philotrox Merriam, 1906

Philotrox Merriam, 1906: 30.
Sunkahetanka Macdonald, 1970: 58.

TYPE SPECIES: *Philotrox condoni* Merriam, 1906.
INCLUDED SPECIES: Type species only.
EMENDED DIAGNOSIS: As its monotypic species.
DISTRIBUTION: As its monotypic species.

Philotrox condoni Merriam, 1906
Figures 26–28

Philotrox condoni Merriam, 1906: 30.
Sunkahetanka geringensis Macdonald, 1970: 58 (referred specimens from Sharps Formation only).

HOLOTYPE: UCMP 89, posterior part of skull and partial left ramus with i3–m3. Collected by L. H. Miller.
TYPE LOCALITY: UCMP loc. 819, Turtle Cove, Oregon, in Middle John Day beds (Merriam, 1906: 30), that is, Turtle Cove Member of John Day Formation (Fisher and Rensberger, 1972). Early Arikareean
REFERRED SPECIMENS: From John Day Formation, Oregon: UCMP 76712, nearly complete skull with left C1, left P2–M2 and right P1–M1 (the rest of the upper teeth are broken off with only their roots remaining), partial mandible with left i3–m3 and right p2–m3, articulated, nearly complete cervical vertebrae series (C1–C6), UCMP locality V-5955. Morgan locality, Site 3, John Day Formation, central Oregon.
From Wounded Knee area, Shannon County, South Dakota, Sharps Formation, early Early Arikareean (the correspondence of SDSM locality number to that of LACM follows Macdonald, 1970): LACM 5471, left maxillary fragment with C1, P2–M1, from

LACM loc. 1821 (= SDSM loc. V5359), "in gully on south side of Sharps Cutoff road in the SW. ¼ of sect. 9, T. 39 N., R. 43 W., near the middle of the Sharps Formation" (Macdonald, 1963: 160); LACM 5895, right maxillary fragment with P3–M1, locality same as above; LACM 9406, left ramus fragment with p3–4, from LACM loc. 1959 (SDSM loc. V544), "along bottom of canyon extending through the N. ½ of sects. 7 and 8, T. 39 N., R. 43 W., near the middle of the Sharps Formation" (ibid.: 161); LACM 13977, partial left ramus with broken c1–m1, from LACM loc. 1955 (= SDSM loc. V541), NW¼, sect. 8, T. 39 N, R. 43 W, middle Sharps Formation (ibid.: 160); LACM 15910, nearly complete skull with entire dentition, from LACM loc. 2005, northeast of Wolff Ranch Badlands, Sharps Formation; LACM 21642, nearly complete skull with left I1–C1, P3–M1 and right I1–C1, P2–M1, from LACM loc. 6898, Groom Ranch, Sharps Formation.
From Quiver Hill localities, Washabaugh County, South Dakota, Sharps Formation, early Early Arikareean: F:AM 63383, partial skull and mandible with badly worn and fragmentary left I3–M2 and right C1–M2, left c1, p3–m2 and right c1, p3–m1, from 1 mi north of Quiver Hill, 18 mi south of Kadoka, SE¼, sect. 17, T. 42 N, R. 35 W, 25 ft above the base of Rockyford Ash (First White Layer of M. F. Skinner fieldnotes); F:AM 63384, edentulous partial skull, from 0.25 mi east of Quiver Hill, in hard grey pitted siltstone, 105 ft above the base of the Rockyford Ash.
From Little Muddy Creek locality, southeast of Lusk, 20 mi south of Keeline and west of Spanish Diggings (see also comments in Referred Specimens of *Enhydrocyon pahinsintewakpa*), Niobrara County, Wyoming, Lower Arikaree Group: F:AM 54095, left maxillary fragment with P3–4.
EMENDED DIAGNOSIS: In contrast to the more primitive *Sunkahetanka geringensis*, *Philotrox condoni* has such derived features as an elongated postorbital region of skull (char. 3) and a correlated long masseteric fossa; a high sagittal crest with a cross section that is uniform in thickness; a strong, posteriorly overhung nuchal crest; a large bulla (more so in John Day individuals); an inflated mastoid process (char. 18); and wider premolars (char. 9). *Philotrox* can be distin-
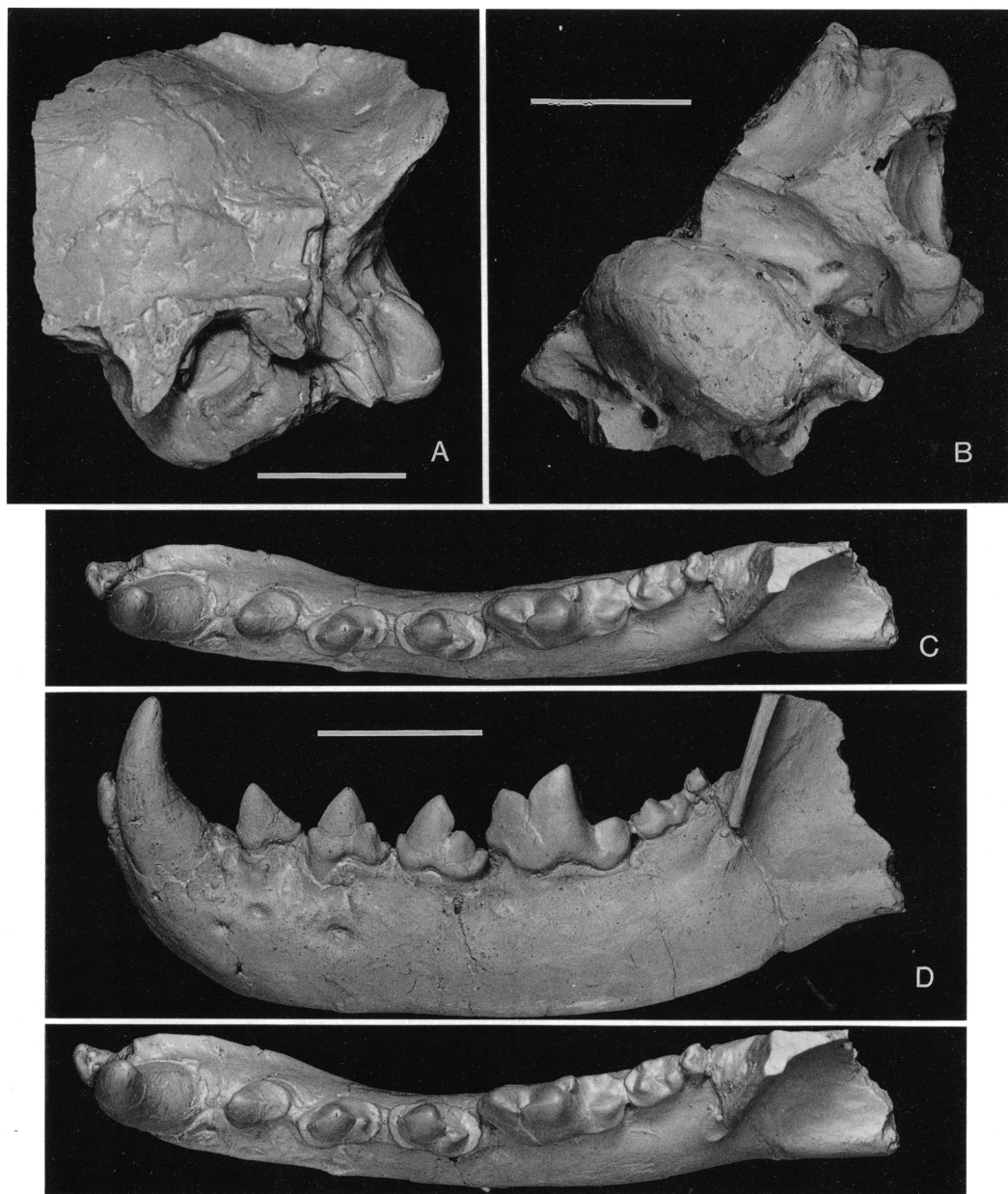
Fig. 26.   Skull and mandible of *Philotrox condoni*, UCMP 89, holotype. **A**, Lateral (reversed from right side) and **B**, ventral views; **C**, occlusal and **D**, lateral views of left ramus. Scales = 20 mm.

guished from *Enhydrocyon* by its lack of the derived characters listed in the diagnosis of the latter.

DISTRIBUTION: John Day Formation of central Oregon, Sharps Formation of Wounded Knee area, South Dakota, and Lower Arikaree deposits of eastern Wyoming. Early Arikareean.

DESCRIPTION: With the referred specimens in the present study, the skull and teeth of *Philotrox condoni* are almost completely known. Although the majority of the speci-

Fig. 27.   Skull of *Philotrox condoni*. **A**, Dorsal and **B**, ventral views of UCMP 76712. Scale = 30 mm.

mens of *P. condoni* are from the Sharps Formation of South Dakota, UCMP 76712 from the volcanoclastic deposits of the John Day Formation, with undistorted skull and nearly complete upper and lower teeth, is the best preserved specimen of this species.

Skull: Six skulls are examined in the present study: F:AM 63383, 63384, LACM 15910, 12642, UCMP 89, and UCMP 76712. The skull of UCMP 76712 is in excellent condition as is evidenced by the in situ preservation of a pair of stylohyoid bones. Together
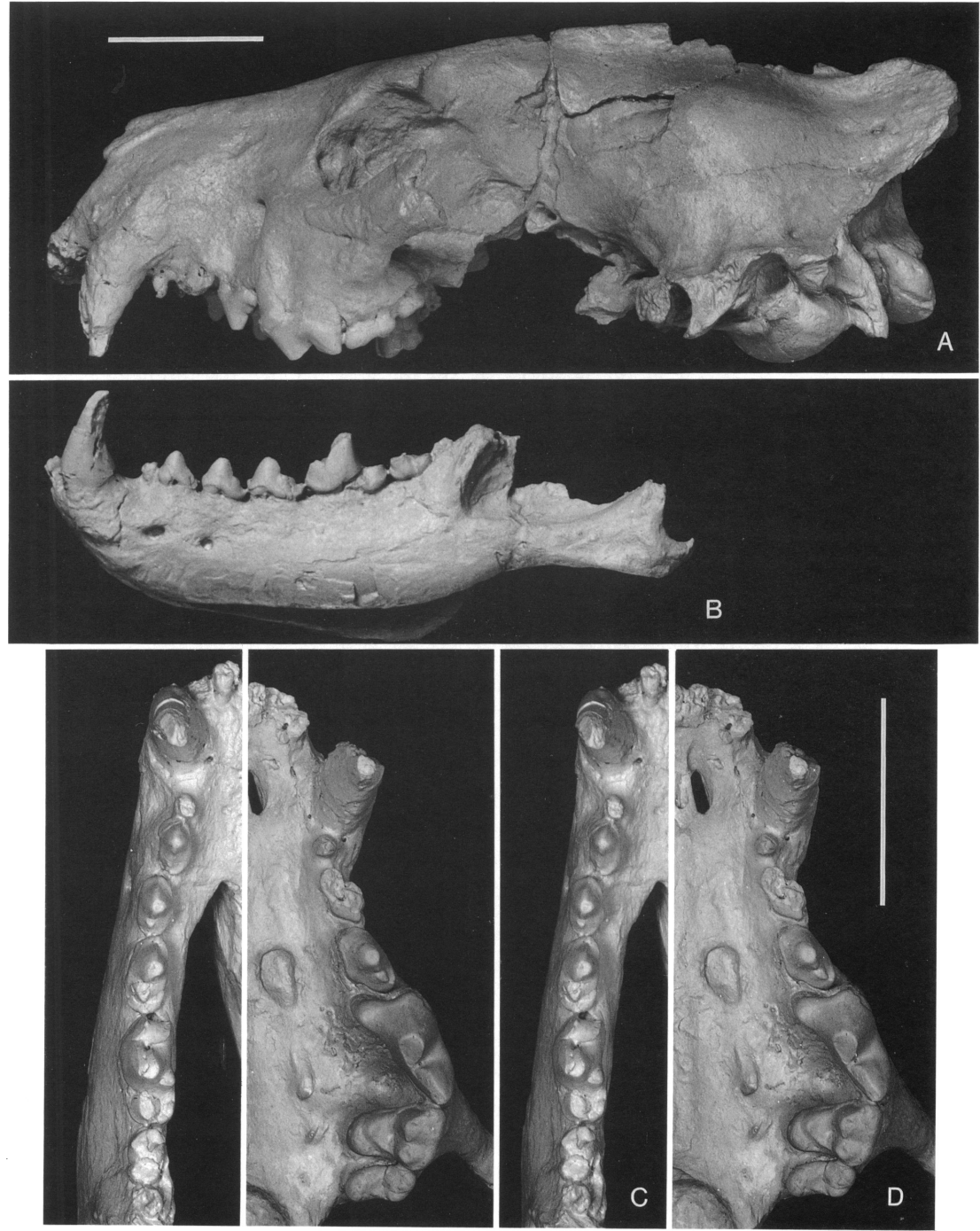
Fig. 28. *Philotrox condoni*. Lateral views of **A**, skull and **B**, mandible, and occlusal views (in stereo) of **C**, lower and **D**, upper teeth of UCMP 76712. Scales = 30 mm.

with other referred skulls, the cranial osteology of *P. condoni* is nearly completely known and a limited sense of variation can be derived from these materials.

The construction of the skull of *Philotrox condoni* shows many intermediate characteristics between the primitive *Sunkahetanka* and the more advanced *Enhydrocyon*. The relative length of the rostrum is short due to the elongated posterior part of skull. The premaxillary has a wide, long posterior process reaching to the level of the infraorbital foramen or beyond; in some individuals (UCMP 76712 and LACM 15910) it nearly touches the anterior process of the frontal. The anterior process of the frontal remains primitively wide at the base in all specimens in contrast to a much narrower frontal processes in *Enhydrocyon*. In F:AM 63383, the lateral border of the left frontal process is seen to be pinched by a sharp posteromedial angle of the maxillary, a characteristic of the more derived *Enhydrocyon*. The postorbital process of the frontal is strong, similar to that of *S. geringensis*. The postorbital constriction is shifted posteriorly due to the elongation of the postorbital region of the skull as compared to that in *Sunkahetanka*. The increased height of the sagittal crest (except in type) is another derived feature in *P. condoni* that suggests its affinity with *Enhydrocyon*. In most individuals, the cross-sectional thickness of the crest is maintained from the top to the base as opposed to a wider-based and tapering, low sagittal crest in *Sunkahetanka*. The nuchal crest is more strongly developed than in *Mesocyon*, *Cynodesmus thooides*, and *Sunkahetanka*. Its lateral wings are extended posteriorly to overhang the occipital condyle (more so in Wounded Knee specimens). The supraoccipital shield is deeply excavated by two large fossae divided in the middle by a vertical central ridge. This pair of fossae occupies almost the entire supraoccipital surface and are presumably for the attachments of the rectus capitis dorsalis major muscles (Evans and Christensen, 1979: 314; Davis, 1964: 169–170). The depth of the fossa appears to be correlated with the posterior extension of the nuchal crest. On UCMP 76712, there is also a pair of shallow pits below these large fossae and immediately above the foramen magnum for insertion of the rectus

capitis dorsalis minor muscle. This latter pair of rounded pits is widely present in *Mesocyon* through *Sunkahetanka*. Corresponding to the large fossa on the supraoccipital for the rectus capitis dorsalis muscle, the fossa for rectus capitis ventralis muscle is also strongly developed. On the basioccipital immediately medial to the posterior lacerate foramen, there is a pair of oval-shaped fossae for the insertion of the rectus capitis ventralis, which, in living *Canis*, originates from the ventral side of the atlas and functions to flex the atlanto-occipital joint (Evans and Christensen, 1979: 315–316).

In the lateral view, the forehead is rather flat. The rostral part of skull is deeper than that of *Sunkahetanka* (although how much of this is due to the dorsoventrally crushed skull of the type of *S. geringensis* is difficult to determine). The zygomatic arch, as is seen in complete right zygoma of F:AM 63383 and remainder basal parts of other skulls, is more laterally arched than in *S. geringensis*.

In the ventral view, the palate of *Philotrox* is longer and wider than that of *Mesocyon*, *Cynodesmus thooides*, and *Sunkahetanka*. On LACM 15910, the posterior palatine border extends approximately 6 mm behind the caudal border of M2, a common phenomenon in individuals with reduced or lost M2. The region between the posterior border of M2 and anterior border of tympanic bulla is significantly longer than in *Mesocyon* through *Sunkahetanka* (except for *Cynodesmus martini*). The outline of the auditory bulla begins to assume the typical pearlike shape in *Enhydrocyon* with a narrow anterior end (particularly in F:AM 63383). The bulla in the type is slightly more inflated than other specimens of the species, once again confirming the tendency for the John Day forms to enlarge their bullae. There is no or only a slight trace (LACM 21642) of a laterally extended tube of the external auditory meatus. The postglenoid foramen is fully enclosed posteriorly by a laterally extended ectotympanic lip in contrast to the exposed posterior half of the foramen in *Enhydrocyon*. The paroccipital process is strong, elongated, and ventrally directed. It is still rodlike, without apparent lateral extension as occurs in *E. pahinsintewakpa* and more derived forms. The extent of fusion between the paroccipital

process and the caudal entotympanic is the same as in *Mesocyon* through *Sunkahetanka*. Although still not fully inflated, the mastoid process begins to look more like that in *Enhydrocyon*. It is smooth-surfaced and has a vertical ridge on its posterolateral side. The mastoid process is still beneath the basal rim of the lambdoidal crest, but has grown fuller than in *S. geringensis*. Despite its many advanced features, F:AM 63383 has a very uninflated mastoid process (see additional comments in Discussion). In fact, its lateral facet has receded approximately 3 mm beneath the basal lambdoidal crest, the kind of mastoid reduction only seen in advanced species of *Osbornodon*.

In UCMP 76712, there is a pair of well-preserved stylohyoid bones, in situ, near the lateral wall of the ectotympanic bone, immediately beneath the external auditory meatus. The stylohyoid on the left side is more complete than the right one. It is a slender element gradually tapering toward the anterior end. The blunt posterior end presumably articulates with the small cartilaginous tympanohyoid, which in turn articulates with the medial base of the mastoid process. The stylohyoid of *Philotrox condoni* is less sharply curved in the middle than in domestic dogs illustrated in Evans and Christensen (1979: 149 and fig. 4–36).

Mandible: The mandibles are slightly more heavily constructed than in *Sunkahetanka geringensis*. The mandibular symphysis is extensively ankylosed in UCMP 76712, but remains separated in F:AM 63383 despite the older ontogenetic stage of the latter (extremely worn teeth). In the type, the lower border of the posterior segment of the horizontal ramus elevates dorsally as also seen in most *Enhydrocyon*. Corresponding to the extended postorbital region of the skull, the masseteric fossa is also anteroposteriorly elongated. The free end of the angular process has a short hook tilting upward. The internal ridge is completely preserved in F:AM 63383 and is rather medially extended. In the lateral side of the angular process, UCMP 76712 lacks a prominent posterior tubercle, which, however, was present in F:AM 63383 and the other species of the genus. The angular process of UCMP 76712 also has a rather sharp ventral edge in contrast to the flattened appearance in F:AM 63383 and in *Enhydrocyon*.

Dentition: The upper incisors in LACM 21642 are the least worn and show no sign of internal basal cusps present in *Enhydrocyon pahinsintewakpa* and more advanced *Enhydrocyon*. The I1–2 are otherwise similar to other *Enhydrocyon* in having a main cusp and two smaller accessory cusps on each side. The I3s in all specimens examined are considerably larger than the I1–2, but are too worn to distinguish the cusp patterns. The canine has relatively smooth surfaces with only a vague posterior ridge. The degree of crowding of the upper premolars is similar to *Sunkahetanka*, with only slight imbrication of some premolars to accommodate each other. The premolars are slightly longer than in *Sunkahetanka*. There is still a single-rooted P1 in *Philotrox condoni*, in contrast to its loss in *Enhydrocyon*. The P1 is small and usually in close contact with the P2. The P2 has a simple principal cusp, with UCMP 76712 showing a shallow notch in the middle of the posterior ridge. The P3 has a well-developed posterior accessory cusp, but still has no anterior or posterior cingular cusp. The P4 is little different from that of *Sunkahetanka* with the exception of its slightly larger size. Its protocone is reduced and close to the base of paracone. A vague anterior ridge is present in front of the paracone. In F:AM 54095, the only referred specimen from eastern Wyoming, there is a small but distinct parastyle at the base of the anterior ridge of the paracone.

The M1 of most *Philotrox condoni* retains the primitive structure and is indistinguishable from that of *Sunkahetanka*. Compared to *Mesocyon* and *Cynodesmus*, the M1 has a more prominent parastyle, slightly increased labial length (LM1), and a narrower waist across the trigon—the initiation of a trend toward an hourglass-shaped M1 in *Enhydrocyon*. The M2 of LACM 15910 is considerably decreased in size relative to that of its M1. There is a large variation in the relative size of the upper molars between the John Day and the Great Plains individuals. The upper molars from the Plains specimens are similar in proportion to *Sunkahetanka*, whereas UCMP 76712 of the John Day Formation has relatively smaller M1 and larger

M2. The direction of this latter variation is the opposite from what is generally shown in *Enhydrocyon*, that is, the reduction of M2. The M1 in UCMP 76712 also tends to be more quadrate due to a shortened mediolateral width (WM1) and a less swollen paracone corner. Its M1 cusps are lower and have less contrast between the high paracone–metacone ridge and the low protocone. The M2 of UCMP 76712 is large due to its elongated width and expanded internal cingulum. The shape and size of M1 and M2 in the rest of the specimens are intermediate between the two extremes represented by UCMP 76712 and LACM 15910.

The lower incisors are closely spaced in UCMP 76712 with a slight indication that i2 is pushed toward the lingual side in contrast to the considerably displaced lower incisors in the type of *Sunkahetanka geringensis*. The left i2 in UCMP 76712 is well preserved enough to show a shallow groove that indicates a bicuspid tooth. The i3 on UCMP 89 has a single main cusp accompanied by a distinct accessory cusp low on its lateral side. The lower canine has a crenulated surface with two ridges, one on the anterolingual side and another on the posterolingual side; neither is as distinct as in *S. geringensis*. The lower premolars are very similar in size and shape to those of *S. geringensis*. The absence of the p1 on UCMP 89 was viewed by Merriam (1906) as indicating normal dentition, taking into consideration the "large" p2 and its closeness to the canine (diastemata between p2 and c1 less than 3 mm), and there is no indication of a porous bony surface on the diastemata to suggest loss and fusion of root canal of p1 during life. The p1 on UCMP 76712 is reduced to a small peg. The large size of the p2 in the type was partly due to a matrix-filled breakage across the main cusp. Elimination of the matrix-filled gap on the type has resulted in a p2 (approximately 1 mm shorter) that is still larger than but much closer to that of *S. geringensis*. The p2 has a single main cusp without additional cuspule at the posterior base as in *S. geringensis*. The p3 has a small posterior accessory cusp; in addition, it has an incipient cingular cusp both anteriorly and posteriorly. The accessory and cingular cusps are much stronger in p4. There is very little difference between the lower molars of *S. geringensis* and *Philotrox condoni*. The reduction of the metaconid of m1 on *P. condoni* is similar to that in *Sunkahetanka* and is far from the reduced state in advanced *Enhydrocyon*. Occupying nearly one-third of the total talonid width, the entoconid shelf of *P. condoni* is wider than in *Sunkahetanka*. In the m2, the protoconids are the dominant cusps and are slightly more anteriorly positioned than the metaconids. The metaconids, although smaller, are still distinctly present. The m3s in all specimens are broken and are approximately the same size as that of *Sunkahetanka*.

DISCUSSION: Except for several referred ramal fragments (Thorpe, 1922a) (presently referred to *Mesocyon coryphaeus*), *Philotrox condoni* has received no attention since its establishment at the beginning of this century. The incomplete nature of the type is obviously partly responsible. Merriam (1906) suggested that *P. condoni* "shows considerable resemblance to the short-faced dogs" such as the "John Day three genera, *Oligobunis*, *Hyaenocyon*, and *Enhydrocyon*," however, "no one of which corresponds closely to the form under discussion." Indeed, *P. condoni* shows trends (high sagittal crest, elongated posterior section of skull, and enlarged mastoid process) toward the eventual emergence of *Enhydrocyon*. Despite a relatively low sagittal crest in the type, those on the rest of the referred skulls are all very high. The loss of the p1 in the type, on the other hand, is more derived than the rest of the sample.

UCMP 76712 has a peculiarly transversely elongated M2 as contrasted to a relatively shortened M1. Such variation can also be observed in *Enhydrocyon pahinsintewakpa* (e.g., SDSM 7961, which has a similarly proportioned M1 [but M2 is lost] as that of UCMP 76712). F:AM 63383 furnishes an example of an intermediate individual between *Philotrox condoni* and *E. pahinsintewakpa*. It has such *Enhydrocyon* characteristics as a laterally pinched anterior process of frontal (on the left side), a high sagittal crest, an extended nuchal crest, a laterally expanded zygomatic arch, and presence of a prominent posterior tubercle on the angular process. On the other hand, F:AM 63383 has a large number of primitive features that indicate its

identity with *P. condoni*: a wide base of anterior process of frontal (on the right side); a rodlike paroccipital process (seen from the remaining basal parts); an uninflated mastoid process (it is more receded than even the more primitive *Sunkahetanka*); postglenoid foramen enclosed posteriorly by ectotympanic lip; shallow, slender mandible; presence of a P1 and p1; small premolars; short upper and lower carnassials; and a relatively unreduced m1 metaconid.

Enhydrocyon Cope, 1879

Enhydrocyon Cope, 1879a: 56.
Hyaenocyon Cope, 1879c: 372.
Sunkahetanka Macdonald, 1963: 214, in part.

TYPE SPECIES: *Enhydrocyon stenocephalus* Cope, 1879.

INCLUDED SPECIES: *Enhydrocyon stenocephalus* Cope, 1879; *E. pahinsintewakpa* (Macdonald, 1963); *E. crassidens* Matthew, 1907; *E. basilatus* Cope, 1879; *E. sectorius* (Cope, 1883), nomen vanum.

EMENDED DIAGNOSIS: *Enhydrocyon* is the terminal genus culminating from a series of more primitive stem genera: *Mesocyon, Cynodesmus, Sunkahetanka,* and *Philotrox.* The genus *Enhydrocyon* acquired a number of synapomorphies that easily distinguish it from the above genera: laterally pinched anterior process of frontal (char. 2); postglenoid foramen not covered by a lateral ectotympanic lip (char. 13); laterally expanded paroccipital process (char. 16); hypertrophied mastoid process (char. 18); presence of internal cusps on upper incisors (char. 25); enlarged I3 (char. 26); loss of P1 and p1 (char. 28); elongated carnassials (char. 34); elevated paracone of M1 (char. 36); anterior extension of M1 internal cingulum to encircle protocone (char. 38); and loss of metaconid on lower molars (char. 43).

DISTRIBUTION: Materials of *Enhydrocyon* are presently known in the northern Great Plains in western Nebraska, western South Dakota, and eastern Wyoming, and in the Columbia Plateau of central Oregon. There is an isolated occurrence in the Canyon Ferry area (Missouri River valley) of western Montana (see Discussion of *E. basilatus*). Species of *Enhydrocyon* span the entire Arikareean land mammal age.

DISCUSSION: In his original description of the genus, Cope (1879a: 56) remarked about the otterlike characteristics of *Enhydrocyon*: "The dentition of this genus refers it to the Canidae, but the form of the skull resembles that of *Putorius vison* and *Lutra.*" The elongated skull behind the orbit is certainly one of the important characteristics of this lineage, which is actually acquired in the more primitive *Philotrox.* The similarity between *Enhydrocyon* and some mustelids is not limited to cranial proportions; the M1 of *Enhydrocyon* also approaches that of mustelids in having an internal cingulum surrounding the protocone. The overall dentition of *Enhydrocyon*, however, is considerably more hypercarnivorous than that of most mustelids.

The genus *Enhydrocyon* became far better known when Matthew (1907) established the Lower Rosebud species *E. crassidens*, based on a nearly complete skeleton. Comparing this skeleton with that of *Daphoenus vetus*, Matthew concluded that "The characters of the skeleton confirm Professor Cope's [1883] view of the affinities of *Enhydrocyon*, ... It is an aberrant type of the Canidae without marked relationship to any other family. Its nearest relative among the Canidae is probably *Temnocyon* of the John Day, which has also the heel of m_1 and trigonid and heel of m_2 trenchant instead of basin shaped ...." Matthew (1930) further elaborated his view of dichotomous developments of trenchant versus basined talonids in fossil Canidae (see History of Study).

Loomis (1931) also placed great importance on the structure of the m1 talonid, and distinguished eight major groups of "Miocene dogs" on the basis of carnassials and the M1. He was impressed by the hourglass-shaped M1 (constricted trigon basin region) in *Temnocyon venator* and *T. wallovianus* (both included in *Paraenhydrocyon wallovianus* in the present study) and placed them in *Enhydrocyon.* Loomis derived the *Enhydrocyon* group from *Brachycyon* Loomis (presently recognized as an amphicyonid carnivoran), which in turn was derived from *Daphoenus* Leidy (another primitive amphicyonid of North America), on the basis of their trenchant talonids on m1. However, when other morphologies are taken into con-

sideration (e.g., the form of mandible, paroccipital process, premolars, etc.; see description of *Paraenhydrocyon*), the similarities of the molars between *P. wallovianus* and species of *Enhydrocyon* are clearly the result of convergence.

Macdonald (1963: 214) assigned his new species *S. pahinsintewakpa* to *Sunkahetanka* based on his belief that the newly recognized genus (type species *S. geringensis*) possessed massive cheek teeth "with premolars greatly expanded owing to thickening of cingula," which is practically the only diagnostic character for *Sunkahetanka*. Due to the considerably enlarged sample size in the present study, *S. pahinsintewakpa* is now known to possess all the advanced features of *Enhydrocyon*. *Enhydrocyon pahinsintewakpa* thus is more derived than *S. geringensis*. The thickening of the premolars merely represents one of many character transformations from *Cynodesmus* to *Enhydrocyon*.

Within *Enhydrocyon*, the Great Plains species, *E. pahinsintewakpa* and *E. crassidens*, appear to be more primitive than the John Day forms, *E. stenocephalus* and *E. basilatus*. The John Day clade is mainly recognized because of its more inflated auditory bulla. Consequently, the enlargement of carnassials and reduction of M2/m3 in both *E. crassidens* and *E. basilatus* must be regarded as independent developments in view of the present phylogeny (fig. 64).

Enhydrocyon stenocephalus
Cope, 1879
Figures 29, 30

Enhydrocyon stenocephalus Cope, 1879a: 56; 1883: 245; 1884: 935. Merriam, 1906: 5. Merriam and Sinclair, 1907: 184. Matthew, 1907: 189. Thorpe, 1922a: 174. Macdonald, 1963: 217.
Enhydrocyon oregonensis Thorpe, 1922a: 173. Macdonald, 1963: 217.

LECTOTYPE: AMNH 6902, cranial fragments of an immature individual with left upper and lower jaw fragments with C1, erupting P3–4, p4–m2, and an isolated I1 or I2. Collected by Charles H. Sternberg.

Two specimens (AMNH 6901 [see Referred Specimens] and 6902) were described

in the original publication (Cope, 1879a: 56) of *Enhydrocyon stenocephalus*. Cope, however, did not expressly designate a type. Matthew (1907: 189) fixed the type as AMNH 6902 because its dentition was described first under the subtitle of "specific characters." Matthew further designated AMNH 6901 as a paratype.

TYPE LOCALITY: The type was collected "in the Oregon White River beds of the John Day River region" (Cope, 1879a: 57). The specimen was labeled, in the AMNH tag, as from "the Cove" (i.e., Turtle Cove), a common usage for early collectors. As mapped in Fisher and Rensberger (1972), the locality Turtle Cove is in sects. 2 and 11, T. 11 S, R. 25 E, Grant County, Oregon. The Turtle Cove Member (sensu Fisher and Rensberger, 1972), extensively exposed in the Turtle Cove area, is the thickest part of the John Day Formation and is well known for its abundance of fossil vertebrates. In the absence of further information, AMNH 6902 is here assumed to be from the Turtle Cove Member, Early Arikareean.

REFERRED SPECIMENS: From the Turtle Cove Member of John Day Formation, Grant County, Oregon: AMNH 6901, complete skull with nearly complete yet badly worn teeth (right P4 and left M2 missing), a paratype of *Enhydrocyon stenocephalus* in Matthew (1907: 189), presumably from the same general region where the holotype was collected; USNM 7745, partial skull with right M1 (endocast figured in Radinsky, 1973: fig. 3); YPM 12730, partial anterior skull with left I1–2, C1, P3–M2 and right I1–2, P2–M2, holotype of *E. oregonensis* Thorpe, 1922.

EMENDED DIAGNOSIS: As the genotypic species, *Enhydrocyon stenocephalus* possesses the typical *Enhydrocyon* cranial proportions with an elongated postorbital region of skull and a high sagittal crest. In addition, it has all of the synapomorphies of the genus (listed in diagnosis of *Enhydrocyon*) that can be used to differentiate it from the more primitive stem groups of *Mesocyon*, *Cynodesmus*, *Sunkahetanka*, and *Philotrox*. *Enhydrocyon stenocephalus* further shares with *E. basilatus* the following derived features that can be used to distinguish them from *E. pahinsintewakpa* and *E. crassidens*: a more rounded and in-

flated bulla (char. 9), a uniformly thickened internal cingulum around protocone of the M1, and a raised protoconid relative to metaconid in m2. Compared to *E. basilatus*, *E. stenocephalus* primitively lacks a lateral expansion of the paroccipital process, a deep notch between mastoid and paroccipital processes, large premolars and carnassials, and retains a small metaconid of m2.

DISTRIBUTION: All four specimens of *Enhydrocyon stenocephalus* are assumed to have been collected from the Turtle Cove Member of the John Day Formation in central Oregon. It is difficult to ascertain the precise stratigraphic level of these specimens, and *E. stenocephalus* is thus assumed to occur in the Early Arikareean of central Oregon.

DESCRIPTION: The present knowledge of *Enhydrocyon stenocephalus* represents a composite from four specimens. Together they make up most of the cranial and dental elements needed for comparison with other taxa. For most of the dental morphology, however, direct comparison among the three specimens is difficult due to their missing or heavily worn teeth. Obviously, this description is critically dependent upon the correct assignment of these specimens whose dentitions are, for the most part, mutually incomparable.

Skull: The single nearly complete skull (AMNH 6901) described by Cope (1879a, 1884) is still the best cranial material available. It is supplemented by the more fragmentary skull of USNM 7745 and anterior half skull of YPM 12730. AMNH 6901 inspired Cope's original comparison of *Enhydrocyon* with short-faced otters. The snout is of a rather massive construction, which is short, broad, and deep. The nasals are broadened in their anterior segment. The posterior process of the premaxillary is thick and extends posteriorly nearly to the level of the infraorbital foramen. The anterior process of the frontal is short and slender and shows a sharply pinched lateral maxillary/frontal suture typical of the genus (fig. 58). The size of the postorbital process varies from a small tubercle in YPM 12730 (a young adult whose permanent dentition is fully erupted but not worn) to a prominent process in AMNH 6901, a much older individual. The skull of *E. sten-*

ocephalus is elongated in the postorbital region between the infraorbital foramen and bulla, which results in the lengthening of the zygomatic arch, the distance between the postorbital process and the postorbital constriction, and the anterior part of the braincase. The sagittal crest is about 10 mm high in AMNH 6901 with uniform thickness like that of *E. pahinsintewakpa*. The nuchal crest is posteriorly extended but not beyond the occipital condyle. Its two wings lateral to the inion are also less extended than in *E. pahinsintewakpa*. A low central ridge is present on the supraoccipital shield.

In lateral view, there is a shallow depression just in front of the orbital rim of the lacrimal bone, marking the posterior extent of attachment of the levator nasolabialis muscle (Evans and Christensen, 1979: 280). There is a slender tubercle, probably composed of lacrimal (suture not distinctly shown in AMNH 6901 and YPM 12730), on the anterior rim of the orbit. The infraorbital foramen is round with a diameter of 5 mm. *Enhydrocyon stenocephalus* shares with *E. basilatus* a triangular pterygoid wing in contrast to a more gently curved ventral border in *E. pahinsintewakpa* and *E. crassidens*.

In the basicranium, AMNH 6901 has one of the most inflated bulla among hesperocyonines. In the lateral view, its anterior end lies in front of the posterior wall of the glenoid fossa. On USNM 7745, however, the bullae are far less inflated, and they may have been somewhat flattened. The ectotympanic sends a small process anteriorly to the posterior wall of the postglenoid process, but stops before the postglenoid foramen. The paroccipital process in AMNH 6901 is broken on both sides. As suggested by the remaining basal parts, it is laterally extended into a blade. The base of the paroccipital process extensively cups the posterior wall of the bulla. The well-inflated mastoid process, typical of *Enhydrocyon*, extends beyond the rim of the basal lambdoidal crest. The lateral face of the mastoid process has a vertical ridge converging toward a ventral tip. On the basioccipital, the area immediately medial to the posterior lacerate foramen is excavated for attachment of the rectus capitis ventralis muscle.

Mandible: The left ramal fragment of the

Fig. 29.   Skull of *Enhydrocyon stenocephalus*. **A**, Dorsal and **B**, ventral views of AMNH 6901. Scale = 30 mm.

type, AMNH 6902, is still the only known specimen of mandible. The horizontal ramus of AMNH 6902 is very shallow, clearly due to its young age, as evidenced by its erupting p3–4.

Dentition: Because of the fragmentary nature of the holotype and the extreme wear on the teeth of AMNH 6901, few teeth in all four specimens of *Enhydrocyon stenocephalus* are directly comparable with one another.
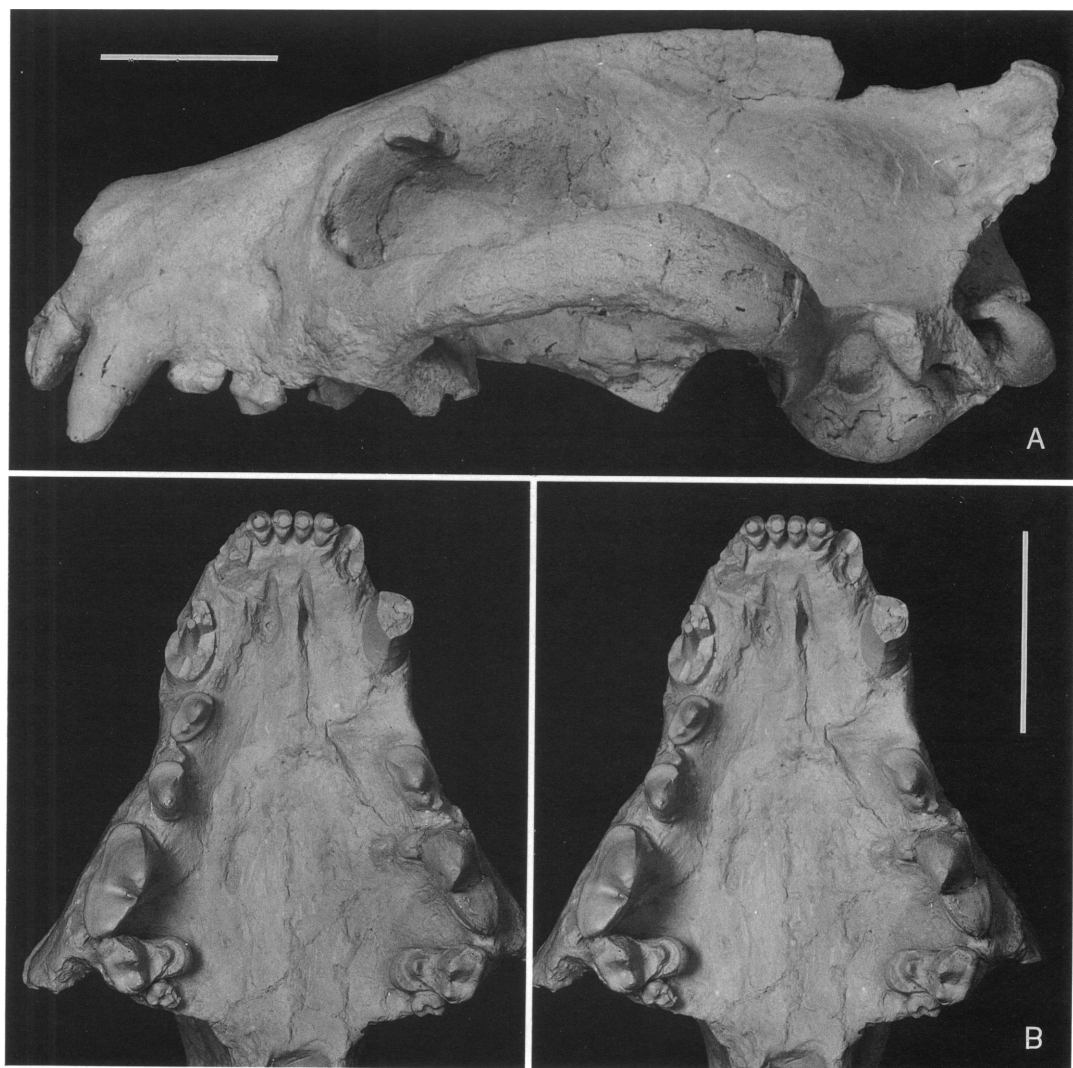
Fig. 30. Skull and upper teeth of *Enhydrocyon stenocephalus*. **A**, Lateral view of AMNH 6901, and **B**, occlusal view (in stereo) of upper teeth, YPM 12730. Scales = 30 mm.

The resulting description is thus necessarily a composite one. *Enhydrocyon stenocephalus* has a dental formula of 3/3 1/1 3/3 2/2(3). The loss of P1 (and presumably p1; that part of mandible is not preserved) is a character shared with all species of *Enhydrocyon*. The presence of m3 cannot be ascertained because of breakage behind the m2. An m3 is probably small, if present.

Upper teeth on AMNH 6901 are too worn to yield much detail. The present description of the upper teeth is therefore mainly based on YPM 12730 and the erupting P2–3 of the type. The I1–2 have a main cusp and an accessory cusp on each side of the incisors. The accessory cusps are lower (those in the lateral side are lower still) than the principal cusp. Thorpe (1922a) described in YPM 12730 a pair of internal cingular cusps on the lingual side of the main cusps near the base of I1 and I2 (fig. 62). Thorpe's observation is further confirmed by an isolated left I1 or I2 in AMNH 6902. The distribution of these complex incisors is more extensive than could be realized when Thorpe made his observations. The internal cusps are now known to be pres-

ent in *E. pahinsintewakpa* (F:AM 25424 and 129097) and *E. crassidens* (F:AM 27560 and 54070). The upper canines are all broken or badly worn so that their full length is not known. Those on YPM 12730 (the size of a female) have a distinct anterior and posterior ridge. The P1 is absent in all specimens examined. The P2 in YPM 12730 is more reduced than that in AMNH 6901 and 6902. It has a distinct posterior accessory cusp, which is further enlarged on P3, and has a vaguely defined cingulum behind the posterior accessory cusp. The P3 has an anterolingual bulge at the base of the principal cusp; its posterior cingular cusp is not clearly defined, as is the case in all *Enhydrocyon*. The P4 remains primitively short and is about the same size as that of *E. pahinsintewakpa*. Its protocone, however, is not extended anteriorly as in *E. pahinsintewakpa*. The M1 is small relative to the P4. Its paracone is enlarged at the expense of the metacone. The waist area at the trigon basin is slightly constricted so that the outline of M1 assumes the hourglass shape typical of the genus. The protocone is surrounded by an internal cingulum of uniform thickness. M2 varies from being small in YPM 12730 (less than 5 mm in transverse distance but double-rooted) to that of a primitively elongated (transversely) M2 with two roots in AMNH 6901. The reduced M2 in YPM 12730 has a peculiar quadrate outline with small, equal-sized paracone and metacone, and a protocone that is positioned close to the paracone–metacone ridge. The internal cingulum is completely absent from the M2 of YPM 12730.

The type is still the only specimen with lower dentition preserved. The lower premolars are more stoutly constructed than those of *Philotrox* but similar to those of *E. pahinsintewakpa*. Both p3 and p4 have distinctly developed posterior accessory cusps and small posterior cingular cusps. Both of these cusps are more enlarged in the p4, which also has an additional anterior cingular cusp.

The lower molars of *Enhydrocyon stenocephalus* have more reduced metaconids and entoconids than those in *E. pahinsintewakpa*. Because of the young age of AMNH 6902, the m1 is quite thin-walled and fragile. The transverse width of the m1 is widened partially due to expansion of matrix filling the

inside of the tooth, as evidenced by sediment-filled cracks up to 0.5 mm wide on the enamel surfaces. In keeping with the short P4 in YPM 12730, the m1 of AMNH 6902 is short compared to *E. crassidens* and *E. basilatus*. Like that of *E. pahinsintewakpa*, the m1 shearing blade, the trigonid, is short. The m1 protoconid on the type is broken off halfway and it is difficult to ascertain the existence of a metaconid. However, because the metaconid on m2 is very reduced, that on m1 is likely to have disappeared completely (loss of m2 metaconid is usually subsequent to loss of m1 metaconid). The m1 talonid includes a prominent hypoconid that has a sharp anterior ridge leading down to the posterior base of the trigonid. There is a tiny entoconid at the posterolingual corner, which is more reduced than in *E. pahinsintewakpa*. Only the trigonid of the m2 is preserved; it has a dominant protoconid and a much smaller metaconid. The high protoconid of m2 is shared with *E. basilatus* and is in contrast to the two Great Plains species of *Enhydrocyon*, which tend to have very low, indistinct trigonid cusps in the m2. The protoconid and metaconid are united by a transverse ridge descending from the tip of the protoconid. The protoconid also has anterior and posterior ridges; the anterior ridge connects with an inconspicuous, cingulum-like paraconid. The degree of metaconid reduction is intermediate between *E. basilatus* and *E. pahinsintewakpa*.

DISCUSSION: Thorpe (1922a) distinguished *Enhydrocyon oregonensis* from *E. stenocephalus* in the following ways: "In comparison with *E. stenocephalus* Cope, the new form [*E. oregonensis*] differs in having less expanded zygomata; nasal bones differently shaped and pointed posteriorly, terminating just anterior to the posterior process; frontal ridges uniting just beyond the postorbital constriction; muzzle 20 per cent longer; less interorbital width; shorter length of superior dental series; longer sectorial; considerably smaller M2; longer and wider M1; less axial length." Of these observations on YPM 12730, only the unique shape of the nasal, the narrower interorbital width, and the smaller M2 are confirmed in the present study; the rest of Thorpe's characters are difficult to verify because of the absence of anatomical structures in at least one of the specimens

(e.g., the zygomatic arch and the upper car-
nassials are missing in AMNH 6901 and
6902, and the outline of the M1 in AMNH
6901 is reduced due to severe wear) or lack
of a clear definition (e.g., the muzzle length
and the axial length). The anterior end of the
nasals in YPM 12730 has a peculiarly straight
transverse plane unlike any other canids,
which commonly have an extension along the
lateral borders of the nasals so that the an-
terior ends are tapered in dorsal view. These
anterolateral processes of the nasals form part
of the dorsal rim of the external nasal open-
ing. In most *Enhydrocyon*, this tapered tip is
shortened because of its shortened rostrum,
but is not truncated as in YPM 12730. The
anterior edge of the nasals in YPM 12730 has
a long, vertical facet, suggesting the possibil-
ity of damage during preparation. As for the
slightly narrower interorbital width of YPM
12730, it is most likely due to its younger
age; as it grew, the orbital rim would probably
have acquired the lateral expansion of AMNH
6901, a much older individual (such an on-
togenetic change can be observed in *Hesper-
ocyon gregarius*). Finally, the small M2 in
YPM 12730 is considered here to be within
the range of variation observable in other
species of *Enhydrocyon*. The reduction in M2
is a general trend in *Enhydrocyon*. Variations
of this character is great in a species with a
relatively large sample size, such as *Philotrox*.

There are some problems regarding the
taxonomic assignment of USNM 7745, a
fragmentary skull with a right M1 only and
roots of the other upper teeth (endocast fig-
ured in Radinsky, 1973: fig. 3). While surely
an *Enhydrocyon*, it possesses some basicra-
nial characters that do not conform to the
present diagnosis of *E. stenocephalus*: a flat,
uninflated bulla and an ectotympanic process
that covers the posterior aspect of the post-
glenoid foramen. Its overall dental structures,
however, suggest that it is best comparable
with *E. stenocephalus*: short P2–4 and rela-
tively unreduced M2 (all deduced from their
alveoli).

Enhydrocyon pahinsintewakpa
(Macdonald, 1963)
Figures 31, 32

Sunkahetanka pahinsintewakpa Macdonald, 1963:
214; 1970: 60.

Enhydrocyon crassidens (Matthew) Macdonald,
1963: 217 (SDSM 53320 and 54180); 1970: 62
(SDSM 7961).

HOLOTYPE: SDSM 53325, complete right
ramus with c1, p2–m1, and alveoli for m2–3.

TYPE LOCALITY: SDSM locality number
V5361, "on the south side of the Gooseneck
road near the junction with the Sharps Cutoff
road in the NE. ¼ of the NW. ¼ of sect. 20,
T. 39 N, R. 43 W, near the top of the Sharps
formation" (Macdonald, 1963: 160). Early
Arikareean.

REFERRED SPECIMENS: From the Ledingh-
am Ranch localities, Sioux County, Nebras-
ka, Lower Arikaree Group: F:AM 25424,
partial upper and lower jaw with nearly com-
plete dentition (left I1–C1 missing), from 3/4
mi northwest of Ledingham Ranch building;
F:AM 25425, left and right rami with com-
plete dentitions, from Tunnel Hill Locality
on the Ledingham Ranch, NW1/4, sect. 29,
T. 25 N, R. 55 W, 1 ft below a marly zone.

From Goshen County, Wyoming, Lower
Arikaree Group: ACM 7645, complete left
ramus with c1, p2–m3, from Goshen Hole
area, no detailed locality data available;
CMNH 13588, partial skull and right ramus
with left P2–M2, broken right P2–M2, and
right p2–m3, from 66 Mountain, sect. 16, T.
20 N, R. 60 W, Lower Arikaree Group.

From the F:AM Muddy Creek locality, 3
mi west of the bridge of Highway 85 where
it crosses the Muddy Creek, about 12–13 mi
south of Keeline, Niobrara County, Wyo-
ming, Lower Arikaree Group (in his field-
notes, C. H. Falkenbach allocated some spec-
imens listed below to an informal stratigraphic
level of low, middle, and high beds. He re-
garded these deposits as referable to the Mon-
roe Creek Formation. The stratigraphy of the
Lusk, Wyoming, area is in need of clarifica-
tion and, until then, the sandy deposits from
Muddy Creek and Little Muddy Creek [next
paragraph] localities are here treated as with-
in Lower Arikaree Group [R. H. Tedford,
personal commun. 1991]): F:AM 54060,
fragment of rostral part of cranium and an-
terior part of mandible, with mostly broken
teeth, from "high" beds; F:AM 54061, partial
cranium and right ramus, with left I1–C1 and
P4, right I1–2 and P3–M1, and right c1–m2,
from above a white layer; F:AM 54062, frag-

ments of left and right maxillae and rami with left C1–M2, right C1–M1, left c1–m3, and right i3–m3, from 1 mi west of Muddy Creek locality, low in the beds; F:AM 54063, fragmentary rostral part of skull and mandible with complete but mostly broken upper and partial lower dentition, the alveoli for the left p2 and p4 were closed through growth of the surrounding bone, from 3 mi west of Muddy Creek locality, low in the beds; F:AM 54064, partial left and right maxillary fragments with left I3–P2, P4–M1 and right I3–P3, below the white layer; F:AM 54065, partial cranium and left ramus with mostly broken upper teeth but with well-preserved left c1–m3, right femur, right astragalus, right calcaneum, and other postcranial fragments, from north side of Muddy Creek locality, east of the bridge, high in the beds; F:AM 54066, left ramus fragment with i2, c1, p2–4; F:AM 54067, partial skull and mandible with left m1 and right p4–m1; F:AM 129095, right ramus fragment with p4–m1, from middle of beds.

From F:AM Little Muddy Creek locality, southeast of Lusk, 20 mi south of Keeline and west of Spanish Diggings, Niobrara County, Wyoming, Lower Arikaree Group (C. H. Falkenbach regarded these deposits as equivalent to the Gering Formation): F:AM 27576, partial left and right rami with entire dentition except for right p2; F:AM 27579, nearly complete skull with complete dentitions except the left and right canines and right M1; F:AM 54092, left ramus fragment with c1, dp4, and m1; F:AM 129097, partial rostral region with right P4–M2 and complete left dentition, partial cervical vertebrae 1–4, from first draw east of Robertson Draw, Little Muddy Creek locality.

From Lower Arikaree Group of Wounded Knee area, Shannon County, South Dakota: ACM 1999, partial skull and right ramus with right p3–m1, from Porcupine Creek, no detailed locality information available; LACM 9193, partial left ramus with p2–m2, referred to *Enhydrocyon crassidens* in Macdonald (1970), from LACM loc. 1964, Monroe Creek Formation (Macdonald, 1970: 62); SDSM 7961 (formerly SDSM 634, which is a duplicate number of the holotype of *Proheteromys ironcloudi* Macdonald, 1970: 43), crushed rostral part of skull with left P2, right I3, left and right P3–M1, from SDSM loc.

V6229, Monroe Creek Formation of east of Bell Butte, SE¼, sect. 8, T. 39 N, R. 42 W (Macdonald [1970: 62], however, listed it as from V1871 also from the Monroe Creek Formation); SDSM 53320, complete skull with all upper teeth except both canines, from SDSM loc. V5360, "in the gullies on both sides of the Sharps Cutoff road in the N. ½ of sect. 17, T. 39 N., R. 43 W., in the middle of the Sharps formation" (Macdonald 1963: 160).

From the type locality of the Turtle Butte Formation, NW¼, sect. 9, T. 95 N, R. 76 W, 4 mi northwest of the village of Wewela, Tripp County, South Dakota (Skinner et al., 1968: 401): F:AM 42965, partial left ramus with p4–m1 and alveoli for c1, p2–3, m2–3, referred to *Enhydrocyon crassidens* in Skinner et al. (1968: 416, fig. 11) (see also Discussion). Skinner et al. (1968: 401) regarded the Turtle Butte Formation to be equivalent to the Monroe Creek and Harrison Formations in western Nebraska. The lower part of the Turtle Butte Formation where F:AM 42965 was collected was equated to the Monroe Creek Formation of Nebraska in Skinner et al.'s correlation charts (ibid.: figs. 7, 9) (i.e., late Early Arikareean).

EMENDED DIAGNOSIS: *Enhydrocyon pahinsintewakpa* is the most plesiomorphic species of *Enhydrocyon*, but has acquired the derived characteristics of the genus: anterior part of nasal transversely widened; anterior process of frontal narrowed and pinched laterally by a sharp maxillary corner (char. 2); postglenoid foramen not covered posteriorly by a lateral ectotympanic lip (char. 13); paroccipital process laterally expanded (char. 16); mastoid process hypertrophied (char. 18); horizontal ramus of mandible deep and robust; presence of internal cusps on upper incisors (char. 25); enlarged I3 (char. 26); loss of P1 and p1 (char. 28); raised paracone on M1 (char. 36); internal cingulum on M1 encircling the protocone (char. 38); and reduction of m1 metaconid (char. 43). *Enhydrocyon pahinsintewakpa* lacks the derived features of *E. crassidens*: a swollen lateral ectotympanic process fused with postglenoid process; a pseudoparastyle on P4; reduction or loss of M2 and m3; and loss of metaconids on m1–2. *Enhydrocyon pahinsintewakpa* differs from *E. stenocephalus* of the John Day

Formation in having a less inflated bulla, a relatively long labial length of M1, an internal cingulum with a thickened posterolingual corner, and a less reduced M2.

DISTRIBUTION: Specimens of *Enhydrocyon pahinsintewakpa* are well represented in the Lower Arikaree Group (Gering/Sharps Formations, Monroe Creek Formation, lower Turtle Butte Formation) of eastern Wyoming, western Nebraska, and southwestern and southcentral South Dakota. Early Arikareean.

DESCRIPTION: Founded on a single ramus from the Wounded Knee area, *Enhydrocyon pahinsintewakpa* is now known for much more complete materials and a good sense of intraspecific variation is possible.

Skull: Three complete (CMNH 13588, F:AM 27579, SDSM 53320) and two partial (F:AM 54061 and 54065) skulls of *Enhydrocyon pahinsintewakpa* are available for the present study. Together with additional but less complete materials, they make up the largest sample of any species of *Enhydrocyon*.

The skull of *Enhydrocyon pahinsintewakpa* is about the same size as that of *Philotrox*, but is more robust with a broad rostrum. The anterior half of the nasal is wide. The posterior process of the premaxillary is long. The lateral suture of the anterior process of the frontal is pinched by a sharply cornered maxillary, and forms a 90° angle with the transverse segment of frontal/maxillary suture (fig. 58). The postorbital process of the frontal is laterally expanded, with rather sharply pointed tips in some individuals. The temporal crests behind the postorbital processes are raised slightly and tend to converge more anteriorly to create a rather high and steep sagittal crest immediately posterior. This raised frontal thus forms the most anterior segment of the sagittal crest. The maximum height of the sagittal crest reaches an estimated 15 mm in F:AM 27579. It is approximately half this height in CMNH 13588. The extremely high sagittal crest in F:AM 27579 is formed by a thin blade with a rather uniform thickness of approximately 3 mm. This is in contrast to that on F:AM 54061 and 54065, which are thicker based and may taper slightly toward the top (F:AM 54061). The conspicuous sagittal crest in *E. pahinsintewakpa* ranks the highest among species of *Enhydrocyon* and

is accompanied by an extended nuchal crest reaching up to 20 mm long in F:AM 27579. In all specimens, the nuchal crest overhangs the occipital condyle. There is a distinct central ridge, the external occipital crest, on the posterior surface of the supraoccipital in CMNH 13588 and F:AM 27579 but not in SDSM 53320. On the occipital shield above the foramen magnum, *E. pahinsintewakpa* still retains a pair of large fossae for the rectus capitis dorsalis major muscles.

In lateral view, the rostral part of *Enhydrocyon pahinsintewakpa* is not as deep as in *E. crassidens*. The depression for the levator nasolabialis muscle immediately in front of the orbit is more prominent than in *Philotrox*. The lacrimal bone forms a small ridge-like tubercle on the anterior orbital rim and is in touch with the anterior process of the jugal. The zygomatic arch is of approximately the same depth as in *Philotrox* and is slightly more arched laterally than that of the latter. In F:AM 27579 and SDSM 53320, there is a shallow groove below the postparietal foramen and along the horizontal parietal/squamosal suture.

In ventral view, the width of the palate is about the same or slightly larger than that in *Philotrox*. The hamulus of pterygoid is similar to *Enhydrocyon crassidens* and has a gently curved ventral edge. The bulla assumes a typical *Enhydrocyon* shape with a rather pointed anterior end, but is less rounded and inflated than in *E. stenocephalus* and *E. basilatus*. On CMNH 13588, the bulla is partially removed and allows examination of the middle ear region. The remaining internal margin of the entotympanic fused with the promontorium indicates presence of a low septum (Wang and Tedford, 1994: fig. 5B). The ectotympanic hugs with the base of the postglenoid process, but lacks the extensive swelling shown in *E. crassidens*. The postglenoid foramen was still walled posteriorly by a lateral lip of the ectotympanic in some individuals (CMNH 13588 [see Wang and Tedford, 1994: fig. 5B] and SDSM 53320), but is naked behind in others (F:AM 27579). The mastoid process is considerably inflated compared to that of *Philotrox*. It has a lateral ridge leading down to a ventral tip. The paroccipital process is oriented mainly ventrally and extensively fused with the posterior wall

Fig. 31.   Skull of *Enhydrocyon pahinsintewakpa*. **A**, Dorsal and **B**, ventral views of F:AM 27579. Scale = 30 mm.
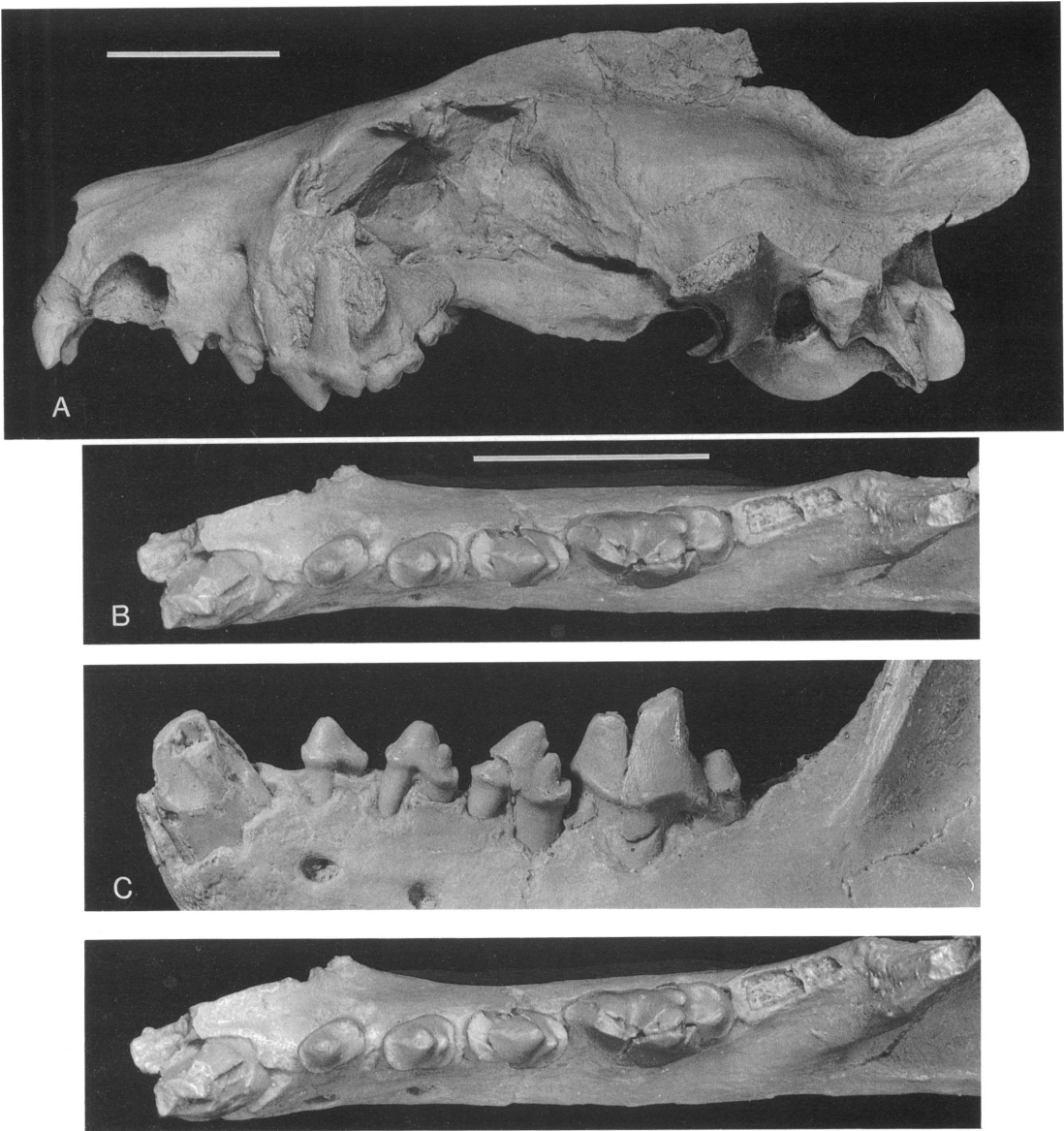
Fig. 32.   Skull and mandible of *Enhydrocyon pahinsintewakpa*. **A**, Lateral view of F:AM 27579; **B**, occlusal view (in stereo) of lower teeth of SDSM 53325, holotype; and **C**, lateral view of lower teeth of SDSM 53325. Scales = 30 mm.

of the bulla. The paroccipital process is expanded toward the lateral side and forms a thin blade on the lateral edge, a derived condition relative to that of *Philotrox*, which has no lateral extension (one Wounded Knee specimen, SDSM 53320, does not exhibit this advanced characteristic). This lateral ridge

continues to the ventral tip of the mastoid process and encloses an elongated pocket.

Mandible: Four specimens (SDSM 53225, ACM 7645, LACM 9193, and F:AM 54065) have well-preserved mandibles, including the angular processes. Beginning in *Enhydrocyon pahinsintewakpa*, the mandible has taken a

more typical *Enhydrocyon* outline: a deep horizontal ramus; a tightly curved ventral border at the anterior end of the horizontal ramus; a deep, anteroposteriorly elongated masseteric fossa (the size of the fossa varies with age; i.e., smaller fossa for younger individuals); a robust ascending ramus; and a short angular process with a prominent posterior tubercle. All these features can be used to distinguish it from mandibles in primitive stem groups of *Sunkahetanka* and *Philotrox*.

In most individuals except the type, the angular process still retains a shallow pocket enclosed by an inflected internal ridge. All have a distinct posterior tubercle (sensu Gaspard, 1964: 251, fig. 1), where the ligament separating the superficial and intermediate masseteric muscles attaches. In ventral view, the angular process is transversely thickened and flattened in contrast to more sharp-edged ventral sides in *Philotrox* and *Sunkahetanka*.

Dentition: A complete set of upper incisors is well preserved in F:AM 25424, 54061, 129097, and SDSM 53320. On the I1–2, there is a large principal cusp accompanied by a small accessory cusp on each side. On specimens with minimum wear (F:AM 25424 and 129097), the I1–2 also have a pair of cingular cusps on the lingual side separated by a vertical groove. The presence of the internal cusps had been used in the diagnosis of *Enhydrocyon oregonensis* (= *E. stenocephalus*) (Thorpe, 1922a). These cusps also appear in *E. crassidens* (status unknown in *E. basilatus*) and therefore is a synapomorphy for *Enhydrocyon*. The I3 is slightly enlarged relative to that in *Philotrox* but is still small relative to that in *E. crassidens*. It has a vertical ridge on its lateral side. The canine has an anterior and a posterior ridge along most of its length. The P1 is absent in all specimens examined. The P2 and P3 are enlarged and slightly rotated so that they fit within the short upper toothrow. The occlusal outline of the P2 and P3 is more quadrate than that in *Philotrox*. The premolars also have better developed posterior accessory cusps than the latter. The anterior cingular cusp is either absent or present as a small bulge on the anterolingual corner at the base of the anterior ridge of the main cusp. The posterior cingulum in P3 is raised to form a cusp. As in *Philotrox*, the P4 of *E. pahinsintewakpa* is not greatly elongated and is significantly shorter than that in *E. crassidens*. The shape of P4 is also not much different between *Philotrox* and *E. pahinsintewakpa*. The P4 protocone is slightly anteriorly positioned, and varies from a distinct cusp (F:AM 25424 and 129097) to a bulge appressed to the base of the paracone (SDSM 7961 and F:AM 27579). There is a prominent ridge on the anterior surface of the paracone, and in certain individuals (F:AM 27579 and 129097) a thickened anterior cingulum is delineated from the base of the vertical ridge. A cingulum is well developed on the anterolabial and posterolingual sides of the P4. The paracone of the M1 is enlarged over the metacone; so is the parastyle. The internal cingulum completely surrounds the protocone but still possesses a posterolingual thickening. This cingulum becomes nearly symmetrical on both anterior and posterior corners of M1s in *E. stenocephalus* and *E. basilatus*. The M1 of SDSM 7961 is markedly smaller than in the other individuals; its outline and relative proportion are similar to UCMP 76712 (*Philotrox*). The M2 is only slightly more reduced than that in *Sunkahetanka* and has a more uniform size than in *Philotrox* (i.e., large size variation in *Philotrox*). The M2 is double-rooted in the majority of individuals (F:AM 25424, 129097, SDSM 53320, and possibly in F:AM 27579). The thickness of the internal cingulum seems to be correlated with the size of the tooth—those having thick internal cingulum also tend to have large M2.

F:AM 25425 has bicuspid i2–3 with a main cusp and a lateral accessory cusp. The i2 accessory cusp is almost the same size and is raised to the same level as the main cusp. The lateral accessory cusp on i3, on the other hand, is much smaller and positioned at the base. Only one specimen (F:AM 54062) may have a p1, as suggested by a labially positioned alveolus away from the main toothrow. All p2s have a single principal cusp only and some toothrows are imbricated slightly. Like the upper premolars, the lower premolars have somewhat quadrate outlines, especially in p3–4, and well-developed posterior accessory cusps. The posterior accessory cusps in the type are more distinct than in most other specimens. The anterior cingulum is usually weak whereas the posterior cin-

gulum is far better developed, although the latter rarely takes the form of a cusp. The length of the m1 remains the same as in *Philotrox*, but is shorter than in *Enhydrocyon crassidens*. The size of the m1 metaconid varies from small in the type and F:AM 54065, to reduced to a bulge in F:AM 25425, to completely lost in the rest of the specimens. The hypoconid is the dominant cusp on the m1 talonid. The entoconid crest is reduced from a wide platform in *Philotrox* to a narrow cingulum in *E. pahinsintewakpa*. The trigonid of the m2 is still primitive in having nearly identically sized protoconid and metaconid even in individuals that have lost the m1 metaconid, in contrast to the much reduced (*E. stenocephalus*) or lost (*E. basilatus* and *E. crassidens*) metaconids of more advanced species. The m2 paraconid is usually inconspicuous or nonexistent. The talonid is made up of a low hypoconid with little or no trace of an entoconid. The small, usually circular m3 (single-rooted) has a low protoconid and even lower metaconid.

DISCUSSION: Despite his formal recognition of *Sunkahetanka pahinsintewakpa* as a distinct species, Macdonald (1963: 216) acknowledged its similarity to *Enhydrocyon crassidens*: "Except for the relatively greater width of the premolars, the metaconid on m1, the relatively greater size of m1, and the presence of a well-developed m3, as indicated by the alveolus, it could well represent a particularly robust individual of *E. crassidens*." Although some of Macdonald's dental characteristics (width of premolars and size of m1) no longer hold true in light of a much larger sample size for both species compared, additional characters (see diagnosis of *E. crassidens*) found in this study appear to justify the separation into two species.

A nearly complete skull (SDSM 53320) and a crushed partial skull (SDSM 54180) from the Sharps Formation were referred to *Enhydrocyon crassidens* by Macdonald (1963: 217). They are here assigned to *E. pahinsintewakpa* because of their possession of the following features: a rodlike paroccipital process (this is in fact a primitive character for *Philotrox*, but is here regarded as a variation within *E. pahinsintewakpa* because of the other advanced characteristics in SDSM 53320), short P4 (not preserved in SDSM

54180), and less reduced M2. Later, Macdonald (1970: 62) referred two more specimens (SDSM 7961 [= SDSM 634] and LACM 9193) from the Sharps Formation to *E. crassidens*. These additional specimens further bear out the above conclusion that individuals from the Sharps Formation are still too primitive (with short m1, well-developed m2 metaconid, etc.) to be *E. crassidens*.

Skinner et al. (1968: 416, fig. 11) figured a partial left ramus with p4–m1 (F:AM 42965) from "type locality of Turtle Butte Formation 1 foot above its contact with the Rosebud Formation," and commented that it "probably represents a smaller individual of the *Enhydrocyon crassidens* population, but in other respects is similar to the type of *E. crassidens* from Porcupine Creek . . . ." Although it has completely lost the metaconid of m1 (so do some individuals of *E. pahinsintewakpa*), F:AM 42965 is here referred to *E. pahinsintewakpa* mainly because of its short m1.

Enhydrocyon crassidens
Matthew, 1907
Figures 33, 34

Enhydrocyon crassidens Matthew, 1907: 190; 1909: 112. Thorpe, 1922a: 175. Macdonald, 1963: 217.

HOLOTYPE: AMNH 12886, crushed skull and lower jaws with nearly entire upper and lower dentition, and a partial postcranial skeleton. Collected by Albert Thomson in 1906.

TYPE LOCALITY: AMNH locality "Rosebud" 12, Porcupine Creek, 3 mi downstream (northwest) of Porcupine Post Office (field note "Porcupine Cr'k, 3 m. below p.o."), in sect. 12, T. 38 N, R. 43 W, Wounded Knee area, Shannon County, South Dakota (Macdonald, 1963). Matthew's (1907) Lower Rosebud Formation was equated with the lower Monroe Creek to lower Harrison Formations in Macdonald (1963: fig. 1), who further restricted the "Rosebud" 12 locality to the Monroe Creek Formation, citing Matthew's fieldnotes as evidence. Late Early Arikareean.

REFERRED SPECIMENS: From Wounded Knee area, South Dakota: AMNH 13799, crushed anterior half of skull and partial right ramus, with left I2–C1 and P3–M1, right I3–

M1, right p3–m2, and postcranial fragments, from "Upper Rosebud" 6 mi west of American Horse Creek. Two specimens (AMNH 12869 and 12870) from the Harrison Formation were referred by Macdonald (1963: 217) to *Enhydrocyon crassidens*, but could not be located for the present study.

From Middle Arikaree Group of Niobrara County, eastern Wyoming: F:AM 27560, nearly complete skull and upper dentition, missing the left and right I3s, from North of Keeline locality, no more information is available for this locality; F:AM 27563, posterior half of right ramus with m1 and broken p4, from North of Keeline locality; F:AM 54070, partial left rostrum with all incisors and broken left C1–M1, right ramus with broken i3–m2, from North of Keeline locality; F:AM 54071, fragment of left maxillary with P2–M1, from North Ridge Highway 85 locality, approximately 10 mi north of Lusk; F:AM 54073, posterior half of right ramus with m1–2, from North Ridge locality, north of Node; F:AM 54074, fragments of left and right rami with broken left m1–2 and right p3, no locality data (this specimen, however, was shipped to AMNH in the box that contained mostly specimens from the North of Keeline locality).

EMENDED DIAGNOSIS: *Enhydrocyon crassidens* can be distinguished from *E. pahinsintewakpa* by having the following derived features: loss of the fossa for rectus capitis dorsalis (char. 6, reversal); extreme reduction or loss of M2 and m3 (char. 40); and complete loss of metaconids in m1–2 (char. 43). *Enhydrocyon crassidens* has two autapomorphies: extensive fusion of the ectotympanic with the postglenoid process (char. 13) and presence of a pseudoparastyle on P4 (char. 37). In addition, *E. crassidens* primitively still has a relatively uninflated bulla, an internal cingulum of M1 that has a posterolingual thickening, and a less enlarged protoconid on m2, characters that help to distinguish it from the John Day *Enhydrocyon*.

DISTRIBUTION: Middle Arikaree Group of eastern Wyoming; Monroe Creek and Harrison Formations of western South Dakota. Late Early to early Late Arikareean.

DESCRIPTION: Although the holotype of *Enhydrocyon crassidens*, AMNH 12886, is still the most complete specimen and forms the main basis of comparison with other species of *Enhydrocyon*, significant additional materials are now available for assessment of intraspecific variation.

Skull: The skull proportions of *Enhydrocyon crassidens* maintain the basic pattern of the genus (i.e., a robust and heavy skull, an elongated postorbital region of the cranium, and a strong zygomatic arch). The nasals tend to be completely fused together in the midline (AMNH 12886 and 13799) and are slightly wider than those in *E. pahinsintewakpa*. The posterior process of the premaxillary is relatively slender and short. As in *E. pahinsintewakpa*, the anterior process of the frontal between the nasal and maxillary is pinched at the base so that there is a 90° angle between the sagittally oriented lateral border of the frontal process and the transversely oriented maxillary/frontal suture. In the less crushed frontal regions of AMNH 13799 and F:AM 27560, the forehead is relatively flat and straight as opposed to a slightly domed frontal region in the holotype. The temporal crests unite near the postorbital constriction whereas those of *E. pahinsintewakpa* converge slightly more anteriorly. The type of *E. crassidens* and F:AM 27560 have a relatively low sagittal crest in contrast to a much higher one in *E. pahinsintewakpa*. AMNH 13799, however, has a much higher crest judging from its preserved anterior end. The cross section of its sagittal crest shows a tapered tip rather than the uniform thickness found in most of *E. pahinsintewakpa*. Individuals with a low sagittal crest also have far shorter nuchal crests. The occipital shield is smooth with a low and gentle central ridge.

In lateral view, AMNH 13799 has a rather prominent depression in front of the orbit for the levator nasolabialis muscle, bordered posteriorly by a conspicuous tubercle on the rim of the orbit. The infraorbital foramen of *Enhydrocyon crassidens* is vertically elongated as opposed to a rounded cross section in *E. pahinsintewakpa*. The zygomatic arch is deep and strongly built.

In ventral view, *Enhydrocyon crassidens* has a broader palate than that of *E. pahinsintewakpa*. The posterior border of the palate is behind that of the last molar due to its reduction or loss of M2. The basicranial regions of *E. crassidens* and *E. pahinsinte-*
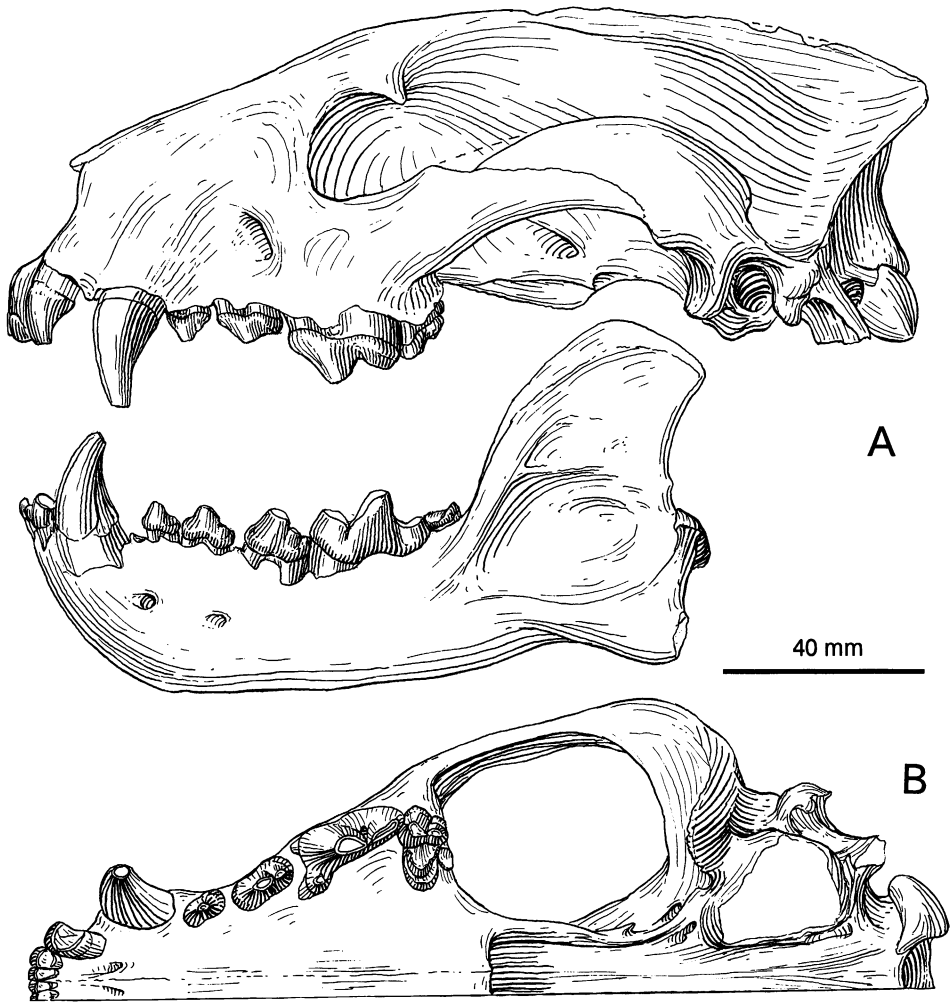
Fig. 33. Skull and mandible of *Enhydrocyon crassidens*, holotype, AMNH 12886. **A,** Lateral view of skull and mandible; **B,** ventral view of left half of skull. Illustrated by Raymond J. Gooris.

wakpa are very similar. Both have less inflated auditory bullae than those of *E. stenocephalus* and *E. basilatus*. As in most *Enhydrocyon*, the postglenoid foramen is exposed posteriorly and not covered by a lateral lip of the ectotympanic. The ectotympanic of some individuals (AMNH 12886 and F:AM 27560) extends toward the postglenoid process to hug its posterior surface; it then thickens to create a swollen tubercle on the otherwise smoothly curved posterior surface. This swollen appearance is not present in AMNH 13799. The mastoid process is highly inflated to the extent that its external surface can be seen in dorsal view rather than hiding beneath the basal lambdoidal crest. Only the basal parts of the paroccipital process are preserved in all *E. crassidens* specimens examined. Inferred from the remaining processes, the paroccipital process is laterally extended to form a thin blade, typical of *Enhydrocyon*. In addition to the extensive fusion of the paroccipital to the posterior surface of the caudal entotympanic, the medial part of the basal paroccipital process is thickened, especially in F:AM 27560, to form a bulge.

Mandible: *Enhydrocyon crassidens* tends to have a solidly fused mandibular symphysis (AMNH 12886 and F:AM 54072) like that of *E. basilatus*. The mandible of *E. crassidens*
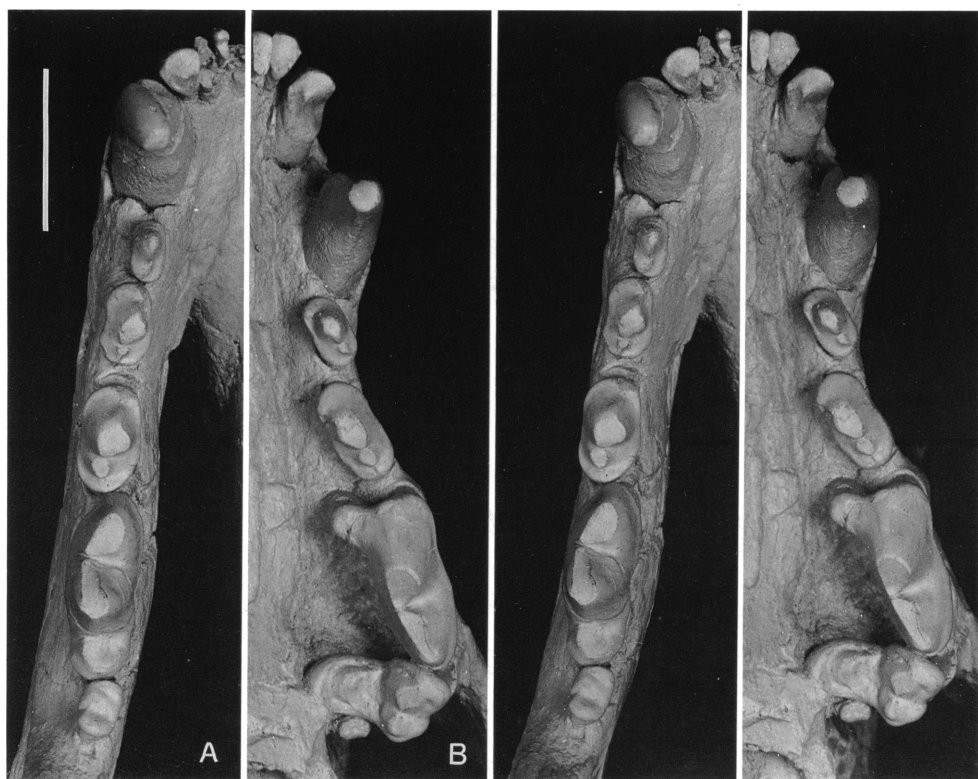
Fig. 34. Occlusal views (in stereo) of **A**, lower and **B**; upper teeth of *Enhydrocyon crassidens*, AMNH 12886, holotype. Scale = 20 mm.

is stoutly constructed and thickens toward the anterior end. The horizontal ramus is noticeably thicker and deeper than that of *E. pahinsintewakpa*. The size and shape of the ascending ramus are quite variable. In AMNH 13799 and F:AM 54073, the ascending rami are high and broad, in contrast to narrower rami of AMNH 12886 and F:AM 27563. The coronoid crest arches backward and extends posteriorly to the level of the posterior border of the mandibular condyle.

Dentition: The dental formula of *Enhydrocyon crassidens* is 3/3 1/1 3/3 1(2)/2(3). Both M2 and m3 are highly reduced or absent (presence of a small m3 alveoli in AMNH 13799 and F:AM 54073, and absence of M2 in F:AM 27560), giving *E. crassidens* the most reduced dentition of all hesperocyonine canids.

Upper incisors of *Enhydrocyon crassidens* are progressively enlarged from I1 to I3. The cross section of the I2 is more rounded than

that of I1. In F:AM 54070, whose teeth are least worn, the I2 has an accessory cusp on either side. In addition, there are two small internal basal cusps, divided by a median groove, on the lingual side of the I2. The existence of internal cusps can also be inferred on F:AM 27560, which has enough enamel left to indicate the remnant of a groove between these cusps. The I3 is almost twice as large as the I2, continuing the trend toward significant I3 enlargement begun in *E. pahinsintewakpa* (e.g., F:AM 54064). In F:AM 54070, there is a low accessory cusp on the medial side of I3 leading to a ridge near the base of the tooth. This medial basal cusp appears to be present on the type AMNH 12886, as is suggested by the remnant of a ridge. The unworn (but broken) upper left canine in F:AM 54070 has a rather sharp ridge on the posterior surface. There is no indication of the existence of a P1 in any of the individuals examined. The upper premolars are less

crowded and less imbricated than in *E. bas-ilatus*. The principal cusps of the upper pre-molars are rather low. The P2, always dou-ble-rooted, has a low anterior cingular cusp and a small posterior accessory cusp. The posterior cingulum of P3 is more distinct than on P2 but is otherwise quite similar. The up-per carnassial with its elongated shearing blade is more hypercarnivorous than that of *E. pahinsintewakpa*. The protocone is mostly at the same level as the anterior basal edge of the paracone but can be slightly anterior (AMNH 13799). Some individuals (F:AM 27560 and possibly F:AM 54071) develop a distinct parastyle, which is absent in the type. The parastyle on M1 is generally well devel-oped, reaching to nearly the same height as the paracone tip. The paracone is much larger than the metacone. The M1 tends to be more slender than in *E. pahinsintewakpa* because of the more medially extended internal cin-gulum surrounding the protocone. The in-ternal cingulum still retains a posterolingual thickening in contrast to the John Day forms, *E. stenocephalus* and *E. basilatus*, that have a uniform thickness of the internal cingulum. The presence of M2 is variable from a small, single-rooted M2 in AMNH 13799, to a tiny residual M2 on the left side of the type, to complete absence in F:AM 27560.

The type of *Enhydrocyon crassidens* has the only preserved, although broken, i1–2, which show the same mediolateral compres-sion as in their upper counterparts. The i3 is twice as large as i2 or i1 but significantly smaller than the I3. The anterolingual and posterolingual ridges on the canine are vague. No specimen has a p1. The p2 has an anterior and posterior ridge on the main cusp. On AMNH 12886, a posterior accessory cusp be-gins to develop on the p3 and becomes far more prominent on p4, which also has a broad posterior cingulum forming a low platform behind the accessory cusp. F:AM 54072, however, shows the strongest development of the cingular cusps, especially those on p4. Like the upper carnassial, the m1 is elongated with a long, slender shearing blade. The m1 metaconid is completely lost. The talonid is relatively narrower than that of *E. pahinsin-tewakpa* and is occupied by a single hypo-conid with a vague cingulumlike entoconid ridge; it is more quadrate and wider than that

in *E. basilatus*. The m2 is relatively small as compared to that of *E. pahinsintewakpa* and *E. basilatus*. The crown of the m2 is rather flat, particularly in the type; the trigonid cusps are low and indistinct in contrast to a much larger m2 protoconid in *E. stenocephalus* and *E. basilatus*. The m2 metaconid varies from being completely lost in F:AM 54074 to being a low ridge in AMNH 12886 and 13799. The m3 is present in AMNH 13799 and F:AM 27563 (both single-rooted), but absent in AMNH 12886.

DISCUSSION: AMNH 13799 is almost iden-tical to the holotype of *Enhydrocyon crassi-dens* in size and shape of its teeth but has a much more robust skull and mandible. It is somewhat transitional between *E. pahinsin-tewakpa* and *E. crassidens*. AMNH 13799 has the following derived characters of *E. crassidens*: extensive fusion between the na-sals, elongated upper and lower carnassials, and residual M2s. On the other hand, it re-sembles *E. pahinsintewakpa* in having a high sagittal crest, less fusion of ectotympan-ic/postglenoid process, and presence of a small m3.

F:AM 27563 has a rather quadrate talonid of m1 not seen in other specimens of *En-hydrocyon crassidens*. In addition, it also re-tains an m3 as is indicated by the presence of an alveolus. This dental peculiarity, in ad-dition to its narrow ascending ramus, may prove to be a distinct species with additional materials.

Enhydrocyon basilatus Cope, 1879
Figures 35–37

Enhydrocyon basilatus Cope, 1879a: 57. Matthew, 1907: 189. Thorpe, 1922a: 173. Macdonald, 1963: 217.
Hyaenocyon basilatus (Cope) Cope, 1879c: 372 (excluding AMNH 6905, type of *H. sectorius*); 1881b: 181 (excluding AMNH 6905); 1883: 246; 1884: 912.
Enhydrocyon sectorius (Cope) Thorpe, 1922a: 174.

HOLOTYPE: AMNH 6904, anterior half of mandible with right i3–c1, left and right p2–4 and roots of m1. Collected by Charles H. Sternberg.

TYPE LOCALITY: Cope (1879a: 58): "Found by Mr. Sternberg in the same region as the *E. stenocephalus*." On the label of AMNH

6904, it is described as "Haystack Valley, Grant County, Oregon." The Haystack Valley Member of the John Day Formation has the thickest deposits (500 ft) near the Haystack Valley, north of the town of Kimberly, although the lower Kimberly Member is also present on the north side of Haystack Valley (Fisher and Rensberger, 1972). The limited locality information of AMNH 6904 is not adequate to place it in the above stratigraphic context. The type of *E. basilatus* is thus within the broad range of Upper John Day Formation (including Kimberly and Haystack Valley members). Late Early to Late Arikareean.

REFERRED SPECIMENS: From John Day Formation, Oregon: AMNH 6918, left ramus fragment with p4; UCMP 76749, nearly complete skull and mandible missing anterior end of skull and jaws, and ascending rami, with left P4–M2, right C1–M2, left p3, m1–2, and right p2–3, m1–3, from UCMP locality number V6013, Bridge Creek 6, Wheeler County.

From Niobrara County, Wyoming, Harrison Formation: F:AM 54072, nearly complete left and right co-ossified rami with c1–m2 of both sides, from 77 Hill Quarry, on C. A. Pinkerton Ranch, 4.5 mi north of Manville, west side of road to Lance Creek in NW¼, SE¼, sect. 11, T. 33 N, R. 65 W.

From Missouri River Valley, Jefferson County, Montana: F:AM 54195, fragment of left maxillary with a single P4 (questionably referred to *Enhydrocyon basilatus*, see Discussion), from Canyon Ferry locality. No more specific locality information is available for F:AM 54195, which was collected by C. Falkenbach in 1942.

EMENDED DIAGNOSIS: *Enhydrocyon basilatus* is a terminal member of the *Enhydrocyon* clade and possesses the following two autapomorphies to be distinguished from its sister-species *E. stenocephalus*: a lateral expansion of the paroccipital process and a deep notch between the mastoid process and paroccipital process (char. 16) and enlarged premolars with distinct anterior cingular cusps (char. 29). In addition, *E. basilatus* has, together with *E. stenocephalus*, characters distinct from *E. pahinsintewakpa* and *E. crassidens*: a rounded and more inflated bulla, an M1 internal cingulum with even thickness, and a high protoconid of the m2.

DISTRIBUTION: Specimens of *Enhydrocyon basilatus* are rare and have been found in ?Kimberly Member of John Day Formation of central Oregon, Harrison Formation of eastern Wyoming, and possibly from Canyon Ferry area of western Montana. Medial and Late Arikareean.

DESCRIPTION: The exceptionally well-preserved skull and mandible of UCMP 76749 furnishes an excellent opportunity for examination of cranial morphology of *Enhydrocyon basilatus*. With little wear on the teeth and mostly unfused bone sutures, UCMP 76749 clearly represents a young individual.

Skull: The anterior tip of UCMP 76749 in front of the canines is broken off. The skull has a short rostrum judging by the crowded and rotated premolars. The shortness of the rostrum is partly due to its young age, as is found in juvenile domestic dogs (Evans and Christensen, 1979). The medial suture of the posterior process of premaxillary is exposed because of the missing anterior nasals. The process has a depth of 4.5 mm in cross section. The anterior process of the frontal is short, as is typical of the genus. The lateral border of the process is sharply constricted by the maxillary, as is common in *Enhydrocyon*. Both postorbital processes of the frontal are broken off in UCMP 76749, but they seem to be short (again a feature of young individuals). The temporal crest is rather smooth, another indication of its young age. The postorbital constriction is posteriorly displaced, due to the elongated temporal region of skull. Most parts of the sagittal crest are broken off; the remaining anterior segment indicates that it is lower than that of *E. stenocephalus*. The nuchal crest is mostly broken off. From the remaining basal part, the nuchal crest does not seem to extended as far backward as in *E. pahinsintewakpa*, although this shortness of nuchal crest and low sagittal crest may again be attributable to its young age and is thus not strictly comparable to adult forms. The posterior surface of the supraoccipital is smooth and has a narrow central ridge (the external occipital crest, Evans and Christensen, 1979), more ventrally extended than in *E. stenocephalus* and connecting to the top of the foramen magnum.

In lateral view, the frontal region above the

orbit is prominently domed. To what extent this is due to the young age is not clear because of lacking adult specimens for comparison. The infraorbital foramen is relatively small and vertically oval in cross section. The lacrimal is a small, rectangular bone bordered by the frontal above, the palatine behind, and the maxillary below and in front. The round opening of the lacrimal canal sits near the suture of maxillary/lacrimal directly above the infraorbital foramen. Unlike the primitive condition in all other species of hesperocyonines, the lacrimal is not part of the anterior orbital rim and does not make contact with the anterior tip of the jugal. Consequently, the anterior orbital rim lacks a small lacrimal tubercle seen in other hesperocyonines.

In ventral view, the palate is transversely broad. On the horizontal lamina of the maxillary, the major palatine arteries leave a pair of distinct longitudinal grooves (20 mm long) leading to the palatine foramen. A triangular pterygoid wing hangs down in lateral view. Although less so than that of *Enhydrocyon stenocephalus*, the bulla is well rounded and inflated, especially at the anterior end medial to the postglenoid process. This globular outline of the bulla is different from the primitively pear-shaped bullae in *E. pahinsintewakpa* and *E. crassidens*. The anterolateral process of the ectotympanic cups the posterior surface of the postglenoid process. There is no lateral lip of the ectotympanic enclosing the postglenoid foramen. The mastoid process is highly inflated and swells laterally beyond the basal border of the lambdoidal crest. The paroccipital process is the most unique among taxa of hesperocyonines. Not only is it anteroposteriorly flattened as in most members of *Enhydrocyon*, it forms an earlike bony blade extending ventrolaterally (fig. 60D). In posterior view, the axis of the paroccipital process points ventrolaterally rather than directly downward as in more primitive *Enhydrocyon*. The paroccipital process is extensively fused with the caudal entotympanic. There is a deep, rounded notch separating the lateral border of the paroccipital process from the mastoid process, in contrast to the unnotched condition in other species of *Enhydrocyon*.

Mandible: F:AM 54072 has the best pre-served mandible among the three specimens in the present study. The left and right rami form a rather large angle in accordance to the short rostrum and the broad palate. The symphysis of the mandible is solidly fused, except in the young individual (UCMP 76749). The horizontal ramus is deep and heavily constructed, a characteristic of the genus; the anterior end of its lower border drops slightly to form a "chin." Also typical of *Enhydrocyon*, the lower border of the horizontal ramus arches slightly downward near the region of m1. UCMP 76749 has the largest portion of the ascending rami preserved, even though both tips are broken off. The remaining basal halves suggest an anteroposteriorly narrow coronoid process, probably another age-related feature. The masseteric fossa is shallow.

Because of its young age, the various facets of muscle attachments on the angular process of UCMP 76749 are not fully ossified, resulting in a rather vaguely defined medial surface. The angular process is short and stoutly constructed, with no pocket excavation into the dorsal facet of the internal ridge. The posterior tubercle of the angular process is also not very distinct.

Dentition: Except for the incisors, the dental morphology is excellently preserved with minimal wear on all of the specimens. *Enhydrocyon basilatus* has a postcanine dental formula of 3/3 2/3, except for F:AM 54072, which has a tiny, peglike p1 on the left ramus.

The following description of the upper teeth is based on UCMP 76749 only. Partial roots of the left and right upper canines are preserved, which indicate strong canine teeth. There is a sharp posterior ridge preserved on the basal part of the right canine. *Enhydrocyon basilatus* represents the ultimate enlargement of its premolars for the genus. The upper premolars are tightly spaced and the anterior ends of P2–3 are forced to rotate approximately 45° lingually from the sagittal plane. This imbrication may be due in large extent to the youth of this specimen. The P2 almost touches the canine and no room is left for a P1. The P2 is unusually elongated contrary to a general tendency of shortening of the P2 in *Enhydrocyon*. The width of the tooth, however, is not increased, and thus P2 has a rather slender outline in the occlusal view. It has a distinct posterior accessory cusp
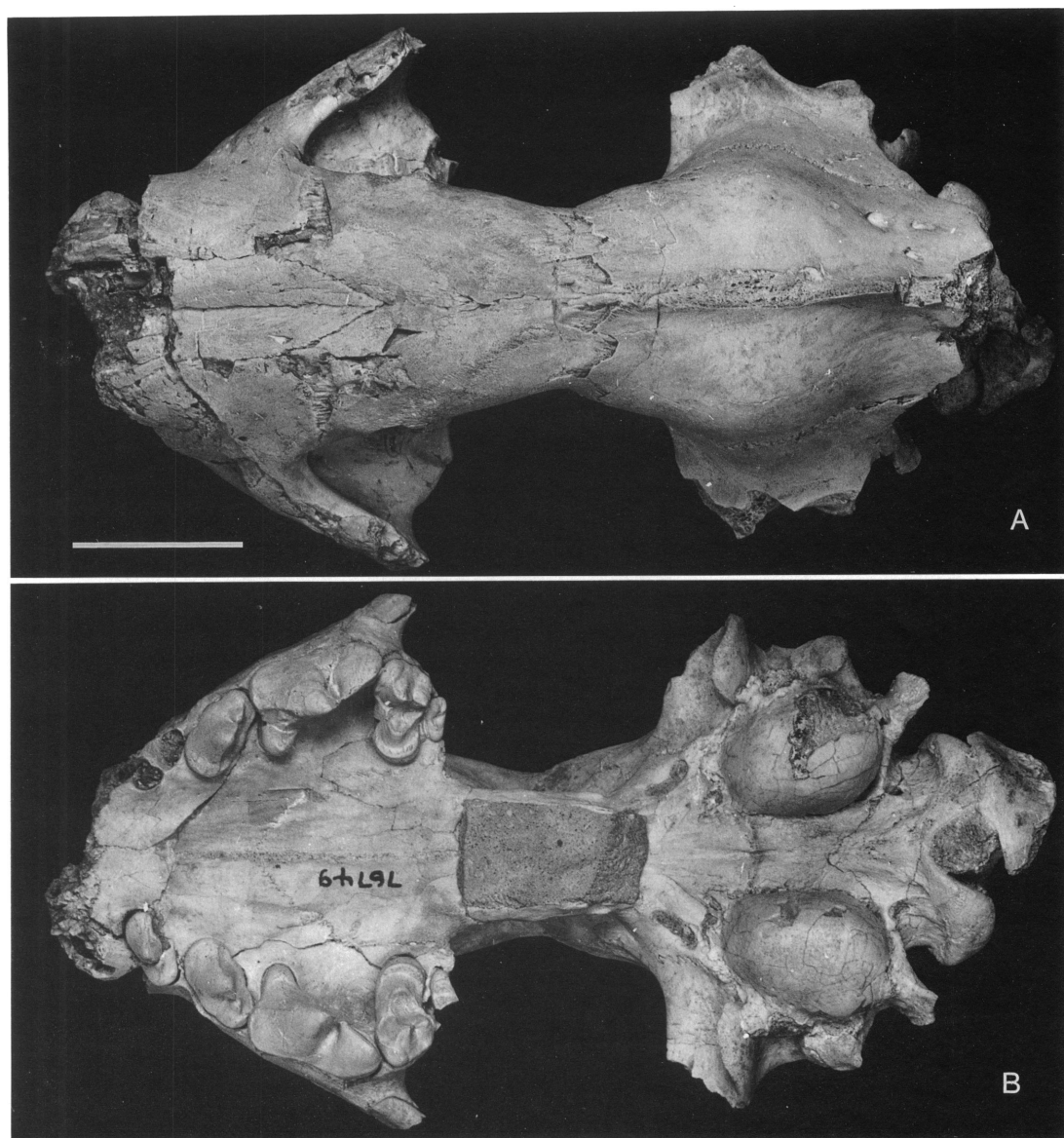
Fig. 35. Skull of *Enhydrocyon basilatus*. **A**, Dorsal and **B**, ventral views of UCMP 76749. Scale = 30 mm.

and small bulges indicative of cingular cusps at either end. The P3 is massive, with a strong principal cusp and a lingually curved anterior crest. There is still no distinct anterior cingular cusp. The posterior accessory cusp is not swollen at the base, as happens in certain individuals of *E. crassidens*. The posterior cingular cusp is a low shelf. The carnassials of *E. basilatus* are among the most hyper-

carnivorous of all hesperocyonines. The size of the P4 is considerably enlarged relative to that of M1. The P4 still retains the bulky construction seen in *E. stenocephalus*, and thus contrasts with the slender upper carnassials of *E. crassidens*. The protocone is small and close to the base of the paracone; the ridge on the paracone leading to the protocone is weak. The anterior ridge of the par-

Fig. 36. *Enhydrocyon basilatus*, UCMP 76749. Lateral views of **A**, skull and **B**, mandible, and occlusal views of **C**, lower and **D**, upper teeth (in stereo). All are reversed from the right side. Scales = 30 mm.
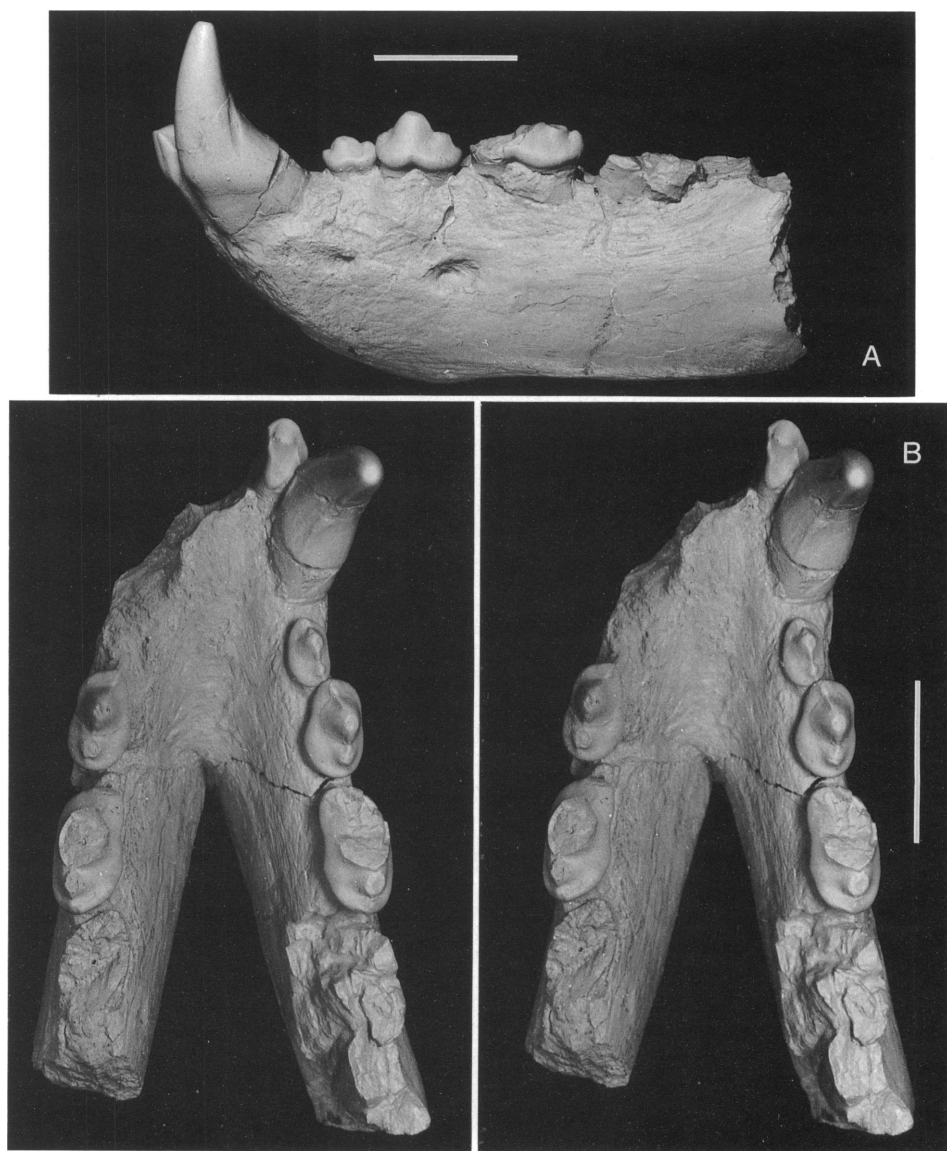
Fig. 37. *Enhydrocyon basilatus*. **A**, Lateral (reversed from right side) and **B**, occlusal (in stereo) views of AMNH 6904, holotype. Scales = 20 mm.

acone is more sharply defined and extended in the basal two-thirds of its length. The anterior cingulum of P4 is inconspicuous. The length along the paracone and metacone of the M1 is reduced relative to that of the talon. The paracone is more prominent relative to the metacone. The parastyle is raised higher than the tip of the metacone. The labial cingulum is indistinct. The sharp-tipped protocone is surrounded medially by an internal cingulum, which forms an encircling platform with no apparent posterolingual swelling seen in *E. pahinsintewakpa* and *E. crassidens*. The M2 is small, slender (anteroposteriorly), and single-rooted. It has a more pointed lingual end than in M1. The paracone and metacone are similar in size. The protocone and internal cingulum form low crests that surround a deep trigon basin.

The lower teeth are known from three spec-

imens. The right i3 in the holotype is closely appressed to the base of the c1. The c1 has a distinct anteromedial ridge and a weak posterior ridge. The right c1 in F:AM 54072 was apparently broken in the middle during life; its anterior breakage plane is still relatively fresh whereas the posterior half is far more polished. Only F:AM 54072 has a vestigial left p1 (4 mm in diameter), which has a low crown surface barely above the dorsal edge of the ramus. The p2s in F:AM 54072 and UCMP 76749 are rotated slightly from the longitudinal axis of the toothrow to accommodate the tight space between p3 and the canine (or p1). In the type, the p2 has a distinct anterior cingular cusp as well as a posterior accessory cusp. In F:AM 54072 and UCMP 76749, however, there is no posterior accessory cusp on p2 and in its place is a gently concave posterior ridge leading down from the principal cusp. The p3s in all three specimens are very similarly constructed with a higher principal cusp than that of the p2. The anterior cingular cusp is better developed than the posterior one; the latter is merely a raised cingulum without a notch to mark a distinct cusp. The posterior accessory cusp is clearly delineated although not greatly enlarged. The p4 in *E. basilatus* is very distinct from that of other species of *Enhydrocyon*. Not only is it greatly enlarged, it also has well-developed anterior and posterior cingular cusps. The posterior accessory cusp is conspicuously large and clearly separated from the main cusp and posterior cingular cusp by deep notches in front and behind. Corresponding to the elongated P4, the m1 is also highly hypercarnivorous. It has an elongated shearing blade (trigonid) relative to its talonid. The m1 metaconid is completely lost. The lateral surface of the m1 is curved (more so in UCMP 76749) so that its anterior and posterior ends bend towards the lingual side. Relative to that of the trigonid, the transverse width of the talonid is narrower than in *E. stenocephalus*. The m1 hypoconid completely dominates the talonid, and the entoconid is reduced to a faint crest on the posterolingual border of the talonid. The reduction of talonid is also exemplified in the outline of the m2; its lingual and labial borders taper toward the posterior end, resulting in a narrower talonid (in UCMP 76749 only). The m2 trigonid maintains a large, dominant protoconid, which is anteriorly connected to a low, lingually bending paraconid ridge. Although the metaconid is nearly lost in UCMP 76749, there is still a transverse ridge leading toward the tip of the protoconid, a feature shared with *E. stenocephalus*. In F:AM 54072, the m2 metaconid is absent. The hypoconid of all specimens is a low longitudinal ridge connected posteriorly and then lingually to a curved entoconid crest, and together they enclose a shallow talonid basin. The high trigonid and low talonid in m2 of *E. basilatus* (especially in UCMP 76749) is distinctly different from a flattened appearance in *E. crassidens* (although the single Great Plains individual, F:AM 54072, also has a relatively low trigonid). The erupting right m3 in UCMP 76749 is almost perfectly circular in outline (probably single-rooted). It has a cingulum-like crest forming a complete circle and a very low main cusp on the labial side.

DISCUSSION: *Enhydrocyon basilatus* was first described (Cope, 1879a: 57) together with the genotype *E. stenocephalus*, and was founded on a single partial mandible, AMNH 6904. In December of the same year, Cope (1879c: 372) referred a maxillary fragment, AMNH 6905, to *E. basilatus* and proceeded to erect a new monotypic genus *Hyaenocyon* (type *H. basilatus*) based on his believe that AMNH 6905 has no M2 and therefore represented a reduced dentition compared with *Enhydrocyon*. Cope (1883) subsequently designated AMNH 6905 as type of a new species *Hyaenocyon sectorius* (which he erroneously used as the type species of *Hyaenocyon*). After further clearing away the matrix from the type of *H. sectorius*, Matthew (1907: 190) was convinced that AMNH 6905 had an alveolus for the M2 after all, and "the validity of the genus *Hyaenocyon* is therefore very questionable, as there are no material differences in the form of the teeth to distinguish it generically from *Enhydrocyon*." Matthew's taxonomic conclusion has been followed by all subsequent authors and his observation on the dentition is confirmed in the present study by an individual (UCMP 76749) that has the M2. The taxonomy of these two species of *Enhydrocyon* came full circle when Thorpe (1922a: 174) stated: "I am inclined to view the latter [*E. sectorius*] as practically

the same or at most as being one a subspecies of the other [*E. basilatus*]." *Enhydrocyon sectorius* remained a junior synonym of *E. basilatus* until Macdonald (1963: 217) once again expressed the opinion that the former is a valid species. During these controversies, AMNH 6904 and 6905 were all that was known about this rare *Enhydrocyon* (see also Discussion of *E. sectorius* below).

One isolated P4 (F:AM 54195) from the Canyon Ferry area is here tentatively referred to *Enhydrocyon basilatus*. Its large size matches that of the two hypercarnivorous species *E. crassidens* and *E. basilatus*. Its relatively robust construction (transversely broad) and lack of a pseudoparastyle, however, make *E. basilatus* the better alternative. If correctly identified, F:AM 54195 will further confirm the distribution of *E. basilatus* east of the continental divide, in addition to the single mandible (F:AM 54072) from the Harrison Formation of eastern Wyoming.

Enhydrocyon sectorius (Cope, 1883), nomen vanum

Hyaenocyon basilatus Cope, 1879c: 372 (excluding AMNH 6904, type of *H. basilatus*); 1881b: 181 (excluding AMNH 6904).
Hyaenocyon sectorius Cope, 1883: 246; 1884: 943. Matthew, 1899: 63. Merriam, 1906: 5. Merriam and Sinclair, 1907: 189.
Enhydrocyon sectorius (Cope) Matthew, 1907: 190; 1909: 107. Macdonald, 1963: 217.

HOLOTYPE: AMNH 6905, fragment of right maxillary with P3, broken P4–M1, and alveoli for C1 and P2.

TYPE LOCALITY: No detailed locality was given in Cope's published references of this species. John Day Formation of Central Oregon.

DISCUSSION: Whereas it is reasonably placed within the genus *Enhydrocyon*, the holotype of *E. sectorius*, AMNH 6905, is too poorly preserved to be assigned to any known species. Its large-sized P4 would suggest either *E. crassidens* or *E. basilatus*. Its small P2 (as indicated by its alveolus), however, is suggestive of either *E. crassidens* or *E. stenocephalus*. Most of the P4 and M1 characters necessary for an adequate identification are missing.

The uncertainty inherent in the poor condition of the holotype of *Enhydrocyon sec-*torius has generated moderate taxonomic controversy (see Discussion in *E. basilatus*), although little knowledge was gained, besides the second-guessing of missing structures. Reference of new materials to this species, therefore, would only perpetuate the ambiguities surrounding the holotype and may add additional confusion about its identity. *Hyaenocyon sectorius* Cope, 1883, is therefore designated as nomen vanum (sensu Chorn and Whetstone, 1978; Mones, 1989).

Osbornodon, new genus

Canis (Linnaeus) Cope, 1881a: 389.
?*Cynodictis* (Bravard and Pomel) Matthew, 1899: 54.
Cynodictis (Bravard and Pomel) Wortman and Matthew, 1899: 130.
Cynodesmus Scott, 1895: 72.
Mesocyon (Scott) Sellards, 1916: 88.
Pseudocynodictis (Schlosser) Matthew, 1918: 189.
?*Cynodesmus* (Scott) Simpson, 1932: 14.
Paradaphoenus (Wortman and Matthew) White, 1942: 5.
Parictis (Scott) White, 1947: 500 (MCZ 3930).
Brachyrhynchocyon (= *Brachycyon* Loomis) Macdonald, 1967a: 1.

TYPE SPECIES: *Osbornodon fricki*, new genus and species.

INCLUDED SPECIES: *Osbornodon fricki*, new genus and species; *O. renjiei*, new species; *O. sesnoni* (Macdonald, 1967a); *O. iamonensis* (Sellards, 1916); *O. brachypus* (Cope, 1881).

DIAGNOSIS: Even in its most primitive forms, *Osbornodon* has 3 synapomorphies that distinguish it from the rest of the hesperocyonines: partially ventrally directed paroccipital process (char. 14, shared with *Mesocyon–Enhydrocyon* clade), which is further extended backward in advanced species; more quadrate upper molars and enlargement of M2 and m2 (char. 39); and basined talonid of m1–2 (char. 45). Species of *Osbornodon* progressively acquire additional derived characters that set the genus further apart from other lineages: relatively long rostrum (char. 1); strongly domed frontal region that is hollowed by a large frontal sinus (char. 4, in advanced species only); paroccipital process expanding posteriorly into a sagittally oriented plate (char. 17, in advanced species); short, mediolaterally flattened angular process (char. 21); and enlarged p4 (char. 33).

ETYMOLOGY: In honor of the late Professor Henry Fairfield Osborn, first chairman of the Department of Vertebrate Paleontology and former President of the American Museum of Natural History. In his unfinished lifetime effort on the evolution of carnivorans, Dr. Childs Frick first recognized this genus as a distinct lineage and intended to name it *Osbornodon*. *Osbornodon* has been informally used in the Frick Collection for the last three decades since Frick's death in 1965.

DISTRIBUTION: *Osbornodon* has the most extensive distribution of all hesperocyonines, both geographically and geologically. Materials are presently known in the northern Great Plains (Colorado, Nebraska, North Dakota, South Dakota, and Wyoming) as well as farther south (Florida, New Mexico, and California). Geologically, *Osbornodon* spans from Orellan to early Barstovian, although a significant gap, most of the Arikareean, is devoid of any representation.

DISCUSSION: Although its advanced species are easily distinguishable from other genera of Hesperocyoninae, the primitive forms of *Osbornodon* are far less distinct, particularly on the basis of isolated teeth. The very derived nature of the genotypic species *O. fricki* helps to put into proper perspective the rest of the more primitive forms, which would otherwise be easily misplaced with other genera based on primitive characteristics. The *Osbornodon*-type dental morphology can be traced to its beginning stage in *O. renjiei* during the Orellan age.

Osbornodon parallels the subfamily Caninae in some features of the skull and dentition: slender rostrum, elongated premolars, quadrate M1s, and basined talonids. The talonid basin in *Osbornodon* is fundamentally different from that of Borophaginae and Caninae in lacking a transverse ridge between the hypoconid and entoconid. The talonid basin in *Osbornodon* is thus surrounded by crestlike entoconid on the medial side rather than a cusp-shaped entoconid as in borophagines and canines.

Osbornodon fricki, new species
Figures 38–40

HOLOTYPE: F:AM 27363, slightly crushed skull with nearly complete upper dentition except left I3 and P1, right ramus with i1–

m3, five lumbar vertebrae, complete pelvis, right humerus and radio-ulna, left radius, partial left and right mana, partial left and right femuri, proximal right tibia, and partial right pes. Collected by Joseph Rak in the 1927 field season.

TYPE LOCALITY: F:AM 27363 is from the Skull Ridge locality, north of Pojoaque Church, south of Arroyo Seco. The only reference of the Skull Ridge locality in the 1927 field season was from a July 18, 1927 letter of Joseph Rak to Childs Frick, in which a block of specimens was described to be from Skull Ridge near Big Wash (= Joe Rak Wash of Galusha and Blick, 1971) 1 mi southeast from Two Sister Hill (probably Three Sisters Buttes). According to this latter description, the locality would be approximately in sect. 21 of T. 20 N, R. 9 E, central Española Basin, Santa Fe County, New Mexico. In his letter to Childs Frick on August 1, 1927, Joseph Rak placed F:AM 27363 within the "bottom 20 feet" of a "color sand" sequence (from top to bottom): "4 feet reddish (skull), 30 feet light brown, 1 foot blue layer, 10 feet light brown, 8–12 inch blue hard layer, 5 feet brown." The Skull Ridge locality is where the lower part (in N½ of sect. 21, T. 20 N, R. 9 E) of a composite type section of the Skull Ridge Member of Tesuque Formation was located (Galusha and Blick, 1971). An Early Barstovian age is indicated for the Skull Ridge Member by Tedford (1981: 1012).

REFERRED SPECIMENS: From the Green Hills Fauna in the Middle Barstow Formation of San Bernardino County, Early Barstovian of southern California (see Woodburne et al. [1982, 1988] for locality and faunal correlations): F:AM 27185, partial left ramus with broken c1, p2–4, m2 and complete m1, locality unknown; F:AM 27224, crushed partial right ramus with c1–m3 (c1–m1 broken), from Third Division in highest Green Hills; F:AM 27311, mandible with left p1–m2, right p2–m2, from Green Hills; F:AM 67066, left and right rami fragments with left m1 and right p3–m1 (m1 talonid missing), from Oreodon Quarry; F:AM 67088, partial left and right rami with left c1–m1 (p3 alveolus only) and right i3–m3, from Lower Green Hills; LACM 25486, left ramus fragment with m2, from "Syncline"; LACM 33808, right m2, from Rainbow Canyon.

From the Yermo Quarry, in Yermo Hills,

5 mi east of Yermo and less than 1 mi north-east of the Toomey railroad station, in SW¼, SWq1, NWq1, sect. 25, T. 10 N, R. 2 E, San Bernardino County, southern California, Middle Barstow Formation, Early Barstovi-an (see Woodburne et al. [1982, 1988] for locality and faunal correlations): F:AM 67086, left maxillary fragment with C1–M2; F:AM 67087, right maxillary fragment with P3–M2; F:AM 67089, partial mandible with left i2–c1, p2, p4–m2 and right i1–c1, p2, p4–m2; F:AM 67090, fragments of mandible with left m1–2 and right p2–m2; F:AM 67091, left maxillary fragment with dP3, P1–M2.

From the Skull Ridge Member of the Te-suque Formation, Early Barstovian of Santa Fe County, New Mexico: F:AM 27361, right maxillary fragment with P4–M1; F:AM 67116, partial left and right rami with worn left m2 and right p2, m2, other teeth broken off, from Skull Ridge.

From the Olcott Formation, Early Barsto-vian of Sioux County, Nebraska: F:AM, 54325, complete right ramus with p3–m1 and partial left ramus with c1, p2–4, from Hum-bug Quarry, "on the hill on the south side of Ranch House Draw near the center of the NW 1/4, NW 1/4, sect. 3, T. 25 N, R. 55 W" (Skinner et al., 1977: 335); F:AM 61172, left maxillary fragment with M1–2, from New Surface Quarry, "on the west side of East Sinclair Draw on a south-facing rim in the central part of the NW 1/4, NW 1/4, NE 1/4, sect. 10, T. 25 N, R. 55 W" (Skinner et al., 1977: 334); F:AM 67111, right ramus with c1, p4–m2, from Humbug Quarry (same as F:AM 54325 above); F:AM 67112, left ramus fragment with p4, from Humbug Quarry (same as above); F:AM 67113, right maxillary fragment with P1–3, from Echo Quarry, extending "along the bottom of An-telope Draw, mainly on the south side, for 1500 feet. The channel deposits are in the southeastern part of the NE 1/4, NE 1/4, SE 1/4, sect. 33, T. 26 N, R. 55 W" (Skinner et al., 1977: 335).

From the Sheep Creek Formation, Late Hemingfordian of Sioux County, Nebraska: F:AM 67092, right ramus with i1–m2, from Thomson Quarry, "on north side of Antelope Draw in the head of a small side wash near the middle of the west line of the SW 1/4, NW 1/4, SW 1/4, sect. 34, T. 26 N, R. 55

W" (Skinner et al., 1977: 325), lower Sheep Creek Formation; F:AM 67093, right ramus fragment with p4–m3, from Long Quarry (lo-cality same as above); F:AM 67094, left ra-mus with m1–2, from Thomson Quarry, "on the east side of Stonehouse Draw, about one-fourth mi below its head in the western part of the SW 1/4, SW 1/4, sect. 33, T. 26 N, R. 55 W" (Skinner et al., 1977: 325), middle Sheep Creek Formation; F:AM 67095, left ramus with p4–m1, from Hilltop Quarry, "on top of a small ridge just south of Antelope Draw in the northwest corner of the NE 1/4, SW 1/4, SW 1/4, sect. 34, T. 26 N, R. 55 W" (Skinner et al., 1977: 327), middle Sheep Creek Formation; F:AM 67096, left ramus fragment with m1–2, from Hilltop Quarry (same as above); F:AM 67097, left m1, from Hilltop Quarry (locality same as above); F:AM 67098, complete skull with left P3–M1 and right P3, alveoli for the rest of the teeth except right P4–M2, from Greenside Quarry, "in a branch of Ranch House Draw, in the northeast corner of the NE 1/4, NE 1/4, sect. 4, so near the section line that it can also be described as in the northwest cor-ner of sect. 3, T. 25 N, R. 55 W" (Skinner et al., 1977: 325), lower Sheep Creek Forma-tion; F:AM 67099, badly weathered skull fragments with left C1–M1, right M1, and postcranial fragments, from floodplain of *Merychippus* Draw, in the same drainage as *Aphelops* Draw (Skinner et al., 1977: 339), but no detailed locality data; F:AM 67100, left maxillary fragment with C1, P3–4, from Thomson Quarry (locality same as F:AM 67092); F:AM 67101, right maxillary frag-ment with P4–M1, from Long Quarry (lo-cality same as 67094); F:AM 67102, left max-illary fragment with P3–4, from *Pliohippus* Draw, "in the northeast corner of the NW 1/4, sect. 32, T. 26 N, R. 55 W, so close to the line between sections 29 and 32 that the site could be in the southeast corner of the SW 1/4, sect. 29, T. 26 N, R. 55 W" (Skinner et al., 1977: 340), Sheep Creek Formation; F:AM 67103, left maxillary fragment with P4–M1, from Thomson Quarry (locality same as F:AM 67092); F:AM 67104, left maxillary fragment with M1–2, from near Antelope Draw; F:AM 67105, left p4, from Long Quar-ry (locality same as F:AM 67094); F:AM 67106, right P4, from Thomson Quarry (lo-

cality same as F:AM 67092); F:AM 67107, left M1, from Long Quarry (locality same as F:AM 67094); F:AM 67108, left M1, no locality data; F:AM 67109, left M2, from floodplain of *Pliohippus* Draw (locality same as F:AM 67012); F:AM 67110, right M1, from Long Quarry (locality same as F:AM 67094).

From the Ginn Quarry, 4.5 mi west and 2 mi south of Hay Springs, in NEq1, NWq1, sect. 24, T. 31 N, R. 47 W, Dawes County, Nebraska, Sheep Creek Formation, Late Hemingfordian: F:AM 67114, partial right ramus with p4–m2; F:AM 67115, right ramus with p2–m2.

DIAGNOSIS: This terminal taxon of the *Osbornodon* lineage can easily be distinguished by a number of highly derived characteristics: wide nasals; extreme enlargement of frontal sinus (char. 4); very high sagittal crest and dorsally elongated nuchal crest; strong, laterally expanded zygomatic arch (char. 19, shared with *O. brachypus*); thickened basal lambdoidal crest overhanging the mastoid process; posteriorly extended paroccipital process (char. 17, shared with *O. brachypus*); elongated P4; development of a pseudoparastyle on P4 (char. 37); short angular process with reduced internal ridge; and enlarged, reclined p4 (char. 33).

ETYMOLOGY: In honor of the late Dr. Childs Frick, whose lifelong interest in fossil carnivorans and extraordinary efforts in field expeditions made possible the unique assemblage of this species in the Frick Collection.

DISTRIBUTION: Specimens of this species are currently known from three middle Miocene depositional regions of North America: (1) Sheep Creek and Olcott Formations of western Nebraska, Late Hemingfordian to Early Barstovian; (2) Middle Barstow Formation of southern California, Early Barstovian; and (3) Skull Ridge Member of Tesuque Formation of northern New Mexico, Early Barstovian. *Osbornodon fricki* is the last representative of the hesperocyonines.

DESCRIPTION: With the exception of two m2s from the LACM, the Frick Collection of the American Museum of Natural History has the entire collection of this unusual and rare species. The combined sample from Nebraska, New Mexico, and California allows a rather complete description of the cranial and dental morphology of *Osbornodon fricki*.

Skull: The holotype, F:AM 27363, is crushed in the basicranial region, which is slightly pushed anteriorly on the left side and posteriorly on the right side. The overall proportions of the skull, however, are more or less preserved. F:AM 67098 is almost completely undistorted and thus complements the deficiencies in the holotype.

The overall proportions of the skull of F:AM 27363 are similar to that of a large-sized living grey wolf. The rostrum is long, as is typical for the derived members of the genus. In dorsal view, the lateral edges of the snout parallel each other most of the way in front of the infraorbital foramen. The incisor-bearing portion of the premaxillary in front of the canines is laterally constricted to form a pinched tip of the snout. The nasal is wider, in dorsal view, than the maxillary; it gradually tapers toward the midline behind the level of infraorbital foramen. The premaxillary sends a long, slender posterior process that nearly touches the anterior process of the frontal.

In the holotype, the postorbital process of the frontal is prominent and a strong temporal ridge originates from it. The forehead above the postorbital process is flat. F:AM 67098, on the other hand, provides a striking example of the inflation of the frontal sinus that differs from the holotype. The entire frontal region of F:AM 67098 is inflated into a great dome. The top of the postorbital process is so swollen that the temporal ridges are nearly obliterated and shifted posteriorly due to differential inflation of the area in front of the temporal ridge. The postorbital process thus becomes less protruded due to the swelling of the frontal region. A 40 × 80 mm rectangle was sectioned off the right frontal of F:AM 67098 that includes the area of the postorbital process. It reveals a very large frontal sinus. The inner surface of the frontal bone is lined by widely spaced, interconnected, thin ridges less than 3 mm high. The frontal sinus expands backward to the level of the posterior end of the zygomatic arch, well past the postorbital constriction, which is usually the limit of the frontal sinus in canids. The frontal inflation is most extreme in F:AM 67098 but is less so in the holotype and in F:AM 67099 (from Nebraska, as is F:AM 67098).
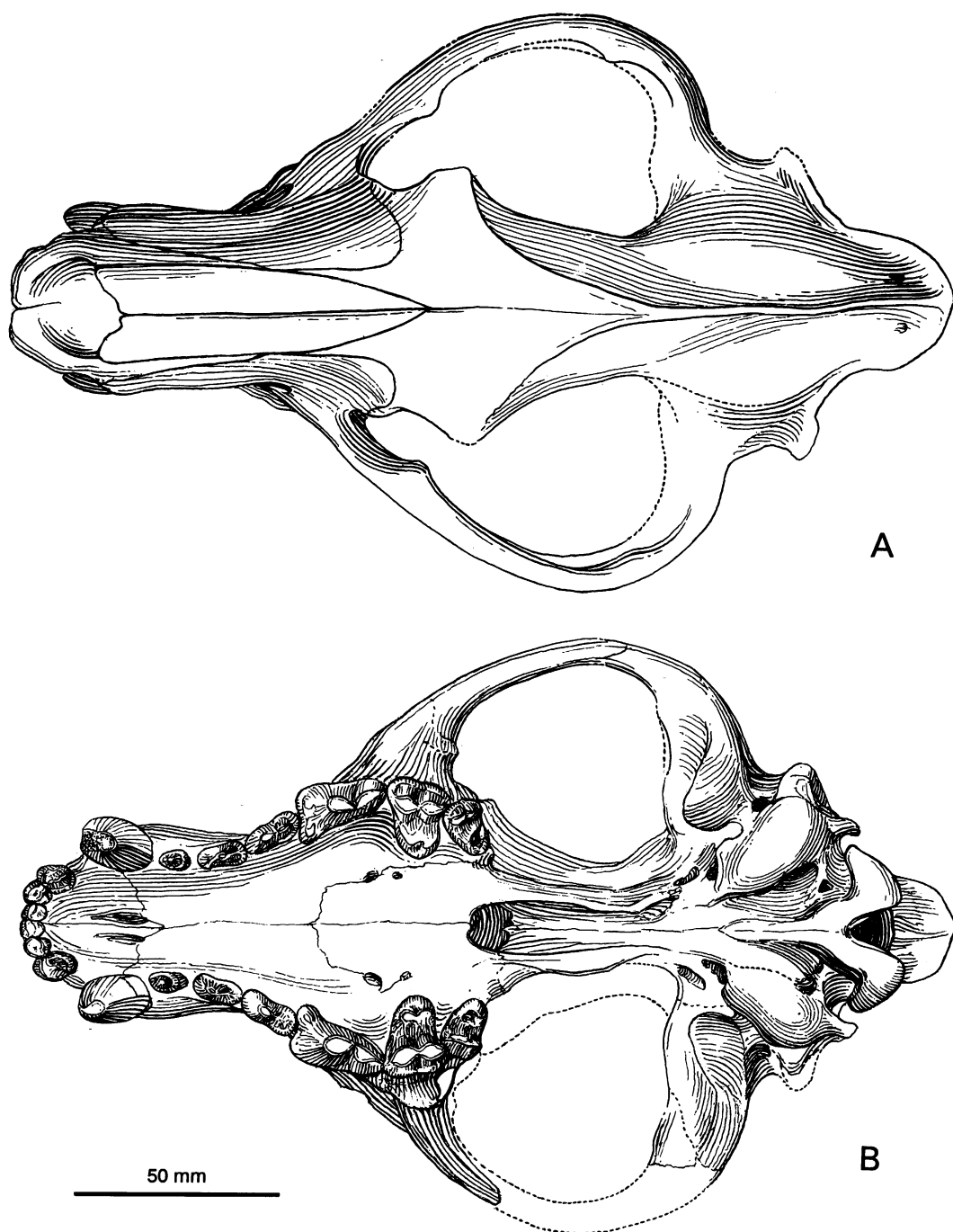
Fig. 38.   Skull of *Osbornodon fricki*, F:AM 27363, holotype. **A**, Dorsal view of skull, and **B**, ventral view of skull, left P1 and P4 drawn from reverse images of right side. Illustrated by Frick's artists.

The sagittal crest reaches a height of up to 20 mm in the holotype. The highest point is near the convergence of the temporal crests.

Posterior to this high point, the sagittal crest gently curves downward, in lateral profile, toward the posterior end. F:AM 67098 and
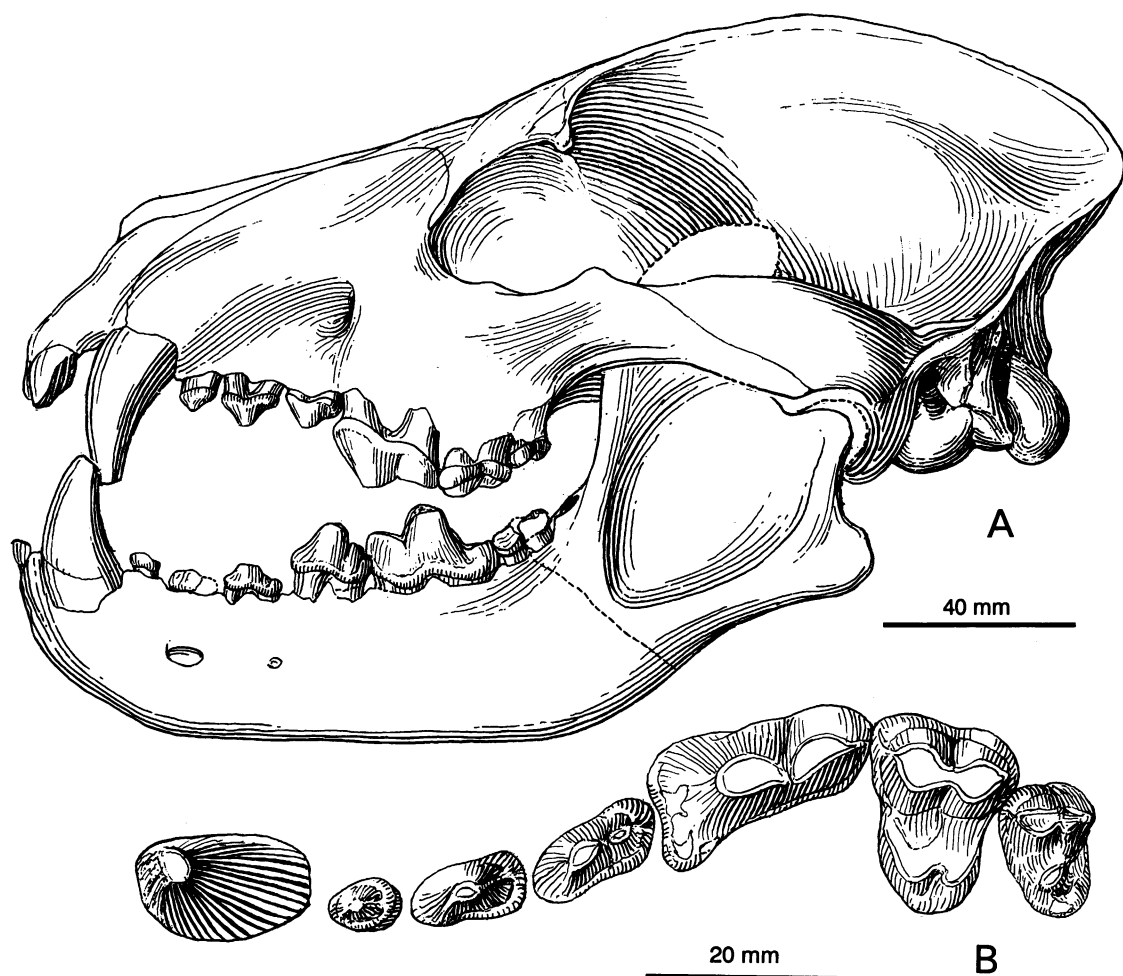
Fig. 39.   Skull, mandible, and upper dentition of *Osbornodon fricki*, F:AM 27363, holotype. A, Lateral views of skull and mandible (reverse of right side); **B**, occlusal view of upper left teeth, P1 and P4 drawn from reverse images of right side. Illustrated by Frick's artists.

67099 vary from the holotype's domed profile and have a straight top border of the sagittal crest in lateral view. In posterior view, the raised sagittal crest also elevates the nuchal crest into a narrow triangle high above the foramen magnum. However, the high nuchal crest does not overhang the occipital condyle as in other taxa with high nuchal crests (e.g., *Enhydrocyon*).

In posterior view, the lambdoidal crest is slightly constricted in the midsection, and then stretches laterally to stop at the mastoid process. Along the dorsal margin of the nuchal crest in posterior view are a pair of distinct grooves for the rhomboideus and sple-

nius muscles. For a robust species such as *Osbornodon fricki*, the supraoccipital shield is quite smooth, unlike the deeply indented supraoccipital surfaces in *Philotrox condoni* and *Enhydrocyon pahinsintewakpa*. There is a narrow and low external occipital crest extending from the tip of the inion down to the dorsal edge of foramen magnum.

In lateral view of F:AM 67098, the premaxillary is procumbent so that the incisors are directed more forwardly than is the case in the holotype, whose upper incisors point downward. The infraorbital foramen is slitlike in cross section in contrast to a rounded cross section in more primitive species of *Os-*

Fig. 40. Skull and mandible of *Osbornodon fricki*. **A**, Lateral view of F:AM 67098, and **B**, lateral view of F:AM 54325, reversed from right side. Scale = 40 mm.

bornodon. Like most other large-sized canids, the zygomatic arch is expanded laterally, making room for the large temporalis muscles, also indicated by the high sagittal crest. The zygomatic arch is deep and strongly built.

In ventral view, the anterior palate region is narrow. The posterior border of the palate is slightly anterior to the caudal edge of the M2. The pterygoid wing has a gentle ventral curve in the holotype but is more ventrally extended in F:AM 67098. The bullae of the holotype are mediolaterally crushed and the present description is mainly based on those on F:AM 67098. The bulla is relatively small, as is characteristic of the genus. It is less inflated and rounded than that of *Mesocyon* and *Enhydrocyon*, probably because of relatively smaller contribution of the caudal en-

totympanic to the ossified bulla, although the actual ecto-entotympanic suture is not clearly visible. The anterior end of the long axis of the bulla tilts toward the midline in contrast to a more anteroposteriorly oriented bulla of other hesperocyonines. In F:AM 67098, the lateral edge of the external auditory meatus forms a short, incomplete bony tube as a lateral extension of the ectotympanic; no bony tube is found in the holotype. There is a pair of prominent muscular tubercles (sensu Evans and Christensen, 1979: 123) between the bullae on the basioccipital/basisphenoid suture. This tubercle is for the insertion of the longus capitis muscle in living domestic dogs (ibid.: 315).

The paroccipital process points mostly downward. It extends backward to form an

anteroposteriorly oriented plate attached to the posterior end of the bulla. An extreme development of this posterior elongation of the paroccipital process can be seen in F:AM 67098 and 67099, in which the process becomes a quadrate plate in lateral view that is almost as wide (anteroposteriorly) as it is long (dorsoventrally) (fig. 60E). This elongated paroccipital process is also seen in *Osbornodon brachypus*. The cupping of the bulla by the paroccipital process is not extensive. The mastoid process is ventrally elongated and remains primitive with an uninflated, rough lateral surface. Its posterior surface is overhung by a prominent basal lambdoidal crest. A similar configuration of the mastoid process is also seen in *O. brachypus* and *O. iamonensis*.

Mandible: The mandible of *Osbornodon fricki* is long, in keeping with the elongated skull. Compared to the holotype from New Mexico, mandibles of the Nebraska individuals (e.g., F:AM 54325) are slightly longer and more slender. The horizontal rami of some California individuals (e.g., F:AM 27185, 27334, and 67090) are swollen due to expansion of the sediments inside (horizontal cracks filled with matrix are seen on the surface of the rami). The ascending ramus is relatively high in contrast to a low coronoid process in *O. brachypus*. The masseteric fossa is also relatively shallow compared to that of the latter. The angular process is short and blunt in *O. fricki*. The internal ridge, which serves to divide the superior (upper) and inferior (lower) rami of the medial pterygoideus muscles, is reduced to a low ridge. The area of attachment for the inferior ramus of the medial pterygoideus is relatively expanded.

Dentition: The upper dentition of the holotype is nearly completely preserved; the wear on its teeth is moderate. The upper incisors are recumbent in the holotype in contrast to the more precumbent condition in F:AM 67098 as reflected by the alveoli of its incisors. The incisor tips are worn, making it difficult to recognize morphological detail. The I3 is nearly twice as large as I2 or I1, and has a large, vertical wear facet on the posterolateral corner. The upper canine is long and relatively slender, and there is a low ridge on both anterior and posterior surfaces. The premolars are widely spaced, corresponding

to the relatively long rostrum (F:AM 67098 has the most widely spaced premolars). The P1 has a single main cusp with a single root and a small ridge both anteriorly and posteriorly. The P2 has strong double roots and a single, low main cusp. An anterior crest leading from the main cusp turns lingually, stopping at the base on the medial side. There is a large, but low posterior cingular cusp on P2. The P3 is also low and has an anteroposteriorly elongated outline. It has a conspicuous posterior accessory and a posterior cingular cusp. The contacts of the upper premolars (excluding P4) with the corresponding lowers are very limited due to their low principal cusps. This is particularly evidenced in F:AM 67098, which has well-worn P4–M1 but has only a slightly flattened tip of the P3 main cusp. In the holotype, the protocone of the P4 is appressed toward the base of the paracone and it is still more reduced in F:AM 27361. There is a low ridge on the anterior face of the paracone in most of the specimens. The California and New Mexico samples tend to have a more distinct ridge that may develop a notch to form a pseudoparastyle, which is best developed in F:AM 27361. A cingulum is present in the medial side in the posterior half of P4. Due to its less acute anterolabial corner of the paracone, the M1 is more quadrate in outline than that of the *Mesocyon–Enhydrocyon* clade. The paracone is larger than the metacone. There is a cingulumlike parastyle raised to the level of the P4 metacone crest. The labial cingulum of M1 tends to be reduced compared to more primitive members of *Osbornodon*. The lingual half of the M1 is wide, as it generally is for the genus. The protocone is small and overshadowed by the high paracone–metacone ridge. In all specimens examined, there is a small, crestlike metaconule continuous with the postprotocrista. However, instead of connecting to the lingual side of the metacone, the metaconule continues posteriorly and is connected with the posterior cingulum. There is a low transverse ridge between the posterior surface of the protocone and the internal cingulum in all individuals from western Nebraska, but not in New Mexico and California specimens. The internal cingulum is raised to form a posteromedial crest on M1. This crest becomes a distinct hypo-

cone in F:AM 67086 but not in any other individual. This hypocone is probably an individual variation since it is not present on the M2 of this individual. The M2 is relatively enlarged. Like the M1, the paracone is larger than the metacone. There is a relatively larger internal cingulum in M2 than in M1.

Three isolated lower incisors are preserved along with the mandible of the holotype (attached to the right mandible during preparation), and there is a broken root of i2 still in situ, indicating that at least one of the three incisors does not belong to the right ramus. Two of the incisors are almost identical, with triangular cross sections and long roots. The third is slightly stronger and has a shorter root. The wear on these incisors makes it difficult to further determine the morphology of the cusps. The lower canine has a long, anterior wear facet caused by the I3. The p1 is small, single-rooted, and single-cusped. The p2 and p3 are almost identical in size whereas p4 is much larger. Instead of the gradually increasing sizes of p2–4 in the majority of hesperocyonines, p4 of *O. fricki* is greatly enlarged whereas the p3 is significantly reduced. This large size difference of premolars is only seen in advanced *Osbornodon* species, and can be found in hypercarnivorous borophagines such as *Epicyon*, *Osteoborus*, and *Borophagus*. Behind the p2 main cusp there is a low cingulum. This cingulum is progressively enlarged in p3 and p4. The p3 and p4 have a posterior accessory cusp, which varies in size. The p4 is a distinctive tooth in the advanced species of *Osbornodon*—not only is it greatly enlarged over that of the p3, but its position is shifted backward toward the m1 so that there is usually a large overlap between p4 and m1 in contrast to the long diastemata separating the more anterior premolars. The strong main cusp of p4 is tilted posteriorly; its distinct posterior accessory cusp occludes with the protocone of P4. This pattern of differential growth of lower premolars also contrasts with the upper premolar series (P1–3), which are far more uniformly sized. On m1, the paraconid–protoconid blade is strongly built. The metaconid is more reduced than in *O. brachypus*, continuing a trend of metaconid reduction that is started in the latter. The metaconid is slightly shifted posteriorly so that it is not

aligned with the posterior face of the protoconid. Although the talonid still maintains an essentially basined structure, the hypoconid of *O. fricki* has become larger than the entoconid. The size and shape of the entoconid varies among individuals, ranging from a low ridge in F:AM 67088 to a more distinct crest in F:AM 27185. The most prominent feature of the m2 is a high trigonid relative to its talonid. In many specimens, the protoconid and metaconid are connected, forming a transverse ridge high above the talonid. The notch between the protoconid and metaconid is shallow such that the two cusps form a more or less continuous blade rather than individual cusps. The talonid of the m2 is a broad basin surrounded labially by a hypoconid ridge and lingually by a low entoconid rim. The m3 is nearly rounded in outline and has a transversely oriented low ridge that represents the protoconid and metaconid.

DISCUSSION: *Osbornodon fricki* is the largest known hesperocyonine in terms of its total skull length. It developed dental features commonly found in hypercarnivorous canids, such as an elongated P4 (seen in parallel in *Enhydrocyon*), a robust p4 joining the lower carnassial as part of a more efficient shearing mechanism (also found in advanced borophagines), and a reduced m1 metaconid. On the other hand, *O. fricki* possesses dental characters that are typical of mesocarnivorous canids: quadrate M1, relatively enlarged M2 and m2, and basined talonid of lower molars. It is this mosaic of characters that distinguishes *O. fricki* from the rest of the hesperocyonines.

Although *Osbornodon fricki* is an end member of a long line of descent, some of its characteristics can be traced to the earlier members of the lineage, for example, relatively long rostrum, slender premolars, quadrate upper molars, enlarged M2, and basined talonids of lower molars. Most of these characters have gone through further modifications in *O. fricki*, but their basic form remains unchanged.

Osbornodon renjiei, new species
Figures 41, 42E–G

?*Cynodictis* sp. maj. Matthew, 1899: 54 (AMNH 1382 and 1386).

?*Cynodictis temnodon* Wortman and Matthew, 1899: 130 (in part as above).
Cynodictis temnodon (Wortman and Matthew) Matthew, 1901: 370 (in part as above).
Pseudocynodictis temnodon (Wortman and Matthew) Matthew, 1918: 189 (in part as above).
Pseudocynodictis sp. Hough, 1948a: 97.

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

TYPE LOCALITY: F:AM Leo Fitterer Ranch locality, 13 mi south and 8 mi west of Dickinson, in sect. 7, T. 137 N, R. 97 W, Stark County, North Dakota. F:AM 63316 was found above the nodular zone in a local channel (the "Fitterer Channel") in unit 5 of Skinner's (1951) stratigraphic column. This was correlated with the "clays above nodules," that is, the "Middle Oreodon Zone," Late Orellan.

REFERRED SPECIMENS: From the "Protoceras beds" near Cheyanne River, Whitneyan of South Dakota: AMNH 1382, partial, laterally crushed skull with left I3, P1–M2, right I2–C1, P2–M2, and the remaining alveoli; AMNH 1386, partial, dorsoventrally crushed skull with left and right P4–M2 and remaining postcanine alveoli. See comments on the holotype of "*Mesocyon*" *temnodon* for historical references of these two specimens.

From Leo Fitterer Ranch locality (see Type Locality), Stark County, North Dakota, Late Orellan: F:AM 63315, right ramus fragment with p2–m1, from above the nodules in talus; F:AM 63317, right P4, from 15 ft above the base of Fitterer Channel deposit that occurs stratigraphically 8 ft above the White Zone (separating the nodular zone from clays above); F:AM 63318, right ramus fragment with p3–m1, from 15 ft above the base of Fitterer Channel.

From Weitzel Ranch, 6 mi north of Mitchell, 0.5 mi east of Highway 29, S½, sect. 22, T. 24 N, T. 56 W, Sioux County, Nebraska, from 80 ft below the Lower Ash, Whitney Member, Brule Formation, Whitneyan age: F:AM 63963, rostral part of skull and mandible with entire dentition except broken left M1–2 and missing right P1–3.

DIAGNOSIS: Smallest of all *Osbornodon*, *O. renjiei* is also the most primitive species of the genus, and is distinguishable from the rest of the *Osbornodon* by its lack of the derived

characters listed in the diagnoses of subsequent species. *Osbornodon renjiei* can be distinguished from other primitive hesperocyonines on several derived characters: a posteroventrally oriented paroccipital process (char. 14, shared with the *Mesocyon–Enhydrocyon* clade); a more quadrate M1 and a relatively enlarged M2 (char. 39); and a basined talonid of m1 enclosed by a well-developed entoconid crest (char. 45) (the latter two synapomorphies also characterize the genus). In addition, it has a tendency for an anteriorly positioned trigonid on m2.

DISTRIBUTION: Late Orellan of southwestern North Dakota; Whitneyan of southwestern South Dakota and western Nebraska.

ETYMOLOGY: In honor of professor Zhai Renjie, the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences.

DESCRIPTION: The selection of F:AM 63316 as the holotype, rather than the two referred skulls (AMNH 1382 and 1386), reflects its more complete upper and lower dentitions. *Osbornodon renjiei* is largely recognized through the tooth morphology. Except for the ventrally bent paroccipital process and the quadrate upper molars, the crushed skulls offer little in terms of useful diagnostic features (particularly their lack of lower molars to indicate the talonid morphology, one of the most important characters of the genus).

Skull: The two referred skulls from the Whitneyan of South Dakota (AMNH 1382 and 1386) form the main basis of comparison for *Osbornodon renjiei*. Both skulls are crushed, mediolaterally in AMNH 1382 and dorsoventrally in AMNH 1386. In addition, the bony surface of AMNH 1382 also suffered severe weathering, and the suture lines are mostly obliterated.

Despite its larger size, the cranial morphology of *Osbornodon renjiei* is little different from that of *Hesperocyon*, as has been suggested by Wortman and Matthew (1899). The rostrum is not elongated, as it is in more advanced *Osbornodon*. The posterior process of the premaxillary is long but not in contact with the anterior process of the frontal. The degree of frontal inflation is difficult to determine because of the distortions on both skulls, but probably is small or absent because of the flat forehead and the relatively
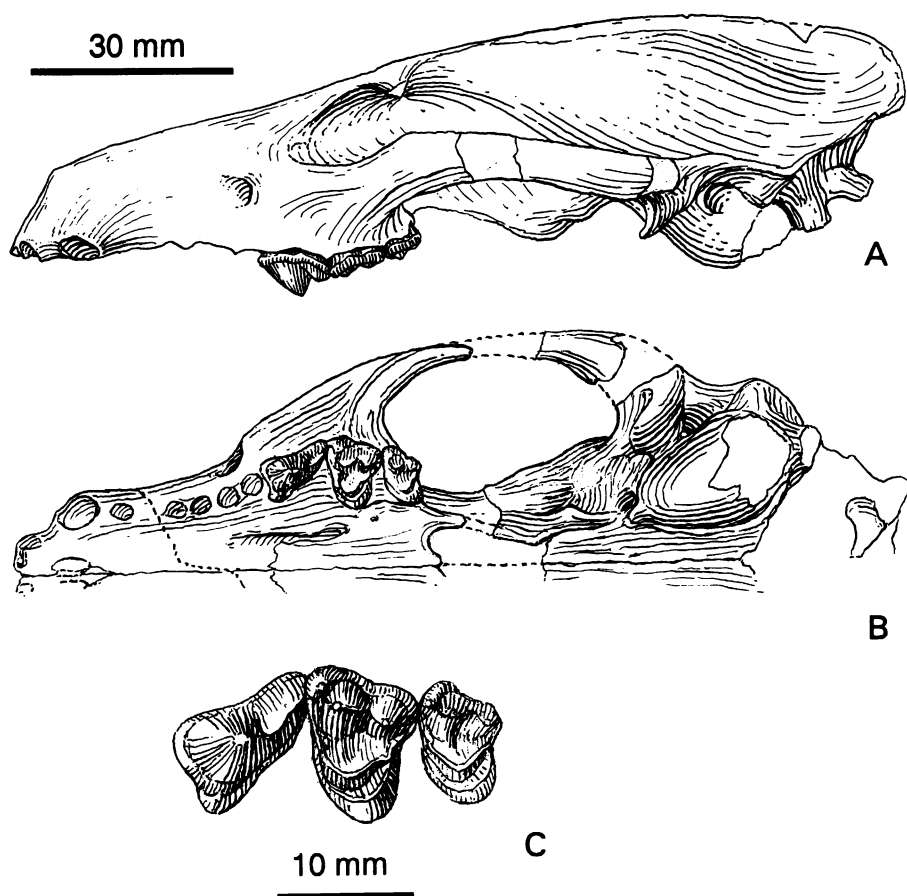
Fig. 41. Skull and upper teeth of *Osbornodon renjiei*, AMNH 1386. **A**, Lateral, **B**, ventral views of skull; and **C**, enlarged occlusal view of P4–M2. The basicranial region and the middle portion of the zygomatic arch in A and B are reconstructed from those of right side. Illustrated by Frick's artists.

anteriorly positioned postorbital constriction. The sagittal crest is low, about 1–2 mm above the top of the skull roof. The dorsal part of the nuchal crest is fan-shaped in the posterior view. The occipital shield has a smooth surface free of distinct muscle scars or pits often found in larger canids.

The pterygoid wings are thick-bladed and form a gentle, ventrally curved outline in the lateral view. The postglenoid process is stout with a thick base. The right basicranium in AMNH 1386 is better preserved despite its damage in the posterior quarter. The bulla is relatively long in contrast to the anteroposteriorly shortened bullae present in more derived species of *Osbornodon*. The paroccipital processes in both of the referred skulls are broken and the remaining basal parts,

especially in AMNH 1386, indicate a predominantly ventrally oriented process, one of the few cranial features more derived than in *Hesperocyon* and shared with the *Mesocyon–Enhydrocyon* clade to the exclusion of the *Paraenhydrocyon* clade. The paroccipital process also exhibits a peculiar anteroposterior compression. The mastoid process is small but not as reduced as in advanced *Osbornodon*.

Mandible: There are only fragments of the horizontal rami (mostly the type) for *Osbornodon renjiei*, offering few useful characters for comparison. Overall, they do not seem to differ from those seen in *Hesperocyon* and *Mesocyon*.

Dentition: The I2 and I3 on AMNH 1382 show a single main cusp although both have
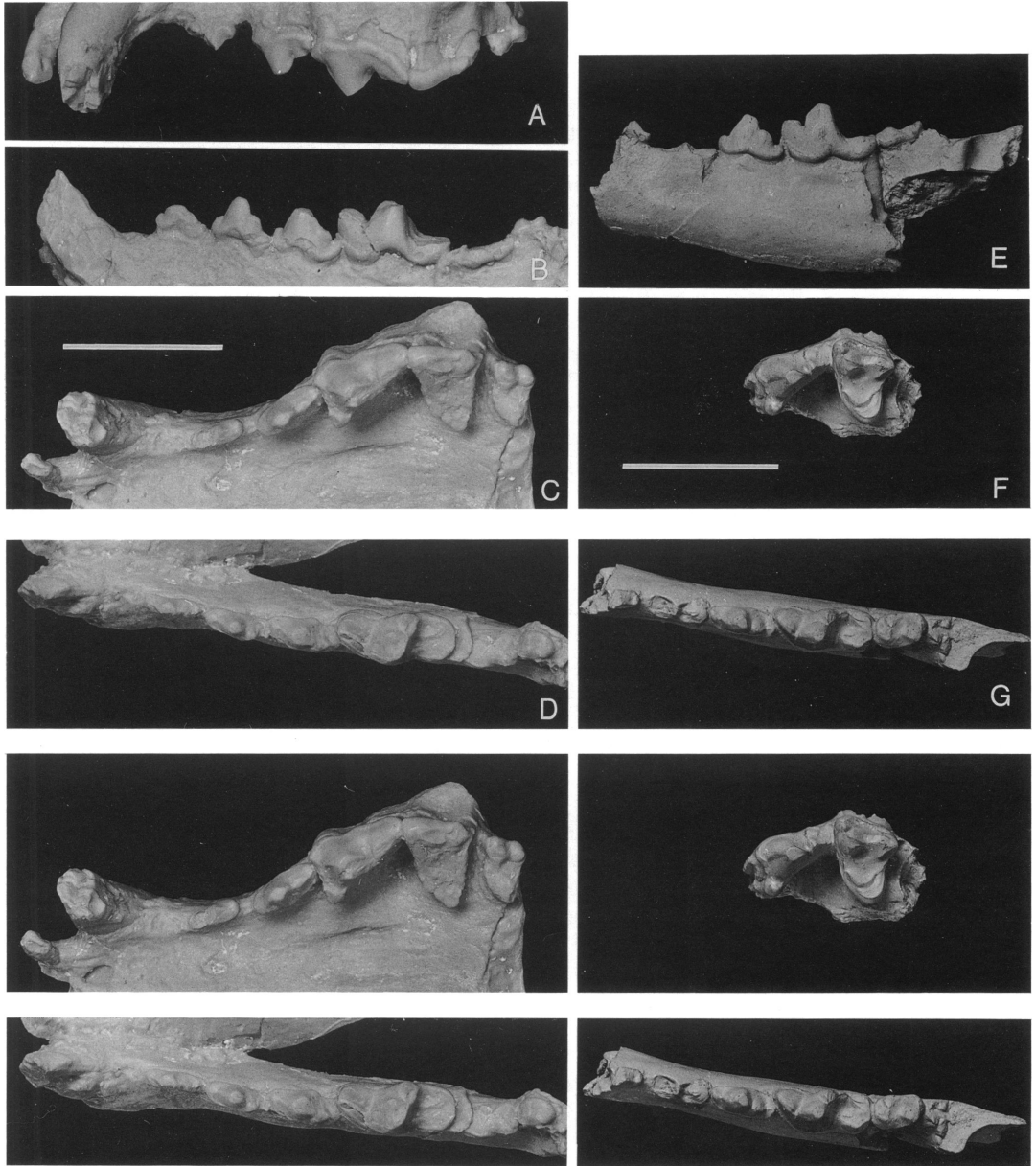
Fig. 42.   Teeth of primitive *Osbornodon*. A–D, *O. sesnoni*, LACM 17039, holotype, photographed from epoxy casts; E–G, *O. renjiei*, F:AM 63316, holotype. A, Lateral view of upper teeth (reversed from right side); B, lateral view of lower teeth; C, occlusal view of upper teeth (in stereo and reversed); D, occlusal view of lower teeth (in stereo); E, lateral view of mandible (reversed); F, occlusal view of upper teeth (in stereo and reversed); G, occlusal view of lower teeth (in stereo and reversed). Scales = 20 mm.

sustained enough wear that an accessory cusp may have been present. There is a small bulge on the I3, indicating the presence of a basal cusp on the lingual surface medial to a long wear facet. The upper canine is slender and long with vague anteromedial and posterior ridges. The P1 is single-rooted and single-cusped. The P2 has an incipient posterior cingular cusp, which becomes a distinct cusp on the P3. The occlusal outline of the P3 is

still primitively short and is distinct from the elongated morphology in *Osbornodon sesnoni* and more advanced species. The size and relative position of the P4 protocone appear to vary in different localities and ages. The North Dakota Orellan specimens have large, anteriorly positioned protocones, whereas those from the South Dakota Whitneyan specimens are smaller and located on the medial side of the paracones; the latter feature was used by Wortman and Matthew (1899: 130) in their diagnosis of *Cynodictis temnodon*. Overall, the size of the P4 protocone is slightly smaller than that of "*Mesocyon*" *temnodon*.

The upper molars are lengthened (anteroposteriorly) and become more quadrate in outline. This is particularly obvious in AMNH 1386, which represents a more extreme case among members of the species (see paragraph below). The rest of the specimens (AMNH 1382, F:AM 63316 and 63963), however, are less quadrate. Although not to be relied upon exclusively, this less transversely elongated appearance of M1 in *Osbornodon renjiei* can be used to distinguish it from *Paraenhydrocyon josephi*, which is of the same size-class and general morphology. The parastyle on M1 is less well developed than in *Paraenhydrocyon*. The distinction of upper molars between *P. renjiei* and "*Mesocyon*" *temnodon* is more subtle and sometimes almost impossible without associated lower teeth. In general, the waist of M1 at the level of the trigon basin is wider in *O. renjiei*. The enlargement of the M2 in *O. renjiei* is also at the beginning stage so that some individuals (e.g., F:AM 63963) with small M2 are indistinguishable from that of "*M.*" *temnodon*, whereas others (e.g., AMNH 1386) clearly demonstrate the *Osbornodon* specialization.

The overall morphology of the upper teeth in AMNH 1386 (P4–M2) is rather different from that of the rest of the sample. Its relatively small P4 with reduced protocone and large M1–2 with quadrate outlines are interpreted here as variation rather than as representing a distinct species because of the more normal appearance of AMNH 1382, presumably from the same locality and stratigraphic level. The skulls of these two specimens are otherwise quite similar. AMNH

1386 is thus tentatively included in *Osbornodon renjiei*.

The lower incisors on F:AM 63963 are worn flat but still show remains of a shallow groove on the lingual side of i2–3. The lower canine has a posterior ridge in the preserved basal segment. The lower premolars are little different from other small, primitive hesperocyonines. A small, simple p1 is present on all specimens examined (single-rooted). Anterior and posterior cingular cusps are present in all p2s, but the posterior cingular cusp is rather vague in the holotype. Some individuals have a posterior accessory cusp on the p2. All specimens, except F:AM 63963, have a posterior accessory cusp on p3. All p4s have acquired the posterior accessory cusp. Like the upper premolars, the lower premolars are not transversely narrowed as in *Osbornodon sesnoni*. The trigonid of m1 is similar to that of "*Mesocyon*" *temnodon* and *P. josephi*. The basined talonid of m1, however, is different from either of the above. The entoconid is noticeably enlarged and raised to approximately the same height as the hypoconid, which still remains the larger cusp of the two (in occlusal view). The talonid basin, or valley, opens posteriorly. F:AM 63315 is unique in having a cingulum on the lateral side of the hypoconid that gives the talonid a widened appearance. Two specimens have an m2 (F:AM 63316 and 63963); both display an anteriorly positioned protoconid–metaconid ridge. The trigonid is thus anteroposteriorly shortened and no room is left for a paraconid. Only F:AM 63963 has an m3 that has a single distinct protoconid with a transverse ridge on its lingual side.

Osbornodon sesnoni
(Macdonald, 1967)
Figure 42A–D

Brachyrhynchocyon sesnoni Macdonald, 1967a: 1; 1970: 61.

HOLOTYPE: LACM 17039, partial skull and mandible with left P1–M2, right I3–C1, P2–M2, left c1, p2–m3, and right c1, p3–m1; postcranial fragments. Collected by Harley Garbani of Los Angeles County Museum of Natural History field party in 1964.

TYPE LOCALITY: "LACM loc. no. 2002, Wolff Ranch Badlands, Shannon County,

South Dakota. Poleslide member of Brule formation in ten foot red layer lying 110 to 120 feet above base of Poleslide member and 130 to 140 feet below the base of the Sharps formation" (Macdonald, 1967a), Whitneyan in age.

REFERRED SPECIMENS: In Poleslide Member of Brule Formation, Whitneyan of southwestern South Dakota: F:AM 63378, left ramus fragment with p4–m1, from north of Cedar Pass, at the base of Leptauchenia beds, Jackson County; SDSM 6836, anterior half skull with left P2–M2 and right P2–3, M1, left ramus with p2–m2, from Wolff Ranch, Shannon County; SDSM 54125, left ramus fragment with p3–m1, from Grass Creek, sect. 23, T. 39 N, R. 45 W, Shannon County.

EMENDED DIAGNOSIS: Besides being larger, Osbornodon sesnoni is more derived than O. renjiei in its elongated and robust paroccipital process (char. 15) and in its slender (high length/width ratio) upper and lower premolars (except P4) with a prominent posterior accessory cusp (char. 29). Compared to O. iamonensis and the more derived Osbornodon, O. sesnoni shows the following primitive characteristics: unelongated rostrum; low sagittal crest; lack of an inflated frontal sinus; a round infraorbital foramen; bulla not shortened; paroccipital process not posteriorly expanded; mastoid process not reduced; p4 not enlarged; and an M2 less enlarged relative to M1.

DISTRIBUTION: Poleslide Member of Brule Formation, Whitneyan of southwestern South Dakota.

DESCRIPTION: Osbornodon sesnoni was founded on a fragmentary skull and mandible with badly worn upper and lower teeth. Additional materials referred to it in this study do not add significantly to the knowledge of its anatomy.

Skull: The holotype lacks most of the basicranial region and is broken into two parts at the postorbital constriction. In dorsal view, the overall form of the skull of Osbornodon sesnoni is little different from similar-sized "Mesocyon" temnodon or Paraenhydrocyon josephi, and has not acquired the elongated skull typical of more derived Osbornodon. The postorbital process of the frontal is less well developed than that in Mesocyon brachyops. The external appearance of the frontal regions suggests an uninflated frontal sinus, unlike O. iamonensis and more derived Osbornodon. The postorbital constriction is not significantly shifted posteriorly as in O. iamonensis and more derived species. The sagittal crest remains unchanged from that in O. renjiei and is far lower than in O. iamonensis. The nuchal crest is partially preserved on the holotype and is slightly posteriorly extended. The infraorbital foramen is still primitively rounded in cross section in contrast to a mediolaterally narrowed, slitlike opening in O. iamonensis and later species.

Mandible: Even with the addition of the partial mandible of SDSM 6836, the holotype is still the primary basis for comparison with the ramus of Osbornodon sesnoni. The horizontal rami of LACM 17039 are relatively deeper and more robust than that of primitive Paraenhydrocyon. The anterior half gradually tapers from a maximum depth underneath m1; this contrasts with that of Paraenhydrocyon, which has a more uniform depth throughout. The ascending rami on LACM 17039 and SDSM 6836 are broken off shortly after the m3, and no angular process is preserved.

Dentition: The upper canines are poorly preserved in all of the specimens. Osbornodon sesnoni begins to exhibit slender premolars characteristic of the genus. The upper and lower premolars are anteroposteriorly elongated, but they remain narrow. The P1 and p1 are single-rooted. The P2–3 and p2–4 commonly have posterior accessory and cingular cusps, whereas the lower premolars (excluding p1) also have anterior cingular cusps. As in more advanced species of Osbornodon, the posterior accessory cusp of the P3 in the holotype is low and the posterior edge of its principal cusp forms a rather steep angle with the plane of the palate, giving the principal cusp an asymmetrical appearance in lateral view. The P4 is little changed from the primitive structure in O. renjiei. It has a small protocone and a well-developed anterior cingulum in front of the parastyle.

The upper molars of the holotype have sustained so much wear that even their outlines have been significantly altered, leaving an impression of a much narrower M1 and M2. On SDSM 6836, an individual with far less wear on the teeth, the M1 exhibits a quadrate

outline typical of *Osbornodon*. The M1 parastyle is poorly developed. Its paracone is slightly larger than the metacone. The M2 is also large but less so than in *O. iamonensis* and *O. fricki*. The enlargement of the M2 takes the form of proportional increase of size rather than just the swollen internal cingulum seen in the latter two species.

The m1 in the holotype has a wide talonid, whereas that on SDSM 6836 is less so. Although worn nearly flat, the entoconid ridge of the holotype can still be seen to be rather wide on the m1 talonid. On the unworn m1 of SDSM 6836, the relatively narrow talonid seems to be a result of a narrow entoconid crest. The occlusal surface of m2 in the holotype is too worn to offer any detail. That of SDSM 6836, however, clearly shows an elongated m2, corresponding to the large M2. The m3 on the holotype still retains two equal-sized cusps: the protoconid and metaconid.

Osbornodon sesnoni exhibits a wear pattern of the premolars that is typical of *Osbornodon*. Despite the severe wear of the upper molars on the holotype, its P3 is still relatively unworn with only the tip of the main cusp flattened off. This lack of wear to the premolars is due to their relatively low main cusps, and is commonly found in more advanced species of *Osbornodon*.

DISCUSSION: Macdonald erected two species under *Brachyrhynchocyon*: *B. sesnoni* Macdonald, 1967, and *B. douglasi* Macdonald, 1970. In neither case did he state the morphological basis of these assignments to the genus *Brachyrhynchocyon* Scott and Jepsen, 1936. The genotypic species *Brachicyon intermedius* Loomis, 1931 (*Brachyrhynchocyon intermedius*, nom. nov. (Loomis) Scott and Jepsen, 1936: 81) is an amphicyonid (R. Hunt, personal commun., 1991), whereas Macdonald's two species are canids. *Brachyrhynchocyon douglasi* Macdonald, 1970, is a junior synonym of *Cynodesmus thooides* Scott, 1893 (see discussion under this species).

Osbornodon iamonensis
(Sellards, 1916)
Figures 43, 44

Mesocyon? iamonensis Sellards, 1916: 88.
Mesocyon iamonensis (Sellards) Simpson, 1930: 160.

?Cynodesmus iamonensis (Sellards) Simpson, 1932: 14.
Cynodesmus nobilis Simpson, 1932: 17. White, 1941: 91.
Paradaphoenus nobilis (Simpson) White, 1942: 5.
Paradaphoenus tropicalis White, 1942: 5.
Parictis bathygenus White, 1947: 500 (MCZ 3930).
Cynodesmus iamonensis (Sellards) Olsen, 1956: 5.

HOLOTYPE: USNM 8836 (formerly FGS 5082), right maxillary fragment with P4–M2. Collected by E. H. Sellards and party in November 1915.

TYPE LOCALITY: 15 mi north of Tallahassee, Griscom Plantation (or Luna Plantation as it is known today), sect. 32, T. 3 N, R. 1 E, Leon County, Florida. The holotype was discovered in a bone-bearing layer in a water well approximately 50 ft below the surface. Bryant et al. (1992: fig. 6) placed the Griscom Plantation local fauna in the lower Torreya Formation (below the Dogtown Member) of Early to Medial Hemingfordian age. The fauna from this limited excavation can best be correlated with that from the Thomas Farm quarry to the south in Gilchrist County, where most of the *O. iamonensis* sample came from.

REFERRED SPECIMENS: From the Thomas Farm locality (all specimens from the Thomas Farm locality are probably from a single quarry [Olsen, 1959]), Gilchrist County, Hawthorn Formation, medial Hemingfordian of Florida: FGS V5255, partial left ramus with p3–m2, holotype of *Cynodesmus nobilis* Simpson (1932); FGS V5256, right maxillary fragment with P4–M1, paratype of *C. nobilis* Simpson (1932); FGS V5259, right maxillary fragment with M1–2, paratype of *C. nobilis* Simpson (1932); MCZ 3563, restored skull with left and right P4–M2; MCZ 3633, left ramus fragment with m1–2; MCZ 3661, crushed skull with left and right P4–M2 and left canine; MCZ 3662, skull fragments with left M2 and right P4–M2; MCZ 3714, left ramus with p2–m2, paratype of *Paradaphaenus tropicalis* White (1942: pl. 4, fig. 1); MCZ 3724, left maxillary fragment with P4–M2 and left ramus with p4–m1, referred to *Paradaphaenus nobilis* White (1942: pl. 3, fig. 1); MCZ 3725, left maxillary fragment with P4–M2, referred to *P. nobilis* White (1942: pl. 2, fig. 1); MCZ 3729, right maxillary fragment with P4–M2, holotype of *P. tropicalis* White (1942: pl. 1, fig. 2); MCZ 3923, max-

illary fragments with left P4–M2 and right P4–M1; MCZ 3930, partial palate with left and right P4–M2; MCZ 3965, left ramus with p2–m2; MCZ 3966, right ramus fragment with p4–m1; MCZ 4044, partial crushed skull with left and right P4–M2; MCZ 4330, right ramus fragment with p3–m2; MCZ 4342, left maxillary fragment with P4–M2; MCZ 4358, crushed skull with left P4–M2 and right P2–M2; MCZ 4521, left ramus with p3–m2; MCZ 7149, crushed skull with left M1–2 and right P4–M1; MCZ 7150, partial crushed skull with left P4–M2 and right P4–M1; MCZ 7151, right ramus fragment with m2; MCZ 7153, crushed skull with left P2–M2 and right P4–M2; MCZ 7309, left ramus with p2–m2; MCZ 7329, partial right maxillary with P4–M2; MCZ 7591, left ramus fragment with p4–m1; MCZ 9850, right ramus fragment with p4–m2; SDSM 523 (formerly MCZ 4331), left ramus with p2–m2.

From western Nebraska: F:AM 128763, nearly complete skull with left and right P4 and right M2, from Dry Creek, Prospect B, SE¼, SE¼, sect. 15, T. 28 N, R. 49 W (Galusha, 1975b: 24), Box Butte County, Nebraska, Box Butte Formation, early Late Hemingfordian; UM 528, crushed skull with left and right P3–M2 and alveoli of the rest of the teeth, near Harrison, Marsland Formation of Sioux County, Nebraska, Late Arikareean; UNSM 25661, crushed rostral part of skull with left and right P3–M2 and alveoli of the rest of the teeth, from Runningwater Formation of Box Butte County, Nebraska, Early Hemingfordian; USNM 25809, partial right ramus with c1 and p2–m2, from Bridgeport Quarry 1, Runningwater Formation, Morrill County, Nebraska, Early Hemingfordian.

EMENDED DIAGNOSIS: *Osbornodon iamonensis* possesses derived characters that set it apart from the more primitive *O. sesnoni*: elongated rostrum (char. 1); inflated frontal sinus (char. 4); slitlike infraorbital foramen (char. 5); shortened bulla (char. 9); posteriorly extended paroccipital process (char. 17); reduced mastoid process (char. 18); ventrally expanded, mediolaterally flattened angular process (char. 21); enlarged p4 (char. 33); and further enlarged M2 (char. 39). *Osbornodon iamonensis* can be distinguished from *O. brachypus* by its relatively lower sagittal crest,

its less posteriorly extended paroccipital process, its lack of a deep masseteric fossa, and its high ascending ramus of mandible. Compared to the highly advanced *O. fricki*, it has the following primitive features: a narrow nasal, a less inflated frontal sinus, a lower sagittal crest, a less laterally expanded zygomatic arch, a less posteriorly extended paroccipital process, and lack of a pseudoparastyle on P4.

DISTRIBUTION: Late Arikareean to early Late Hemingfordian of western Nebraska and medial Hemingfordian of Florida.

DESCRIPTION: With its relatively large number of specimens, the Museum of Comparative Zoology collection furnishes the primary basis for description of the Thomas Farm canids. The depositional environment at the Thomas Farm, however, almost invariably resulted in flattening of the skulls, although the teeth are usually well preserved. Fortunately, a skull from Dry Creek, Nebraska (F:AM 128763), is almost completely free of distortion; this specimen, plus a mediolaterally crushed skull (UM 528) also from western Nebraska, is of prime importance in the morphological interpretation of the crushed materials from Florida.

Skull: *Osbornodon iamonensis* is the most primitive species that clearly exhibits many of the advanced characteristics of the genus. Both the middle and rostral sections of the skull are anteroposteriorly elongated. The posterior process of premaxillary is still primitively short and is separated from the anterior process of frontal by 10 mm. The nasal is still transversely narrow, unlike the widened condition in *O. fricki*. The frontal region domes above the postorbital process of the frontal, indicating a well-developed frontal sinus. On the fragmentary frontal bones of MCZ 4044, a large frontal sinus can be seen to expand backward beyond the postorbital constriction. The sagittal crest (F:AM 128763 has the highest sagittal crest of all specimens examined) is much higher than that in *O. sesnoni* but falls short of the extreme cases in *O. brachypus* and *O. fricki*. The lateral profile of the sagittal crest is slightly arched. The nuchal crest is not posteriorly elongated and stops anterior to the posterior edge of the occipital condyle. The zygomatic arch is rather slender in contrast to the much deeper ones in *O. brachypus* and *O. fricki*. The infraor-
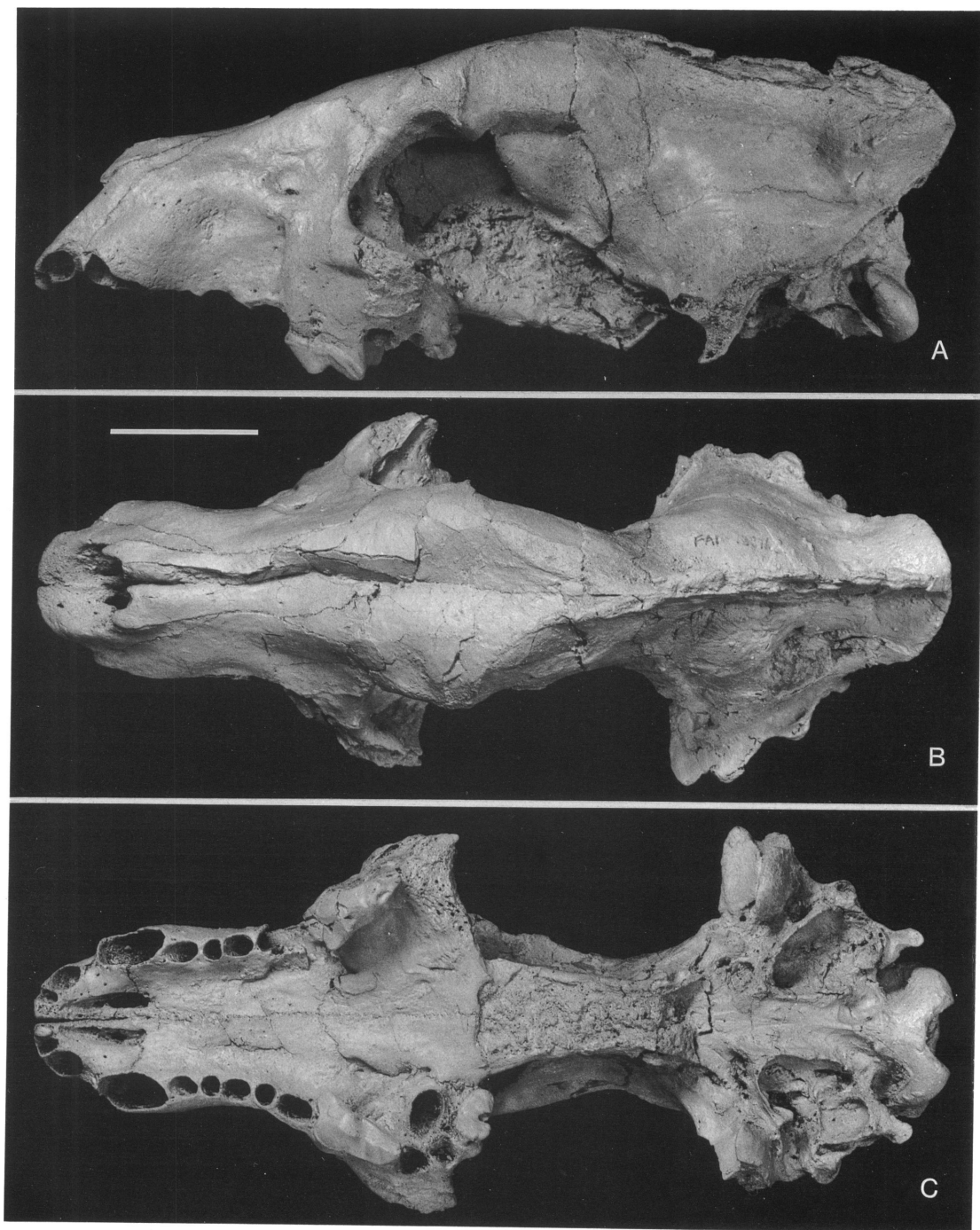
Fig. 43. Skull of *Osbornodon iamonensis*. **A**, Lateral (reversed from right side), **B**, dorsal, and **C**, ventral views of F:AM 128763. Scale = 30 mm.

bital foramen begins anteriorly at the level of the P3–4 junction and is a narrow slit instead of a rounded cross section in *O. sesnoni*.

In ventral view, the anterior half of the palate is relatively narrow because of the narrow rostrum. On F:AM 128763, the pterygoid wing hangs down in a gentle curve similar to that seen in *Osbornodon renjiei*. No specimen has a complete bulla. The most complete is on F:AM 128763, which has both bullae broken off at the base but still has the ectotympanic ring and parts of entotympanic that are ankylosed to the basioccipital. The size of the bulla, judging from its outline, is small and short, a characteristic of the genus. The middle ear region in F:AM 128763 is fully exposed on both sides. On the mediodorsal free edge of the entotympanic is a low septum, which is strongly developed in the anterior segment in contrast to the more posteriorly located septum in *Hesperocyon* (in addition, the septum in *Hesperocyon* is located at the ectotympanic/caudal entotympanic suture). Through the opening of the right posterior lacerate foramen can be seen a small space for the inferior petrosal sinus, which is walled on the medial side by a flange formed by the basioccipital. The ectotympanic sends a thin blade of bone laterally to cover the posterior wall of the postglenoid foramen. The paroccipital process points about 45° downward from the horizontal axis of the skull and is posteriorly expanded. This posterior expansion is, however, far from the extreme cases in *O. brachypus* and *O. fricki*. The base of the paroccipital process is swollen on the medial side and cups the posterior caudal entotympanic. The mastoid process is quite small and is overhung by a thick basal lambdoidal crest. Its posterior surface is excavated deeply beneath the lambdoidal crest, as is also seen in *O. fricki* and to a lesser extent in *O. brachypus*. There is a shallow fossa for the rectus capitis ventralis muscle in front of the occipital condyle on the basioccipital.

Mandible: The overall construction of the mandible of *Osbornodon iamonensis* is quite primitive. The horizontal ramus of *O. iamonensis* is slenderly built, similar to that of *O. fricki* and *O. brachypus*. The lower border is relatively straight as opposed to the more arched appearances in the mandible of *O. fricki*. The coronoid crest is relatively higher

and more erect than that of *O. brachypus*. The masseteric fossa is less excavated than in *O. brachypus*.

On MCZ 3714, a complete angular process is preserved. The angular process is dorsoventrally deep as a result of the ventral expansion of the area of insertion for the inferior ramus of the medial pterygoideus muscle. The ventral border of the angular process is rather sharp compared to that in the *Mesocyon–Enhydrocyon* clade. The overall mediolaterally flattened appearance of the angular process is further amplified in *Osbornodon brachypus* and *O. fricki*.

Dentition: The relatively large number of the Thomas Farm specimens furnishes a good opportunity to evaluate the morphological variation in the teeth. Most of *Osbornodon iamonensis* premolars (especially those of the uppers), however, are missing from the skulls, due to their relatively wide spacing and loosely rooted condition.

The dentition of *Osbornodon iamonensis* is at an early stage of a trend toward hypercarnivory, with few specializations that are typical of the advanced species of *Osbornodon*. The I1–P2 are not known in any of the specimens examined. Judging from the alveoli, the I3 is much larger than I1 or I2. The premolars are evenly spaced without large diastemata. The P1s are single-rooted and P2s double-rooted. The P3 is characteristic of the genus with a slender occlusal outline, a low principal cusp, and a distinct posterior accessory and cingular cusp. The principal cusp of P3 is more reduced than is seen in *O. brachypus* despite the latter's more advanced cranial morphology. The P4 is longer than in the more primitive species of *Osbornodon*. Its protocone is small and slightly anteriorly located. There is a distinct ridge along the anterior edge of the paracone that terminates at the anterior cingulum. This ridge is developed into a pseudoparastyle in *O. fricki*. The M1 is rather quadrate in outline due to a square anterolabial corner and a broad internal cingulum. The paracone is not much larger than the metacone. The M1 parastyle is little more than a slightly enlarged cingulum. The protocone is slightly shifted lingually, making room for a larger trigon basin. The metaconule is poorly differentiated from the postprotocrista and is much less
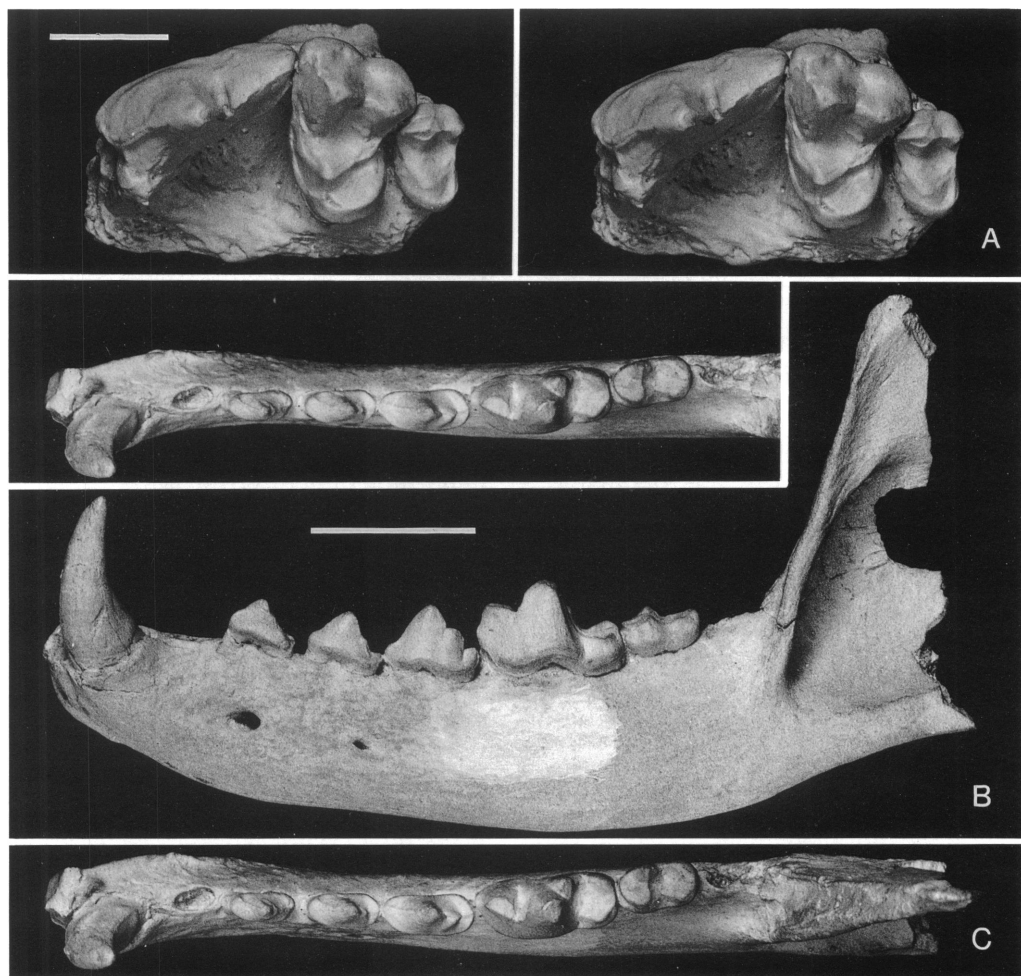
Fig. 44. *Osbornodon iamonensis*. **A**, Occlusal view (in stereo) of USNM 8836, holotype, scale = 10 mm; **B**, lateral and **C**, occlusal (in stereo) views of UNSM 25809, scale = 20 mm. Photographs of plaster casts.

prominent than in borophagine canids. It is shifted posteriorly and connected with the posterior cingulum away from the metacone, as seen in some arctoid carnivorans. Not only is the shape and size of M2 highly variable, it is also most unusual among hesperocyonines. The M2 is significantly enlarged with a posterolingually expanded internal cingulum that gives it a distinct oval outline. Like the M1, the paracone is similar in size to the metacone. Between the preprotocrista and the broad internal cingulum is a large shallow basin. The posterior edge of the internal cingulum occludes with the m3.

The lower canine is slender, with a weak

posterior ridge and a more distinct antero-medial ridge. The premolars are elongated, as is characteristic of the genus. The p1 has a single root. The main cusps of p2 and p3 are low. The p2–4 begin to develop a low posterior cingular cusp that is slightly expanded caudally. A posterior accessory cusp appears on p3 and is prominent on p4. The p4 is relatively enlarged, beginning to take on a hypercarnivorous appearance more apparent in more derived species of *Osbornodon*. The trigonid of m1 is indistinguishable from most primitive hesperocyonines with no reduction of its metaconid. The m1 talonid, however, is basined, due to the enlargement

of entoconid, in contrast to the predominantly trenchant talonids in most genera of hesperocyonine. The entoconid and hypoconid are similar in height, and enclosed within these two cusps is a talonid basin. The entoconid is very close to the medial border of the talonid and swells slightly at the medioposterior corner. This medial placement of the entoconid is distinguishable from that of a more laterally positioned entoconid ridge in *Osbornodon brachypus* (F:AM 54122), which also has a more dominant hypoconid. There is a small cingulum at the anterolateral corner of the m2. The talonid is similarly enclosed by a narrow entoconid ridge. The long talonid of m2, together with m3, occludes with an anteroposteriorly lengthened M2. This enlarged M2/m2 complex is characteristic of *Osbornodon* and is not found in any other hesperocyonines.

DISCUSSION: Simpson (1932: 19) erected the species *Cynodesmus nobilis* from a sample of eight specimens from Thomas Farm and remarked that it "closely resembles '*Mesocyon*' *iamonensis* Sellards from the Griscom Plantation." However, all of the differences cited by Simpson to distinguish these two species can also be seen in, or are even exceeded by, the Nebraska sample of *O. iamonensis* in the present study. Simpson was particularly impressed by a relatively larger M2 with a stronger "hypocone" in *C. nobilis*. This, too, can be seen in UNSM 25661 from Box Butte County, Nebraska.

The diversity of the Thomas Farm canids was further increased when White (1942) named another species, *Paradaphaenus tropicalis*, on the basis of its large hypoconid on m1. White's diagnosis of the M2 in *P. tropicalis* is almost the reverse of Simpson's contrast between *Cynodesmus nobilis* and *Mesocyon iamonensis* (i.e., *P. tropicalis* has a smaller M2 than in *C. nobilis*), and *Osbornodon iamonensis* was not mentioned in White (1942).

Olsen's (1956: 10) review of the Thomas Farm canids demonstrated that only two midsized canids are represented in the Thomas Farm deposit: *Cynodesmus iamonensis* Sellards and *Tomarctus canavus* Simpson. In light of the rather uniform cranial morphology in the Florida and Nebraska samples, I follow Olsen's taxonomic treatment and consider *C. nobilis*, *P. tropicalis*, and *Osbornodon iamonensis* conspecific. The contrasts proposed by him between the two remaining species reflect some of the fundamental differences in the morphology of M1/m1 between hesperocyonine and borophagine canids, for example, the presence (*T. canavus*) or absence (*O. iamonensis*) of a well-developed M1 metaconule and a cross-ridge between hypoconid and entoconid of m1. Having considerably reduced the nominal diversity of the Thomas Farm canids, Olsen (1956: 10) was still puzzled about the implication that "two true dogs very similar in size should have coexisted in nearly equal abundance" in the Thomas Farm locality.

Osbornodon iamonensis is phylogenetically the first advanced member of the genus. Many derived characters in advanced *Osbornodon* can be seen in *O. iamonensis* at their initial stages. These include the inflated frontal sinus, high sagittal crest, posteriorly extended paroccipital process, enlarged p4, reduced P3, elongated P4, and enlarged M2.

Osbornodon brachypus
(Cope, 1881)
Figure 45

Canis brachypus Cope, 1881a: 389; 1883: 242.
Cynodesmus brachypus (Cope) Scott, 1895: 72. Matthew, 1907: 186; 1909: 112. Peterson, 1910: 209, 213. Cope and Matthew, 1915: pl. CXIXa, b, c.
?*Cynodesmus brachypus* (Cope) Stevens, 1991: 46.

HOLOTYPE: AMNH 8140, crushed skull and lower jaws with left C1, P2–3, M2, right P2–3, M1–2, left p1–m3, and right p1–4, m2–3, plus most of the postcranial skeleton (Cope, 1883: 242, fig. 8a; Cope and Matthew, 1915: pl. CXIXa, b, c). Collected by J. C. Isaac in 1880.

TYPE LOCALITY: The holotype was found in "a sandy bed of the Ticholeptus division of the Loup Fork formation, east of Laramie Peak, Wyoming Territory" (Cope, 1881a: 390). Schultz and Falkenbach (1947: 176) remarked that: "The location 'East of Laramie Peak,' . . . is probably the area north of Wheatland in Platte County, Wyoming," and "The fossilization of the Frick specimens [of *Merychyus arenarum* Cope] is similar to that of the material found by J. C. Isaac." Schultz

and Falkenbach further suggested that the east Laramie Peak locality occurs in rocks equivalent to the Marsland Formation, Late Arikareean age.

REFERRED SPECIMENS: F:AM 54122, posterior half of left ramus with m1–2, maxillary fragment with left P1–2 and partial P4, right P4, and numerous fragments, from 2 mi south to 5 mi north of Jay Em, Goshen County, Wyoming, Upper Arikaree Group, Late Arikareean.

EMENDED DIAGNOSIS: *Osbornodon brachypus* is intermediate in size between *O. iamonensis* and *O. fricki*. In contrast to *O. iamonensis*, but as in *O. fricki*, *O. brachypus* has a laterally expanded zygomatic arch (char. 19), a very high sagittal crest, an extremely posteriorly extended paroccipital process forming an anteroposteriorly oriented plate (char. 17), and a reduced internal ridge on the angular process. In contrast to *O. fricki*, *O. brachypus* primitively possesses a narrow nasal, a less extremely inflated frontal sinus, a relatively short P4, no pseudoparastyle on P4, and a less enlarged p4. The mandible of *O. brachypus* is different from the rest of the species of *Osbornodon* by having two autapomorphies: a low coronoid process (char. 24), which is shifted laterally to enclose a deep masseteric fossa (char. 22).

DISTRIBUTION: Both the holotype and the only referred specimen (F:AM 54122) are from eastern Wyoming, in the Marsland Formation, Late Arikareean.

DESCRIPTION: Little was said about *Osbornodon brachypus* in Cope's (1881a) original description and his subsequent discussion (1883), in which only the astragalus was figured despite the large number of postcranial elements preserved in the holotype. The majority of Cope's illustrations of this species were published only posthumously (Cope and Matthew, 1915). Even then, sketchy descriptions were the only published information about this species. Except for the single referred mandible fragment (F:AM 54122), the holotype remains the only example of the species and provides the main basis of the following description.

Skull: Although the skull of the holotype is badly crushed, recent preparation reveals a significant amount of information that was previously obscured by matrix. Areas of the fractured cranial bones are actually much better preserved than would be suspected and are quite free of distortion (e.g., right pterygoid, right bulla, left paroccipital process, etc.).

The elongated *Osbornodon brachypus* skull is typical of the genus. The rostrum is long with correspondingly widely spaced premolars. The nasal is narrow, in contrast to its widened appearance in *O. fricki*. The posterior process of the premaxillary does not extend as far posteriorly as in *O. fricki* — there is a 15-mm-long contact between the maxillary and the nasal. The postorbital process is not greatly inflated. There is a considerable posterior displacement of the postorbital constriction, indicating a large frontal sinus. The sagittal crest is largely broken away except the short anterior segment. From its remaining portion, the sagittal crest can be estimated to be extremely high, approaching the level of *O. fricki*. The zygomatic arch is laterally expanded but less strongly arched than in *O. fricki*.

The pterygoid wing is ventrally extended and, as in F:AM 67098 of *Osbornodon fricki*, has a quadrate ventral angle for the hamulus, in contrast to a gentle curve in *O. iamonensis* and *O. renjiei*. The left bulla of the holotype is not distorted and exhibits the typical outline of an *Osbornodon*: small size, anteroposteriorly shortened, and rather oblique orientation of its long axis to the sagittal plane. The caudal entotympanic has a slightly more inflated appearance than that of *O. fricki*. The ectotympanic sends a long, thin, liplike blade to surround the posterior wall of the postglenoid foramen. Unlike *O. fricki*, no bony tube is developed for the external auditory meatus. The paroccipital process on the holotype is greatly elongated posteriorly to form a longitudinal plate. The size of this plate is matched only by *O. fricki*. As was noted by Cope (1881a), the fusion between the base of the paroccipital process and posterior bulla wall is extensive. The mastoid process is typical of the advanced species of the genus with a basal lambdoidal crest overhanging it, although the degree of reduction of the mastoid is less apparent than in *O. iamonensis* and *O. fricki*.

Mandible: The horizontal rami of the type are mediolaterally flattened. The lower border of the mandible is quite straight and the depth of the ramus uniform. Two prominent features of *Osbornodon brachypus* jaws are a
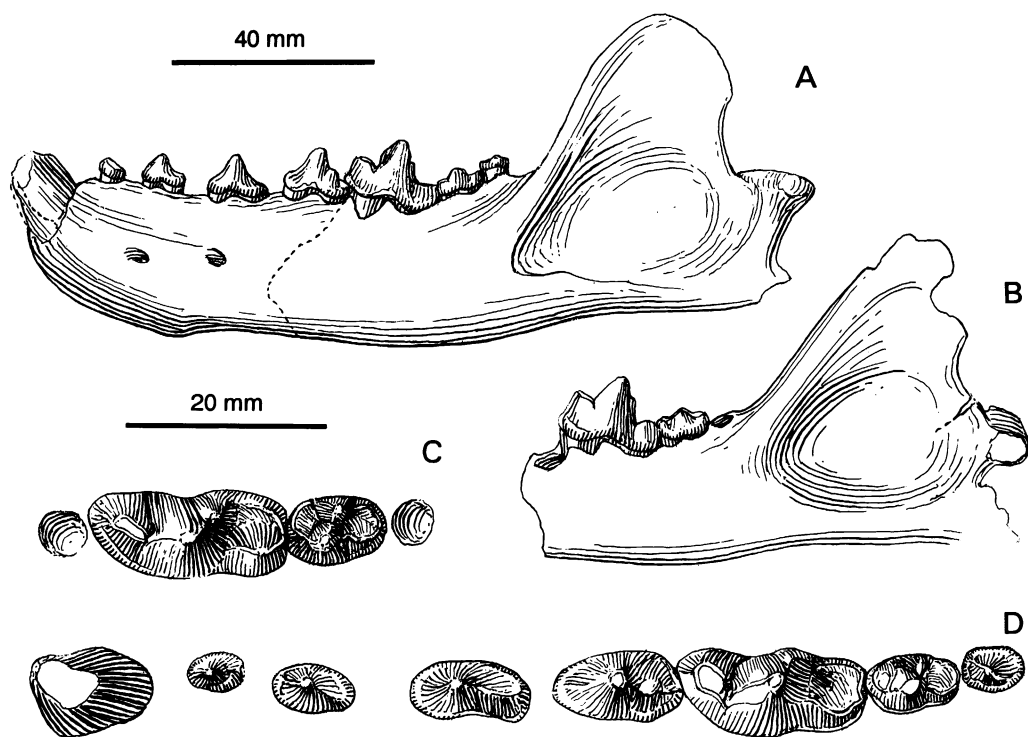
Fig. 45. Mandibles of *Osbornodon brachypus*. **A**, Holotype, AMNH 8140, lateral view of left mandible (partially reconstructed from the right mandible); **B**, left mandible of F:AM 54122; **C**, occlusal view of left m1–2 of F:AM 54122; and **D**, occlusal view of lower left dentition, holotype, AMNH 8140, canine reconstructed from that of right side. Illustrated by Frick's artists.

large distance between m3 and the condyloid process and a low coronoid crest, as had been noted by Cope (1881a). The anteroposteriorly elongated masseteric fossa corresponds to the elongated midsection of the skull. The height of the ascending ramus is considerably lower than any other species of *Osbornodon*. The anterior border of the coronoid crest reclines posteriorly in contrast to the much more erect coronoid crest in *O. iamonensis* and *O. fricki*. The ascending ramus is laterally displaced so that instead of the relatively straight coronoid crest of most hesperocyonines, the crest forms a gentle sigmoid curve in anterior view. The laterally displaced anterior coronoid crest encloses a large, deep masseteric fossa. This deep fossa differs from the somewhat comparable features in *Paraenhydrocyon* in that the fossa of the latter is ventrally bordered by a shallow pocket absent in *O. brachypus*. Both specimens of *O. brachypus* have preserved the basal part of an angular

process. On the holotype, the remaining anterior segment of the internal ridge is very reduced (less so than in F:AM 54122) and indicates a shallow facet for the superior ramus of the medial pterygoideus muscle, as is the condition in *O. fricki*. The angular process exhibits a sharp-edged lower border first shown in *O. iamonensis*.

Dentition: The teeth on the holotype (AMNH 8140) suffer severe weathering (mostly etching of the enamel) that has damaged much of the surface details. Partial roots of the left I2–3 are preserved in the holotype. The root of the I3 is twice as large as that of I2. Both upper canines are broken in the middle and show a posterior ridge on remaining basal halves. The upper and lower premolars are more widely spaced than those of *Osbornodon iamonensis* and *O. fricki*. The single-rooted left P1 seen in F:AM 54122 is composed of a single cusp. The P2 and P3 are relatively less reduced than in *O. iamonensis*

and *O. fricki*. Their main cusps are sharp and have a concave curve on the posterior edges, similar to those of *Paraenhydrocyon wallovianus*. The P3 has a posterior accessory cusp whereas the P2 does not. Cope (1881a) claimed that *Canis brachypus* had small upper sectorials (P4) even though the P4s on the holotype are mostly broken off and the remaining alveoli presumably were the basis of his judgement. Cope used Huxley's (1880: 248) terminology "microdont" to describe this short upper carnassial. The isolated left and partial right P4 on F:AM 54122 confirm Cope's estimation and show that it is no more elongated than that of *O. iamonensis*. The P4 protocone is slightly anteriorly located. As in *O. iamonensis*, there is a distinct narrow ridge in front of the paracone. The only information about M1 is from the lateral half of the right M1 in the holotype. Its paracone and metacone are closely spaced. The labial cingulum is low, and the M1 parastyle probably is, too (enamel chipped off). The M2 is smaller than in most individuals of *O. iamonensis*. The outline of M2 is similar to that of *O. iamonensis* in having a broad medial border formed by an enlarged internal cingulum.

No lower incisor is preserved and the right lower canine in the holotype is too badly weathered to be described. The lower premolars resemble the uppers in their concave posterior edges and sharp tips. The p1 has a single root. The size increase of the premolars from p2 to p4 is gradual in contrast to that of *Osbornodon fricki*, which has nearly identically sized p2–3 and a drastically larger p4. The p2 and p3 have one single main cusp whereas the p4 has an additional large posterior accessory cusp. The m1–2 in F:AM 54122 are much less weathered and thus better lend themselves to description. The metaconid is reduced compared to that in *O. iamonensis*, but is less so than in *O. fricki*. The hypoconid and entoconid are both ridgelike. In contrast to the nearly equal-sized talonid cusps in *O. iamonensis*, the hypoconid of *O. brachypus* is larger than the entoconid. The m2 protoconid is larger than the metaconid and the protoconid–metaconid ridge is not anteriorly positioned as in some *O. iamonensis* and more primitive species of *Osbornodon*. The hypoconid crest is low. The m3 is double-rooted with a low protoconid.

DISCUSSION: Cope (1881a, 1883) compared *Canis brachypus* to living coyote (*C. latrans*) and pronounced it "the oldest species of true dog known to me from American formations." This was followed by Scott (1895: 72) and Peterson (1910: figs. 6, 10), who used it as an example of a species close to the "true" canid line, as opposed to the more aberrant "canid" *Daphoenodon superbus*. Three characters were listed by Cope (1881a: 389) to support his hypothesis: "the small sectorial teeth, the elevated sagittal crest, and the small feet." Matthew's (1907, 1909; Cope and Matthew, 1915) reference of *Canis brachypus* to *Cynodesmus* was similarly influenced by the small P4 (microdont teeth) and reinforced, in a different way, the image of *Cynodesmus* as a genus ancestral to the living *Canis*. The many synapomorphies shared between *Osbornodon brachypus* and *O. fricki* clearly remove *O. brachypus* from the ancestry of living canines.

Paraenhydrocyon, new genus

Temnocyon (Cope) Cope, 1881b: 179.
Hypotemnodon (Eyerman) Wortman and Matthew, 1899: 130.
Mesocyon (Scott) Matthew, 1907: 185.
Enhydrocyon (Cope) Loomis, 1936: 50.

TYPE SPECIES: *Paraenhydrocyon wallovianus* (Cope, 1881).

INCLUDED SPECIES: *Paraenhydrocyon wallovianus* (Cope, 1881); *P. josephi* (Cope, 1881); *P. robustus* (Matthew, 1907).

DIAGNOSIS: Members of *Paraenhydrocyon* may be distinguished from other genera of hesperocyonines in having a posteriorly directed and laterally extended paroccipital process (primitive), a loss of suprameatal fossa (char. 7, reversal), a deeply pocketed angular process (char. 20), a long, slender mandible with a deep masseteric fossa (char. 22), and narrow premolars (char. 29). The derived taxa (*P. robustus* and *P. wallovianus*) have high, sharp principal cusps on premolars and reduced or absent accessory cusps, and a deeply pitted trigon basin of M1 for reception of the m1 hypoconid.

ETYMOLOGY: *para*, Greek, beside, near, by; designating the many parallel features developed by the present genus and *Enhydrocyon*.

DISTRIBUTION: The available record indi-

cates a restricted distribution for the primitive members of *Paraenhydrocyon* (*P. josephi* and *P. robustus*) within the northern Great Plains. The most derived species, *P. wallovianus*, has a much wider range, probably including much of the mid-continent of North America. *Paraenhydrocyon josephi* has the longest geological range among species of hesperocyonines, spanning the Whitneyan through Arikareean ages. *Paraenhydrocyon robustus* and *P. wallovianus* are mostly confined to the Late Arikareean.

DISCUSSION: *Paraenhydrocyon* shares with *Enhydrocyon* tendencies to develop hypercarnivorous carnassial teeth. The reduction or loss of the metaconid in the lower first and second molars and the semicircular internal cingulum of the upper first molar make isolated molars of the two genera difficult to differentiate. Loomis (1936) first noted this dental similarity and placed *Temnocyon venator* (= *P. wallovianus*) into *Enhydrocyon*. The overall shape of the premolars and the general proportions of the skulls, however, are so different between *Paraenhydrocyon* and *Enhydrocyon* that they clearly belong to different evolutionary lineages.

The laterally extended paroccipital process in *Enhydrocyon* also bears superficial similarity to that of *Paraenhydrocyon*. However, the convergent nature of this similarity is apparent when their fundamentally different character transformations are understood. In *Enhydrocyon*, the development of the laterally expanded paroccipital process is achieved through a downturned and elongated rodlike structure (still seen in certain individuals of *E. pahinsintewakpa*, e.g., SDSM 53320), whereas in *Paraenhydrocyon*, the paroccipital remains primitive in its backward orientation and lacks any elongation or thickening.

The high-tipped and simple-cusped premolars are quite similar to those of amphicyonids, which is the reason Cope (1881b, 1884) linked *Paraenhydrocyon wallovianus* closely to *Temnocyon altigenis*. Merriam (1906) further suggested that *P. wallovianus* may be an individual of *Temnocyon altigenis*. As noted by Stevens (1991), however, the basicranium of AMNH 81086 (holotype of *Temnocyon venator*), the only specimen of *P. wallovianus* with this region well preserved, is unambiguously canid (see description be-

low). It is this combination of *Enhydrocyon*-like molars and amphicyonid-like premolars that makes *Paraenhydrocyon* a unique lineage distinct from the rest of hesperocyonines.

Paraenhydrocyon wallovianus
(Cope, 1881)
Figures 46–48

Temnocyon wallovianus Cope, 1881b: 179; 1883: 239; 1884: 905. Matthew, 1899: 62; 1909: 107. Merriam, 1906: 5. Merriam and Sinclair, 1907: 184.
Temnocyon venator Cook, 1909: 262. Olsen, 1958: 596.
Enhydrocyon venator (Cook) Loomis, 1936: 50.
Enhydrocyon wallovianus (Cope) Loomis, 1936: 50.
Mesocyon venator (Cook) Stevens, 1991: 45.

HOLOTYPE: AMNH 6858, crushed rostral part of skull with all incisors, right C1–M1, and left P1–M2 (Cope, 1884: pl. LXX, fig. 10). Collected by J. L. Wortman.

TYPE LOCALITY: As is common for many published specimens in E. D. Cope's collection, little is known about the precise localities. Cope (1884) only listed the type of *Paraenhydrocyon wallovianus* as from "John Day Bad Lands, Oregon." The greenish matrix of AMNH 6858 may suggest the Turtle Cove Member of the John Day Formation, although coloration of the sediments is no longer a reliable indicator of stratigraphic positions in the John Day region (Fisher and Rensberger, 1972).

REFERRED SPECIMENS: AMNH 13764, heavily weathered partial skull with left P2, P4–M2 and right P1–M1, from 9 mi south of Lusk, Marsland Formation of Niobrara County, Wyoming, late Late Arikareean; AMNH 81086 (holotype of *Temnocyon venator* Cook, HC 223, originally in the Harold Cook Collection and later purchased by the American Museum of Natural History), partial skull and lower jaws with left P2, P4, right P2, P4–M2, left c1, p2, m1–2, and right c1, m1–2, from the *Syndyoceras* Quarry or AMNH Cook Quarry (see Distribution) in the Harrison or Marsland Formation of Sioux County, Nebraska, Late Arikareean or Early Hemingfordian; F:AM 27555, rostral part of the skull with heavily worn left P3–4 and

right I1–3, P4–M1, from North of Keeline, upper Lower or Upper Arikaree Group of Niobrara County, Wyoming, late Early or Late Arikareean; F:AM 54050, nearly complete left ramus with entire dentition, from 5 mi southeast of Guernsey, Platte County, Wyoming, stratigraphic position uncertain, possibly Upper Arikaree Group, Late Arikareean; F:AM 54110, partial mandible with left and right c1–m3 and postcranial fragments, from North Ridge, 0.5 mi west of Highway 85, Harrison Formation of Niobrara County, Wyoming, Late Arikareean; TMM 40879-9, crushed skull and mandible with partial skeleton, from Delaho Formation, Brewster County, Texas, Late Arikareean.

EMENDED DIAGNOSIS: *Paraenhydrocyon wallovianus* is the largest and most derived among the three known species of the genus. Characters that distinguish it from *P. josephi* and *P. robustus* include (autapomorphies): short angular process that is vertically expanded (char. 21), prominent paracone and large parastyle on M1 (char. 36), and extreme reduction or absence of metaconid on m1 and absence of metaconid on m2 (char. 43). In addition, *P. wallovianus* shares with *P. robustus* the following synapomorphies: slender premolars (char. 29), reduction of premolar accessory cusps (char. 30, reversal), and reduced metaconid on m2 (char. 43).

DISTRIBUTION: In different parts of his article, Cook (1909) mentioned two different localities for the holotype of *Temnocyon venator*, AMNH 81086. One is from 2 mi north of Agate Spring Quarry, presently known as the American Museum Cook Quarry (Marsland Formation). The other is from 0.5 mi west of Agate Spring Quarry, the *Syndyoceras* Quarry (upper part of Harrison Formation). Based mainly on the appearance of matrix associated with the specimen (from personal reports of R. Hunt), Stevens (1991) suggested that AMNH 81086 came from the *Syndyoceras* Quarry. Recent reexamination of the matrix from these two quarries by R. Hunt suggests to him that sediment associated with AMNH 81086 cannot be unequivocally assigned to either quarry; that is, the possibility that the type of *Temnocyon venator* came from the American Museum Cook Quarry still exists. However, the preservation in

specimens from *Syndyoceras* Quarry seems to indicate that AMNH 81086 was from the *Syndyoceras* Quarry (AMNH 81086 is virtually undistorted on parts that were preserved as opposed to the more crushed condition of the American Museum Cook Quarry specimens). AMNH 81086 is thus tentatively assumed to be from *Syndyoceras* Quarry (i.e., upper part of Harrison Formation, Late Arikareean). TMM 40879-9 came from the lower member of the Delaho Formation, Brewster County, Texas, of "early late Arikareean" age (Stevens, 1991). Together with the holotype (AMNH 6858) from the John Day Formation, the present sample suggests a widespread geographic distribution of *P. wallovianus* in the Late Arikareean of North America.

DESCRIPTION: Stevens' (1991) recent description of this species was detailed and little more needs to be added other than a better appreciation of the intraspecific variation through additional specimens referred herein. To avoid redundancy, the following description is focused on significant characteristics in the context of the phylogenetic relationships proposed herein. *Paraenhydrocyon wallovianus* provided the central concept of the genus and its morphology is contrasted with other genera as well as more primitive species of *Paraenhydrocyon*.

Skull: *Paraenhydrocyon wallovianus* has a slightly longer rostrum than that in the *Enhydrocyon* lineage and consequently has less crowded premolars. The infraorbital foramen is large and rounded. The height of the sagittal crest remains the same throughout the *Paraenhydrocyon* lineage and is much lower than that of *Enhydrocyon*. In posterior view, the top part of the nuchal crest is semicircular and is elevated relative to that in *P. josephi* so that the middle segment of the lambdoidal crest has a constricted appearance in posterior view. The supraoccipital lacks a thin, vertical ridge, the external occipital crest (Evans and Christensen, 1979), that is often well developed in *Enhydrocyon*.

AMNH 81086 has a well-preserved basicranial region except for the broken bulla. Only the part of entotympanic that attaches to the basioccipital and promontorial region is preserved. On the medial side of the promontorium, along the free dorsal edge of the

caudal entotympanic, there is a low, longitudinally oriented ridge with small cross ridges, here interpreted as the dorsal extension of a low septum unique to canids (Hunt, 1974). This is in contrast to the condition in *Hesperocyon* in which the septum is restricted to the ectotympanic/caudal entotympanic suture on the *ventral* edge of the caudal entotympanic. Breakage of the inflected entotympanic lying under the basioccipital allows observation of the cross section of the internal carotid canal embedded between the entotympanic and petrosal, another typical canid feature. The well-preserved left paroccipital process in AMNH 81086 shows it to be a slightly down-turned and dorsoventrally flattened plate, and there is little fusion of the paroccipital process with the bulla. The paroccipital is more laterally expanded than in *P. josephi*. Although more inflated than in *P. josephi*, the mastoid process is much smaller than in any *Enhydrocyon* of equivalent size.

Mandible: The horizontal ramus is long with a rather uniform depth. On the anterior end of the horizontal ramus, the lower border quickly turns upward to form a tight curve in contrast to a more gently tapered anterior end in most primitive hesperocyonines. The masseteric fossa is deep and expanded ventrally, creating a shallow groove on the ventral border of the fossa. The angular process is short, as is the case in the more primitive *Paraenhydrocyon robustus*. The internal ridge is reduced in AMNH 81086 but probably remains slightly larger on F:AM 54050, which has only the basal part of the angular process preserved.

Dentition: The robustness of the upper and lower canines, especially that of the holotype, exceeds that of *Mesocyon* but is less so than the advanced members of *Enhydrocyon*. One of the most distinctive dental features of *Paraenhydrocyon wallovianus* is its simple, sharp premolars that are anteroposteriorly elongated in occlusal view. The main cusps of upper and lower premolars are slightly curved posteriorly and most of them lack a strong posterior accessory and cingular cusp typically present in *Enhydrocyon*. In addition, the premolars in *P. wallovianus* are far less crowded than those in *Enhydrocyon*.

The P4 is less elongated than in advanced, more hypercarnivorous forms of *Enhydro-*

cyon but resembles *Mesocyon* in its proportions. Its protocone varies from a distinct cusp isolated from the paracone in the type to one that is closely appressed to the base of the paracone in AMNH 81086. The M1–2, on the other hand, are more *Enhydrocyon*-like. The degree of domination of paracone over metacone shown by *Paraenhydrocyon wallovianus* is reached only by advanced members of the *Mesocyon–Enhydrocyon* clade. The hourglass-shaped M1 (the "waist" by Stevens, 1991), particularly that in TMM 40879-9, is strikingly similar to the outlines of some *Enhydrocyon*. The trigon basin is deeply excavated, a derived feature shared with *P. robustus*. This deep excavation, or a V-shaped valley in posterior view, is formed by precisely controlled movement of the trenchant talonid (hypoconid) of m1 during mastication. The resultant wear pattern on M1 is such that the protoconule and metaconule ridges are ground off early in life, whereas the tips of the trigon cusps remain unworn. This deep valley occurs on the M2 as well, forming a continuous trough that occludes with the longitudinally trenchant m2. This occlusal precision of upper and lower molars and lack of grinding action are not seen even in the most hypercarnivorous *Enhydrocyon*.

The lower incisors are small and compressed into a tight row. The i3 has a small lateral accessory cusp similar to that of *Paraenhydrocyon robustus*. The reference of additional materials, especially F:AM 54050, a nearly complete lower jaw, to *P. wallovianus* implies larger variation in the premolars than is implied by the sample Stevens (1991) studied. The p1–4 of F:AM 54050 are the most robust of all specimens examined. Not only are they transversely widened, thus lacking the slender appearance usually found in *Paraenhydrocyon*, but the p4 also has a stronger posterior accessory cusp than is found in TMM 40879-9. In addition, the ramus of F:AM 54050 is strongly built with a strikingly large masseteric fossa. F:AM 54050 is from southeast of Guernsey, Platte County, Wyoming, a locality with uncertain stratigraphic position in the Upper Arikaree Group. This robustness of F:AM 54050 may be an indication that it is stratigraphically higher than the Harrison Formation where most *P. wallovianus* specimens come from.
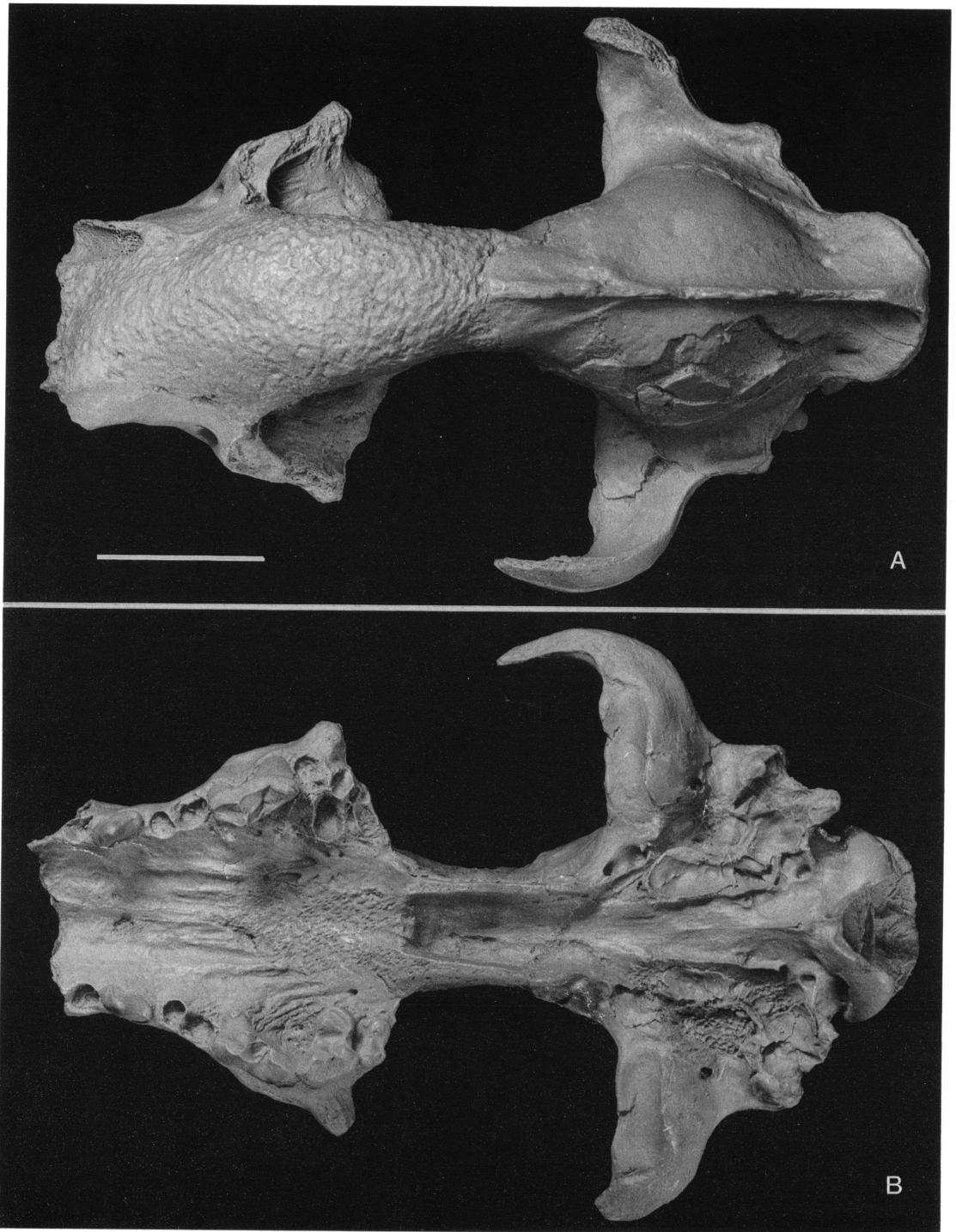
Fig. 46.   Skull of *Paraenhydrocyon wallovianus*. **A**, Dorsal and **B**, ventral views of AMNH 81086. Photographs of epoxy cast. Scale = 20 mm.

Fig. 47. *Paraenhydrocyon wallovianus.* Lateral views of **A**, skull (reversed from right side) and **B**, mandible of AMNH 81086. Photographs of epoxy cast. Scale = 20 mm.

The lower molars are highly hypercarnivorous. The shearing blade on the trigonid of m1 is long relative to the talonid. Its metaconid is completely lost (TMM 40879-9 and F:AM 54050) or is present as a residual cusp (in AMNH 81086 and F:AM 54110). That of m2 is lost in all specimens except possibly in F:AM 54110, whose m2 is worn flat beyond recognition. The m3 has a single cusp: the protoconid, with extended anterior and posterior ridges. The trenchant talonid in m1 plus the entire m2–3 form a more or less continuous ridge aligned in a straight line. This ridge, made up of m1 hypoconid, m2 protoconid and hypoconid, and m3 protoconid, occludes precisely within the valleys in the trigons of upper molars (see above description). The tendency in the *Paraenhydrocyon* lineage is clearly toward precise shearing.

DISCUSSION: In his most comprehensive treatment of North American Tertiary can-

ids, Cope (1884: 905) opened his description of *Temnocyon wallovianus* with the following statement: "This species of *Temnocyon* is more nearly related to the *T. altigenis* [an amphicyonid] than to any other member of the genus. Its anterior dentition is much like that of the species named, but the tubercular molars are not larger than those of the *T. coryphaeus.*" Merriam was reluctant to recognize *Temnocyon wallovianus* as a valid species (Merriam, 1906: 5; Merriam and Sinclair, 1907: 184) and expressed the suspicion that "this species should possibly be included in *T.* [*Temnocyon*] *altigenis*" (Merriam, 1906: 23). Based on the carnassials and M1, Loomis (1936: 49), however, was convinced that "Cook's *T.* [*Temnocyon*] *venator* is surely an *Enhydrocyon.*" Loomis' statement was rejected by Macdonald (1963), who pointed out that the "compressed premolars" (of *T. venator*) are a characteristic of *Temnocyon.* Isolated upper or lower first molars of *Paraen-*
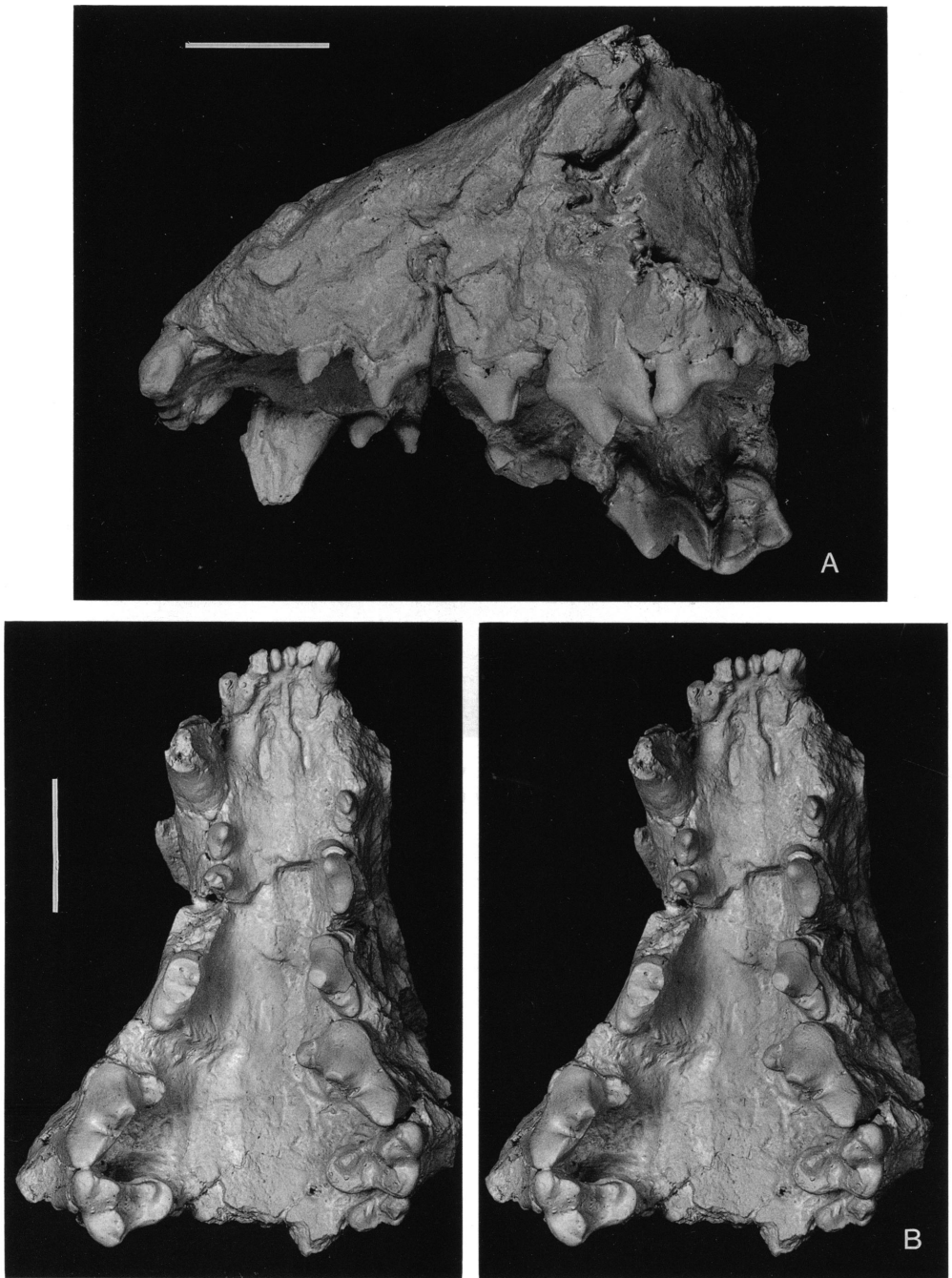
Fig. 48.   Skull of *Paraenhydrocyon wallovianus*. **A**, Lateral and **B**, ventral (in stereo) views of AMNH 6858, holotype. Scales = 20 mm.

hydrocyon wallovianus and *Enhydrocyon*, however, are considerably similar in having an hourglass-shaped M1 and the reduction of the metaconid on m1. In addition to the molars, *P. wallovianus* seemingly also shares with advanced *Enhydrocyon* a laterally expanded paroccipital process. However, as described above, both the detailed morphology

of the paroccipital process and the pathways through which their respective morphology evolved are fundamentally different.

Paraenhydrocyon wallovianus is the largest and, so far as known, terminal member of the genus. Stevens (1991: 60) pointed out that "Mesocyon robustus is exactly what an ancestor for M. venator should be." However, she allowed her stratigraphic analysis and a preconceived size relationship to overrule the morphology in concluding: "The much smaller size, and the more or less comparable age of M. robustus relative [to] M. venator remove M. robustus as a suitable ancestor for M. venator," and "Mesocyon venator must have been derived from near or within M. coryphaeus, as a lineage which reduced a crushing, but increased a piercing/slicing dentition through the premolarization of m1–m2" (ibid.: 61). The present study confirms Stevens' morphological observation about the relatedness of P. robustus and P. wallovianus; the available evidence suggests that P. robustus is the sister-species of P. wallovianus. Contrary to Stevens' claim, however, M. coryphaeus is far removed from P. wallovianus in the many characters discussed in the phylogeny section.

Cope (1881a: 179) had long ago recognized the deep valleying in the trigon of the upper first molar of Temnocyon wallovianus as being distinct from T. coryphaeus: "First superior tubercular molar [M1] with a wide median fossa, bounded within by a tubercle," in contrast to the "narrower basin, bounded within by a V-shaped crest" in the latter. Furthermore, the highly hypercarnivorous lower molars ("premolarization" in Stevens, 1991) suggest a predominantly predaceous lifestyle of Paraenhydrocyon wallovianus. Stevens (1991: 61) speculated that P. wallovianus may have led a scansorial life: "The suggestion is ventured that M. venator [= wallovianus] as a lone, non-cursorial hunter might have climbed trees (suggested by its postcranial anatomy) and there waited to drop on a passing oreodont."

Paraenhydrocyon josephi
(Cope, 1881)
Figures 49–51

Temnocyon josephi Cope, 1881b: 179; 1884: 912.

Temnocyon coryphaeus (Cope) Cope, 1884: 911 (AMNH 6861).
Hypotemnodon (Temnocyon) coryphaeus (Cope) Wortman and Matthew, 1899: 130 (AMNH 6861).
Hypotemnodon (Temnocyon) josephi (Cope) Matthew, 1899: 63. Wortman and Matthew, 1899: 130 (AMNH 6908).
Mesocyon coryphaeus (Cope) Thorpe, 1922a: 168–169 (YPM 12702 and 12704).
Mesocyon josephi (Cope) Schlaikjer, 1935: 133. Barbour and Schultz, 1935: 412. Stevens, 1991: 46.
Mesocyon hortulirosae Schlaikjer, 1935: 133. Olsen, 1956: 1. Stevens, 1991: 46.
Mesocyon robustus (= M. hortulirosae) (Matthew) Macdonald, 1963: 213.

HOLOTYPE: AMNH 6878, anterior half of skull with complete upper teeth except broken canines and incisors (Cope, 1884: pl. LXX, fig. 9). Collected by Mr. J. L. Wortman in 1879.

TYPE LOCALITY: Cope's (1884: 914) description about the type locality is brief and vague: "Found in the John Day beds of the John Day region, Oregon."

REFERRED SPECIMENS: From John Day Formation, Oregon, Arikareean (see comments about John Day localities under Type Locality and Referred Specimens of Mesocyon coryphaeus and Enhydrocyon stenocephalus): AMNH 6861, nearly complete skull with left and right I1–C1, left P4, right P4–M1, left and right i1–c1, and postcranial fragments, from Haystack Valley, Grant County (figured in Cope [1884: pl. LXXIa, fig. 1] as Temnocyon coryphaeus; its partial left ramus is not located); AMNH 6863, partial left and right lower jaws with left p2–m3 and broken right p3–m2, from Camp Creek; AMNH 6908, left maxillary fragment with P1 and broken P4–M2; AMNH 6910, nearly complete skull with almost all teeth (some broken), and postcranial fragments; YPM 12702, complete skull and mandible, from Turtle Cove, Grant County, Turtle Cove Member; YPM 12704, badly crushed and weathered rostral part of skull with left P2–4 and right P4–M2, from Turtle Cove, Turtle Cove Member; YPM 12723-1, left ramus fragment with m1, from Bridge Creek.

From the Arikaree Group of Niobrara County, Wyoming: F:AM 27556, right ramus fragment with p2–4, from Upper Arikaree

Group, north of Keeline, Late Arikareean; F:AM 27577, left P1, P4–M2 and right M1, from Harrison Formation, North Ridge, 10 mi north of Lusk, Late Arikareean; F:AM 54097, crushed skull and mandible with nearly complete dentition except for incisors, partial postcranial skeleton, from 3 mi west of Muddy Creek locality, which is 3 mi west of Highway 85, Upper Arikaree Group, Late Arikareean; F:AM 54098, skull and mandible fragments with left P2, P4–M2, and left c1, p2, from Muddy Creek, Lower Arikaree Group, Early Arikareean; F:AM 54099, fragment of rostral part of skull with most pre-P4 teeth, locality same as F:AM 54098; F:AM 54100, mandible fragments with broken left c1–m3 and right m1–3, locality same as F:AM 54098; F:AM 54106, complete skull and mandible with heavily worn dentition, right I1–2 missing, from north of Jeriah, Harrison Formation, Late Arikareean; F:AM 54107, complete skull and dentition, missing right zygomatic arch, associated partial left and right fore- and hindlimbs, from north of Keeline, Upper Arikaree Group, Late Arikareean; F:AM 54108, partial skull and mandible with nearly complete, heavily worn teeth, from North Ridge, 14 mi east of Highway 85, Harrison Formation, Late Arikareean; F:AM 54109, partial left ramus with p1–m1, from North Ridge, Harrison Formation, Late Arikareean.

From Arikaree Group of Goshen County, Wyoming: F:AM 54115, complete skull and mandible, atlas–axis, partial thoracic–lumbar vertebrae, and right hindlimb bones, from 4 mi east of Tremain, Lower Arikaree Group, Early Arikareean; F:AM 54117, right maxillary fragment with P4–M2, from 1/2 mi east of Tremain railroad station, Lower Arikaree Group; MCZ 2102, holotype of *Mesocyon hortulirosae* Schlaikjer (1935), almost complete skull and mandible with entire upper and lower dentition except right P1, left C1, left m3, and right p1, from east end of Bear Creek Mountain, NW¼, sect. 36, T. 20 N, R. 62 W, approximately 191 ft above the "Brule-Gering" contact, above *Daemonelix*-bearing beds (measured section in Schlaikjer, 1935: 112), Harrison Formation, Late Arikareean; MCZ 2882, paratype of *M. hortulirosae*, an incomplete pair of lower jaws with premolars and molar teeth, from 66 Moun-

tains, probably the equivalent of Gering Formation, Early Arikareean; MCZ 2883, rostral part of skull and mandible with most of upper and lower dentition, partial fore- and hindlimbs, from 2 mi northwest of Lone Tree Canyon; UCMP 80391, slightly crushed skull and mandible with nearly complete teeth, from Bear Creek Mountain, Upper Arikaree Group, Late Arikareean; UW 10253, rostral part of skull with left and right P3–M2, from 10 mi east of Slater and north to northeast of Redding Ranch.

From Morrill County, Nebraska: F:AM 27753, partial left ramus with p2–m3, from 8 mi southwest of Bridgeport, Gering? Formation, Early Arikareean; MCZ 5092, nearly complete mandible with all teeth except left c1 and p3, from 1.5 mi southwest of Chimney Rock, Gering Formation, Early Arikareean.

From White River Group of Shannon County, South Dakota: F:AM 63380, right ramus fragment with m1–3, from southwest of Indian Stronghold, Brule Formation, Whitneyan.

EMENDED DIAGNOSIS: *Paraenhydrocyon josephi* is approximately the same size as "*Mesocyon*" *temnodon* or *Osbornodon sesnoni* and slightly smaller than *P. robustus*. *Paraenhydrocyon josephi* can be distinguished from similar-sized *Mesocyon* and *Osbornodon* by having 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 (char. 20); a dorsoventrally flattened paroccipital process (char. 16) that is pointed posteriorly (primitive); an angular process of mandible with a deeply pocketed fossa for the superior ramus of the medial pterygoid muscle (char. 22); and absence of a small suprameatal fossa (char. 7, reversal). *Paraenhydrocyon josephi* can be distinguished 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.

DISTRIBUTION: From Brule Formation of southwestern South Dakota; Gering–Harrison Formations of eastern Wyoming and

western Nebraska; and from the John Day Formation of central Oregon. All specimens from the John Day area were collected more than 100 years ago and have poor locality data. YPM 12704 was collected from the Turtle Cove and Thorpe (1922a) placed it (referred to *Mesocyon coryphaeus*) in the Middle John Day Formation, that is, the Turtle Cove Member of Fisher and Rensberger (1972). The rest of the John Day specimens are assumed to be from the Turtle Cove Member (Early Arikareean). Whitneyan to Late Arikareean.

DESCRIPTION: The addition of several nearly complete skulls to the original *P. josephi* sample not only supplies many additional anatomical details but also gives a better sense of temporal and geographical variation since the present sample comes from the John Day area as well as the northern Great Plains, and spans the entire Whitneyan through Arikareean ages.

Skull: In almost every respect, the cranial proportions of *Paraenhydrocyon josephi* are like those of an enlarged *Hesperocyon*. Skulls from the John Day area are slightly larger and have more elongated rostra. The nasal is long and slender. The posterior premaxillary process is a thin strip. The frontal domes slightly, especially above the postorbital process area. On the early, smaller skulls, there is a shallow depression on top of the postorbital process of the frontals, indicating absence or weak development of a frontal sinus. In F:AM 54115, a 20 × 20 mm opening was made in the skull roof. A moderately sized frontal sinus is present in the frontal bone. The sinus is 2 mm past the postorbital constriction and does not invade the postorbital process. The sagittal crest is a thin blade reaching a height of 3 mm near the top of the cranial cavity and 8 mm in front of the nuchal crest. In posterior view the nuchal crest resembles a semicircle. The surface of the supraoccipital is smooth with a low, oval dome indicating the position of the vermis of the cerebellum. There is no fossa for the rectus capitis muscle.

The infraorbital foramen is rounded. The zygomatic arch is slender; the postorbital process of the jugal is small. On UCMP 80391, the posterior margin of the palate at the midline is 5 mm behind the posterior edge of M2;

most specimens, however, have the two borders at nearly the same level. The bulla is well inflated (more so in John Day individuals), particularly near the anterior part of the ectotympanic/entotympanic suture. The left bulla of MCZ 2102 was opened (Wang and Tedford, 1994: fig. 5A). It shows a low septum in the same position as in *Paraenhydrocyon wallovianus*, but the septum lacks the small cross-ridges seen in the latter. As in *Hesperocyon*, the paroccipital process is posteriorly oriented and is not fused with the bulla. It is dorsoventrally flattened and has a flat ventral facet and a rounded dorsal surface. The lateral edge of the paroccipital is stretched (more so in Late Arikareean individuals) into a sharp blade, an important characteristic defining the genus *Paraenhydrocyon*. The mastoid process is little different from that of *Hesperocyon* in having a small lateral facet beneath the basal corner of the lambdoidal crest.

Mandible: Two specimens (F:AM 54108 and UCMP 80391) have a sharp-edged, triangular flange on top of the coronoid process. This triangular flange also occurs in one specimen of "*Mesocyon*" *temnodon* (F:AM 63367). The horizontal ramus of the mandible is slender and has a nearly constant depth. This is in contrast to the anteriorly tapered rami of the *Mesocyon–Enhydrocyon* clade. A distinctive feature of *Paraenhydrocyon* mandible is a deeply excavated masseteric fossa. The fossa sinks into its ventral border, forming a shallow pocket at the bottom of the fossa. A deeply pocketed angular process is another distinctive feature of *P. josephi*. The internal ridge (aréte interne; Gaspard, 1964: 251, fig. 2) of the angular process extends mediodorsally to form a thin bony blade that encloses an elongated pocket for the insertion of the superior medial pterygoideus muscle. The inferior medial pterygoideus muscle inserts on the medial surface of the internal ridge outside the pocket. In UCMP 80391, the angular process is elongated beyond the posterior margin of the condyloid process and terminates in an upward hook. The above pocket for the superior medial pterygoideus is also reduced in UCMP 80391 because of its lack of inward extension of the internal ridge.

Dentition: The teeth of *Paraenhydrocyon*

Fig. 49.   Skull of *Paraenhydrocyon josephi*. **A**, Dorsal and **B**, ventral views of YPM 12702. Scale = 30 mm.

josephi are, in general, very primitive. Five skulls have the upper incisors preserved; however, all are too worn or broken to distinguish individual cusps. The canines are moderate-sized. The upper premolars are little different from similar-sized hesperocyon-ines such as "*Mesocyon*" *temnodon* and *Osbornodon renjiei*. The P1 is single-rooted. Only P3 has a posterior accessory cusp and a posterior cingular cusp, although P2 may have an incipient accessory cusp as well. There is a distinct anterior cingulum in front of the
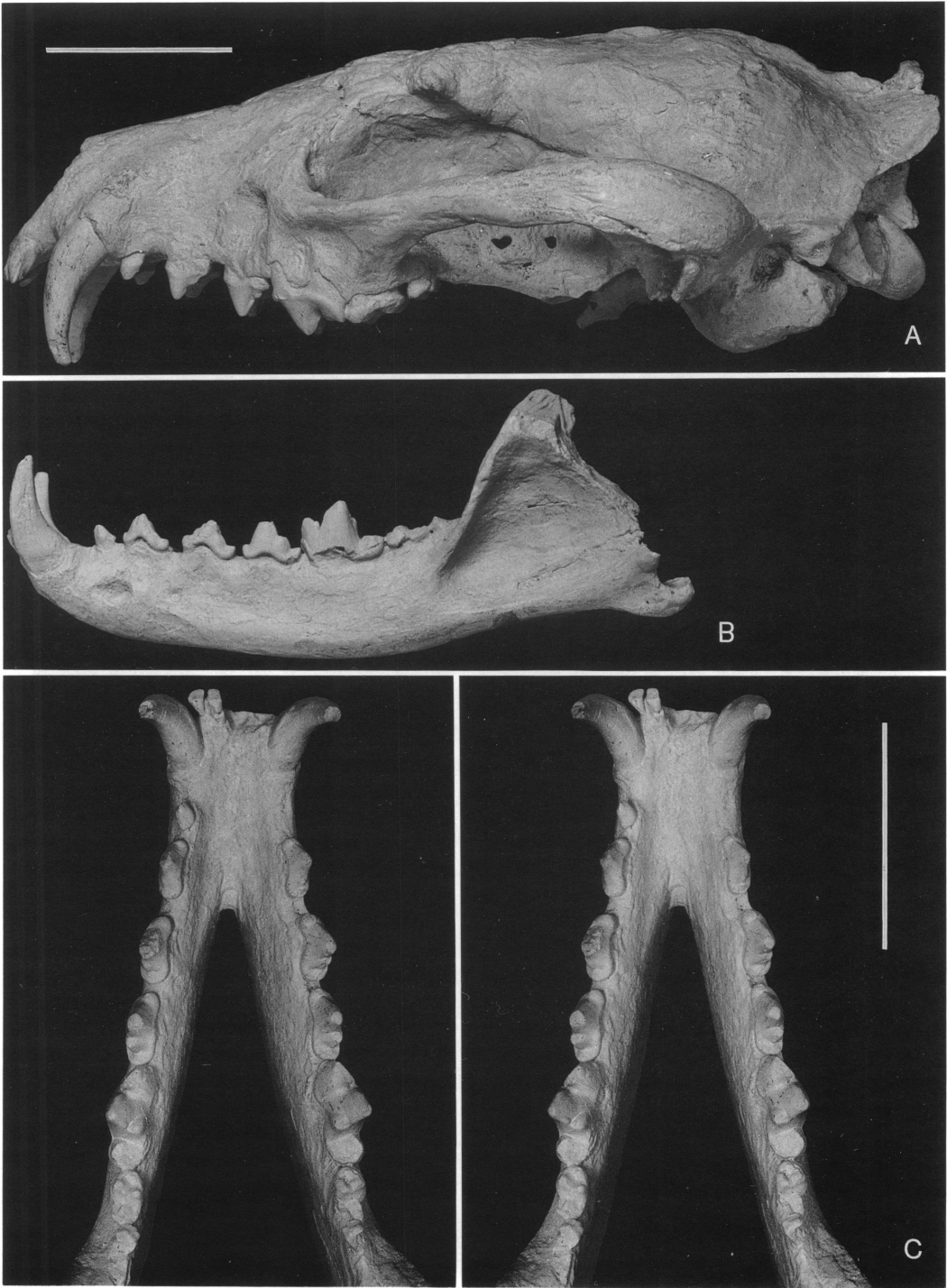
Fig. 50. *Paraenhydrocyon josephi*. Lateral views of **A**, skull and **B**, mandible, and occlusal view (**C**, in stereo) of lower teeth of YPM 12702. Scales = 30 mm.
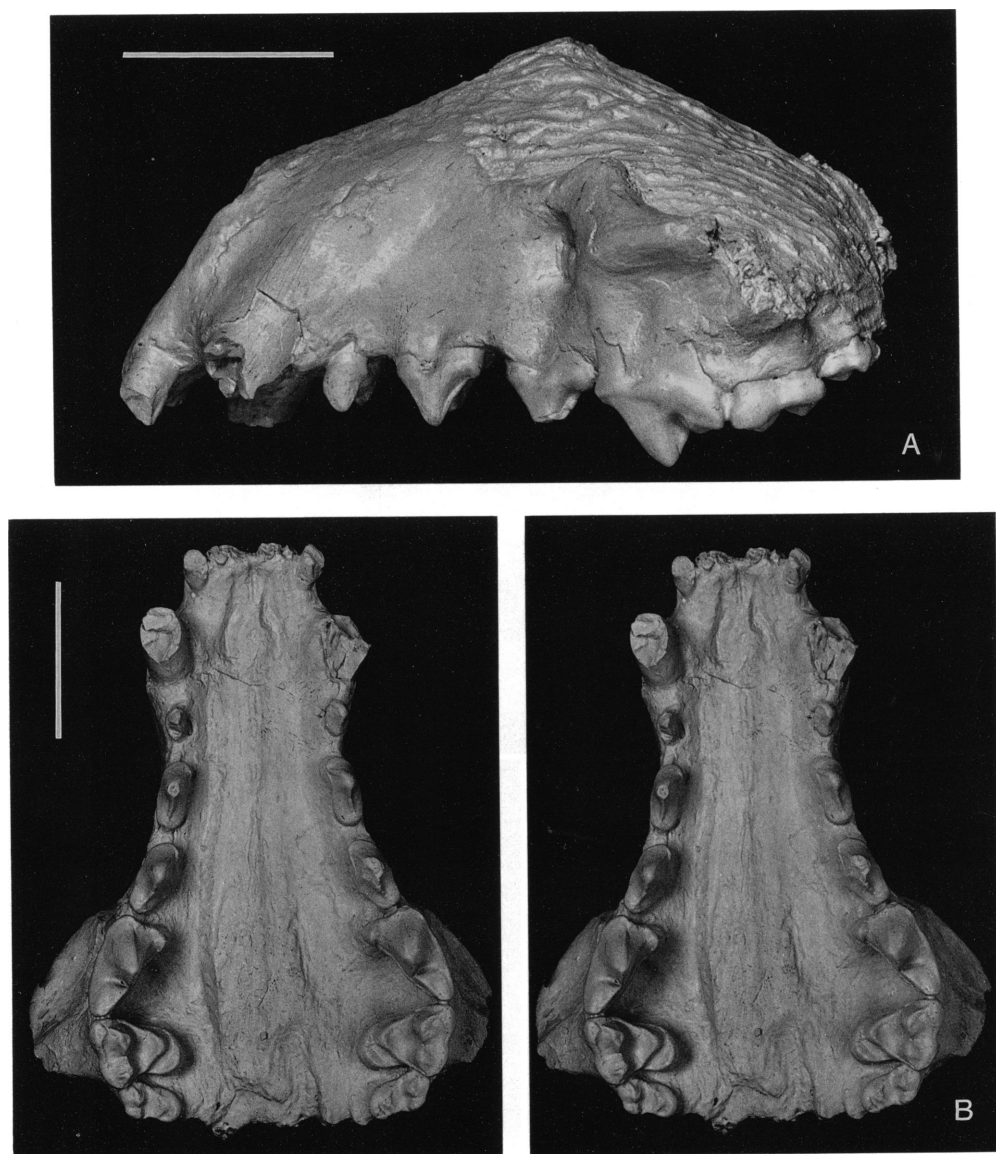
Fig. 51. Skull of *Paraenhydrocyon josephi*. **A**, Lateral and **B**, ventral views (in stereo) of AMNH 6878, holotype. Scales = 20 mm.

paracone of P4, which is best developed and almost cusplike on UCMP 80391. The protocone is usually positioned slightly anterior of the anterior border of the paracone. The M1 tends to have a transversely slender outline with a somewhat sharp-cornered parastyle, which is better developed than in "*M.*" *temnodon* and *O. renjiei*. The M2 is usually not enlarged relative to the M1, as is the case

with *Osbornodon*, although AMNH 6910 has an unusual, transversely elongated M2 similar to one individual of *Philotrox condoni* (UCMP 76712).

Only on MCZ 5092 is detailed cusp morphology on the lower incisors well preserved. The i1 is bicuspid, as is indicated by a vague central groove on the tip. The tip of the i2 has two shallow grooves to divide the flat top

into three cusps. The i3 is also tricuspid with the lateral cusp significantly lower than the medial two cusps. In general, the lower premolars have better developed accessory and cingular cusps than their upper counterparts. The p1 has a single root. A small anterior cingular cusp can be seen in 60% (6/10) of the p2s and in 70% (7/10) of the p3s. The occurrence of the posterior cingular cusps is closely correlated with the presence of the anterior ones; a posterior accessory cusp is unambiguously present on most of the p3s and on all p4s. In occlusal view, the m1 has a more slender appearance and a narrower talonid than that of "*Mesocyon*" *temnodon* and *Osbornodon renjiei*, but these distinctions are certainly not infallible. Taken in isolation, they cannot be reliably used as the sole criterion of identification. The narrowing of the talonid results from the narrowing of the entoconid shelf, which lacks the quadrate posterior corner seen in "*M.*" *temnodon* and *O. renjiei*. The m2 has a primitive *Hesperocyon*-like trigonid with a well-developed metaconid that is equal to or slightly smaller than the protoconid. The m3 is present as a double-rooted tooth in all specimens.

DISCUSSION: The many more-or-less complete skulls and mandibles of *Paraenhydrocyon josephi* from the Early Arikareean (AMNH 6861, 6910, 27753, F:AM 54115 and 63380, MCZ 2102, 2882, and 5092, UW 10253, YPM 12702) offer a good sense of variation within the species. The more variable features include the size of the auditory bulla, the development of accessory cusps of premolars, and the size and shape of upper molars. The Late Arikareean sample, represented by equally well-preserved skulls (F: AM 54097, 54106, 54107, 54108, 54109, UCMP 80391), shows a slight size increase (among the Great Plains individuals) and some random variation that does not seem to lead in any particular direction. The increase in body size through time and the associated robustness of the dentition are probably anagenetic events.

One individual, UCMP 80391, however, has acquired features that are not seen in any other individual: a well-developed parastyle on P4, an elongated angular process that has lost the deep medial pocket, and a more posteriorly positioned posterior palatine border

(see description above). This puzzling combination of features does not seem to lead to any particular lineage of hesperocyonines and is here tentatively regarded as variation within this species.

Paraenhydrocyon robustus
(Matthew, 1907)
Figure 52

Mesocyon robustus Matthew, 1907: 185. Thorpe, 1922b: 429. Schlaikjer, 1935: 139. Barbour and Schultz, 1935: 412. Macdonald, 1963: 213 (holotype only). Stevens, 1991: 46.
Mesocyon hortulirosae (Schlaikjer) Macdonald, 1963: 213.

HOLOTYPE: AMNH 12884, partial left and right rami with nearly complete left and right dentition. Collected by the American Museum of Natural History 1906 expedition.

TYPE LOCALITY: AMNH Rosebud locality 7 from 4 mi south of Porcupine Creek, sects. 1 or 6, T. 38 N, R. 42 W, Shannon County, South Dakota (see Stevens [1991] for a recent review). Harrison Formation of Late Arikareean age.

REFERRED SPECIMENS: AMNH 12871, right ramus fragment with p1, p4 and partial c1, probably from the same locality as the type; F:AM 27554, left maxillary fragment with C1–M2, partial left and right rami with entire lower dentition, and partial skeleton, from 16 mi northeast of Lusk, Niobrara County, Wyoming, Upper Arikaree Group, Late Arikareean; F:AM 27557, partial right ramus with i2–m3 and some limb bones, from 12 mi south of Jay Em, Goshen County, Wyoming, stratigraphic position uncertain, possibly upper Lower or Upper Arikaree Group, late Early or Late Arikareean.

EMENDED DIAGNOSIS: *Paraenhydrocyon robustus* is limited in diagnosable features to only the mandible and teeth. *Paraenhydrocyon robustus* is 15% smaller than *P. wallovianus* and 8% larger than *P. josephi* (calculated on the species means of p1–m3 length). *Paraenhydrocyon robustus* can be distinguished from the latter by absence of a distinct anterior cingulum on P4; narrowed premolars (char. 29) with reduced accessory and cingular cusps (char. 30); and reduced metaconids of m1–2 (char. 43). On the other hand, *P. robustus* retains the following prim-
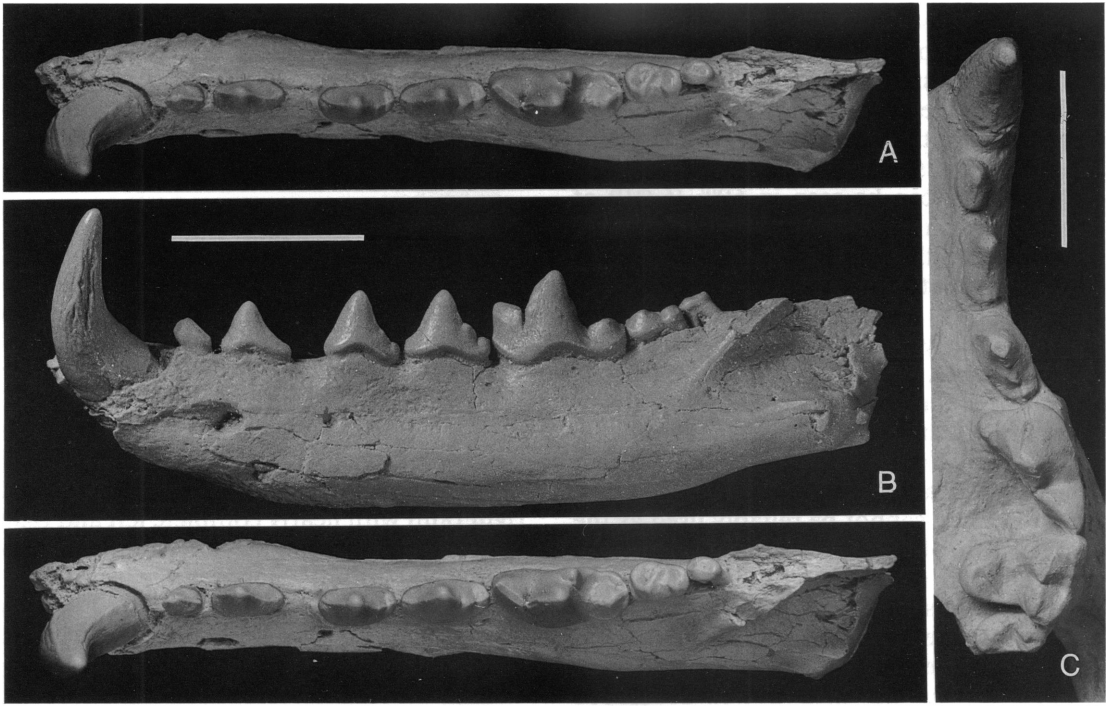
Fig. 52. *Paraenhydrocyon robustus*. **A**, Occlusal view (in stereo) and **B**, lateral view of AMNH 12884, holotype, photographs of epoxy cast; and **C**, occlusal view of F:AM 27554. Scales = 20 mm.

itive dental features that can be used to separate it from *P. wallovianus*: less enlarged M1 paracone and less reduced metaconids of m1–2, which are completely lost in *P. wallovianus*.

DISTRIBUTION: Harrison and Marsland Formations of eastern Wyoming and western South Dakota. Late Arikareean.

DESCRIPTION: Since the first discovery of the lower jaws of a single individual of *Mesocyon robustus* by W. D. Matthew (a second ramus fragment, AMNH 12871, was mentioned by Matthew [1907], but it is so poorly preserved that the identification cannot be determined), only two specimens have been added to the original sample.

Skull: Very little can be learned from a partial left maxillary of F:AM 27554. It has a slender zygomatic arch that seems to be more dorsally arched than in *Paraenhydrocyon josephi*. The infraorbital foramen is rounded.

Mandible: The mandible retains the deep, ventrally positioned masseteric fossa found in *Paraenhydrocyon josephi*. The horizontal rami are similar to those of *P. josephi* in their rather uniform depth throughout most of their length. Both left and right rami of the holotype are deformed. There are longitudinally oriented cracks on the ventral surface that were formed by expanding matrix. The expanded mandible may have contributed to Matthew's conclusion of the "robustness" of the holotype.

F:AM 27554 is the only specimen of *Paraenhydrocyon robustus* that has a complete angular process. The angular process is peculiarly shortened with a rounded, blunt tip. In addition, in contrast to that of *P. josephi*, its internal ridge is not greatly mediodorsally extended to enclose a deep fossa for the superior medial pterygoideus muscle; the area for muscle attachment is much reduced.

Dentition: Information about the upper teeth can be learned only from the referred specimen, F:AM 27554, which has considerably more robust teeth than in the holotype. The upper premolars are evenly spaced and are anteroposteriorly shorter than those seen in *Paraenhydrocyon josephi* and *P. wallovi-*

anus. The P1 (single-rooted) and P2 are single-cusped, whereas the P3 has both a small posterior accessory and cingular cusps. The size of the P4 protocone is reduced and there is no parastyle; the anterior ridge of the paracone is still present. The M1 has a large parastyle, a high paracone–metacone blade, and a much lower protocone. The unique interlocking mechanism between a trenchant talonid of m1 and a V-shaped valley on trigon of M1 of advanced *Paraenhydrocyon* (see also description of *P. wallovianus*) is partially formed in *P. robustus*. The M1 protocone is not yet enlarged to prevent lingual movement of the m1 hypoconid. However, the wear pattern on M1 indicates that transverse movement is limited. The internal cingulum is less well developed, especially its anterior segment, than in *P. wallovianus*. The M2 is similarly worn into a shallow trough continuous with that of M1.

The lower incisors are small and the i3 has a lateral cusp below the main cusp. The canine on the type has a crenulated surface. The premolars resemble those of *Paraenhydrocyon wallovianus* in their degree of reduction of the accessory and cingular cusps. F:AM 27557 is slightly more primitive in retaining a small posterior accessory cusp on p3–4. The p1–3 of the other specimens have a single, slender main cusp and the p4 has a posterior accessory and cingular cusps. There is a 3-mm diastema between the p2 and p3 in the holotype. The occlusal outline of m1 is slender, as is typical of the genus, with a narrowed talonid that has a rounded posterolingual corner (as contrasted with a more quadrate appearance of the same corner in *"Mesocyon" temnodon*). The m1 metaconid is intermediate in size between *P. josephi* and *P. wallovianus*. The entoconid shelf appears as a narrow, low cingulum in contrast to the dominant, high hypoconid. The metaconid on m2 is smaller relative to the protoconid. The m2 of the holotype has a reduced cusp pattern such that the crown surface is nearly flat and recognition of its cusp morphology is difficult. The m3 has two roots, and it is present on all specimens except the left ramus of the holotype.

DISCUSSION: Schlaikjer (1935: 139) recognized the similarity between *Mesocyon hortulirosae* (*Paraenhydrocyon josephi*) and *P.*

robustus, but emphasized "the incipient development of the metaconid on M_2" of the latter as a distinct character. Macdonald (1963: 213) rejected this argument: "the metaconid on M_2 of *M. robustus* is hardly more than a large wrinkle in the enamel" and suggested that *M. hortulirosae* is "very likely synonymous with *M. robustus*." Although it is difficult to make comparisons based on the nearly flattened m2 on the holotype, *P. robustus* does seem to occupy a more derived position in the phylogeny by having more reduced accessory cusps on the premolars than does *P. josephi*.

Macdonald (1963: 212, 1970: 58) referred five specimens from the Wounded Knee Sharps Formation of South Dakota to *Mesocyon robustus*. All of them are referred to *"Mesocyon" temnodon* in the present study because of their well-developed accessory cusps in premolars and their lack of a deep masseteric fossa.

F:AM 27554 and 27557 are tentatively included in *Paraenhydrocyon robustus*. F:AM 27557 has primitively retained an anterior cingular cusp on p4 and F:AM 27554 has rather broad premolars. Their intermediate size and reduced metaconids on the lower molars, however, suggest a phylogenetically transitional position, as is demonstrated by the type of *P. robustus*.

Caedocyon, new genus

TYPE SPECIES: *Caedocyon tedfordi*, new genus and species.

INCLUDED SPECIES: Type species only.

DIAGNOSIS: As monotypic species.

DISTRIBUTION: As monotypic species.

ETYMOLOGY: *caeduus,* Latin, fit for cutting, *caedo,* cut, cut down, kill; in reference to the precise occlusion pattern of its dentition. *kyon,* Greek, dog; common ending for doglike carnivorans.

Caedocyon tedfordi, new species
Figures 53, 54

HOLOTYPE: UW 10251, rostral part of skull with left I3–M1 and right C1–M2.

TYPE LOCALITY: UW locality no. V-76006, Dog Skull locality, north of Klutz Canyon, 10 mi east of Slater, north to northeast of Redding Ranch, in NE½, SE¼, NE¼, sect.
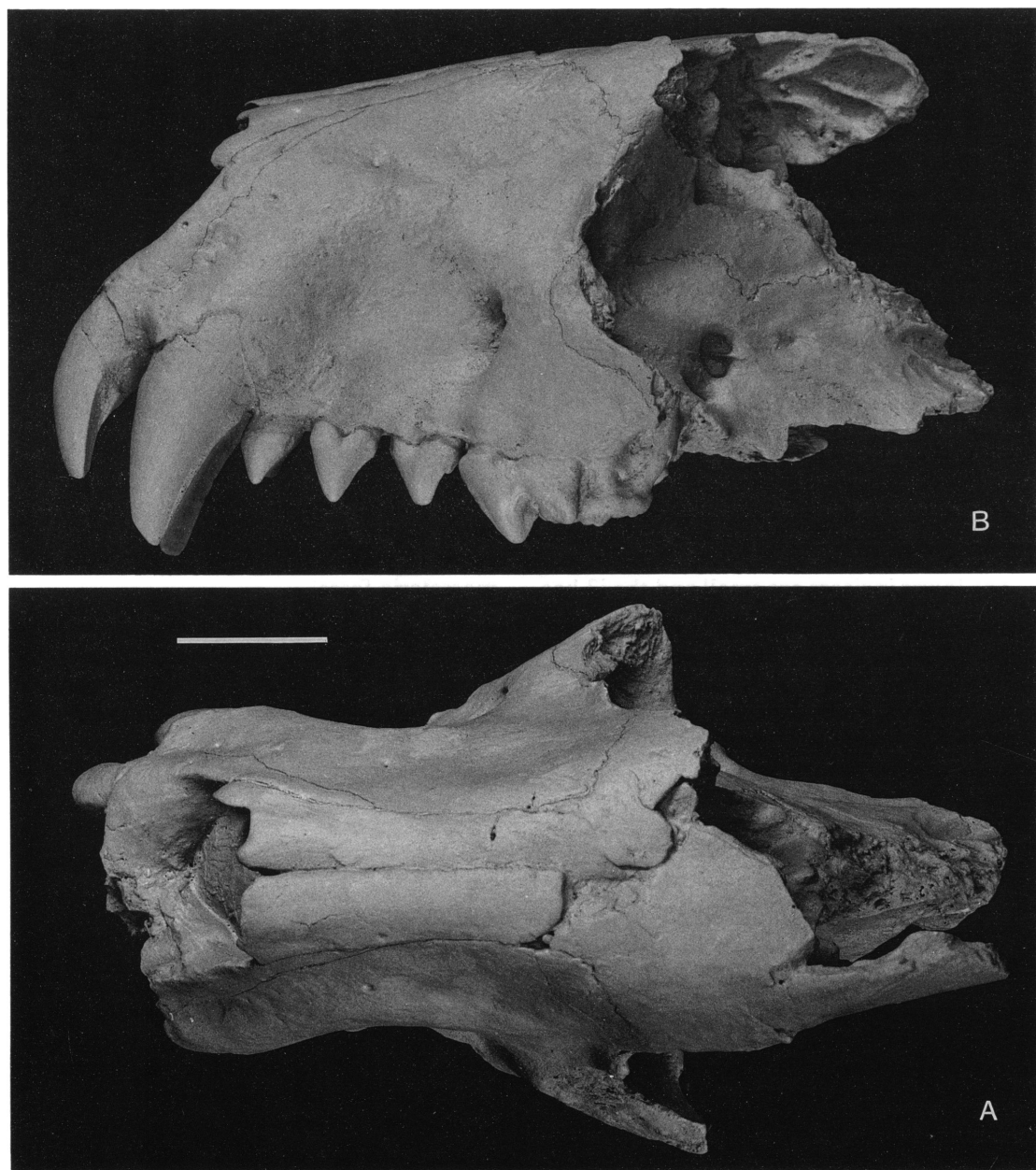
Fig. 53.   Skull of *Caedocyon tedfordi*. **A**, Lateral and **B**, dorsal views of UW 10251, holotype. Photographs of plaster cast. Scale = 20 mm.

15, T. 22 N, R. 65 W, Goshen Hole area, Goshen County, Wyoming. The nearest section measured by Schlaikjer (1935: 113) was from approximately 1 mi north of YBO Pass in NW¼, sect. 5, T. 21 N, R. 64 W. The YBO Pass section is 5 mi to the southeast of the

UW loc. V-76006, and contains a sequence of 200-ft-thick sandy deposits above the Brule clay. UW V-76006 is topographically in the same level as the YBO Pass; both are along the southeast escarpment of the Goshen Hole area. UW V-76006 is thus assumed to be
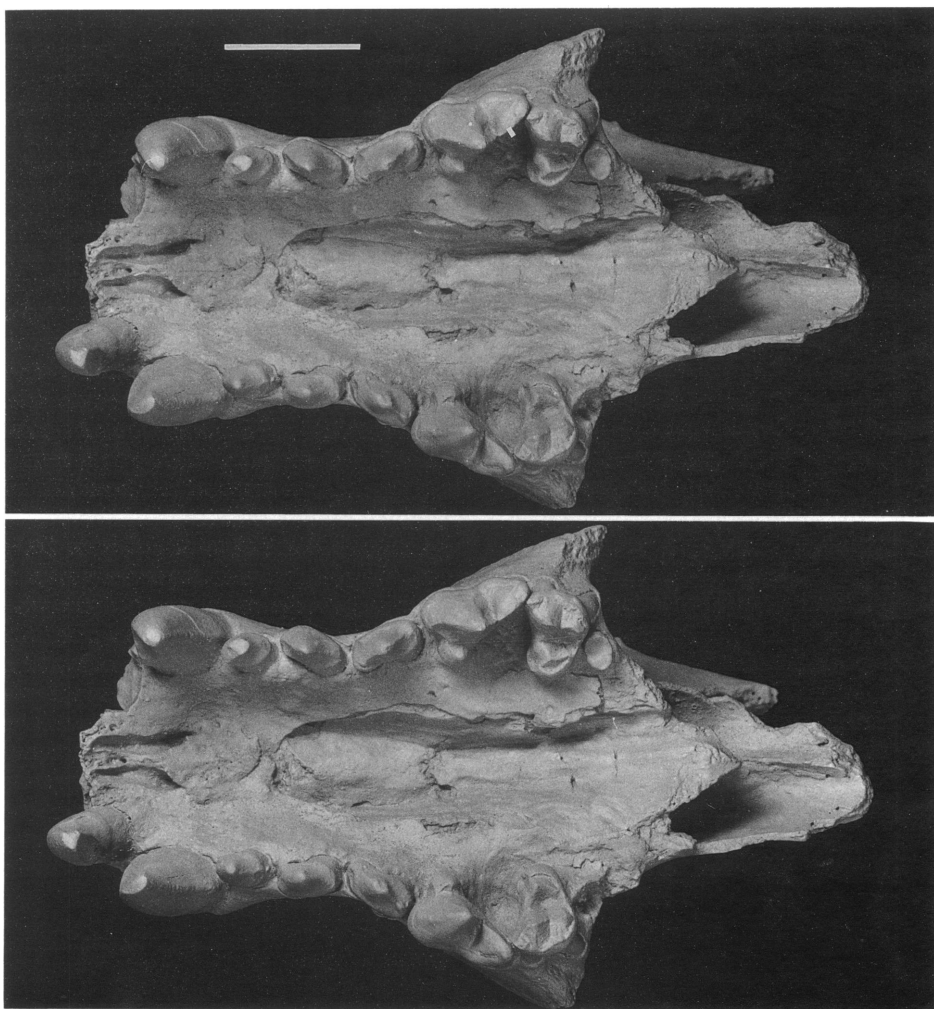
Fig. 54. *Caedocyon tedfordi*. Occlusal view (in stereo) of UW 10251, holotype. Photographs of plaster cast. Scale = 20 mm.

equivalent to the YBO Pass section (i.e., Lower Arikaree Group). This same locality produced a partial skull of *Paraenhydrocyon josephi* (UW 10253; see Referred Specimen of this species).

REFERRED SPECIMEN: None.

DIAGNOSIS: *Caedocyon tedfordi* is highly apomorphous and distinct from other lineages of hesperocyonines. It has a short but strong rostrum, which is broad and deep. The frontal region is slightly domed with a reduced postorbital process of the frontal and an extensive frontal sinus (char. 4). The teeth are mainly characterized by the enlarged I3

(char. 26) and shortened cheek toothrow (char. 27) with short, high premolars and reduced molars. The M2 is reduced (char. 40). Another distinct feature is its precise occlusal pattern that greatly limited lateral movement of the lower jaws.

DISTRIBUTION: As in type locality.

ETYMOLOGY: This species is named in honor of Dr. Richard H. Tedford, curator and chairman of the Department of Vertebrate Paleontology, American Museum of Natural History. Dr. Tedford's lifelong research on carnivorans has greatly enriched the understanding of their phylogeny and evolution,

and his knowledge of canid systematics and biostratigraphy has significantly improved the quality of this study.

DESCRIPTION: An excellent cast of the holotype is available for the present study and forms the basis for the description.

Skull: The holotype is a well-preserved rostrum that is broken off near the postorbital constriction. Being significantly larger than *Paraenhydrocyon wallovianus*, the overall construction of the holotype of *Caedocyon tedfordi* is stout with a short and broad rostrum in dorsal view. The rostrum is also very deep in lateral view. The premaxillary is massive, into which is anchored an enlarged caniniform I3. The posterior process of premaxillary is short and slender, and does not reach back to touch the anterior process of the frontal as it does in borophagines that have enlarged I3s. The nasals are short, extending posteriorly to the level of the antorbital rim. The frontal region is swollen such that its postorbital process (preserved on the left side) is a small, inconspicuous bump surrounded by the inflated frontal bone. The internal surface of the frontal bones can be observed due to the breakage near the postorbital constriction. The frontal sinus is large but does not seem to invade the postorbital process. The maxillary is deep and houses a large, oval-shaped infraorbital foramen. The lacrimal forms a prominent process on the antorbital rim. This lacrimal process touches the anterior tip of the jugal bone.

The palate is very wide, despite compressive deformation that has reduced its original width. The incisive foramen is narrow and long, and is more anteriorly located than in *Paraenhydrocyon*. The posterior border of the palatine extends far behind the posterior border of the M2, because of the considerably shortened toothrow (see below).

Dentition: The dental morphology of *Caedocyon tedfordi* is as unusual as that of its skull. Some of the autapomorphies cannot easily be compared with known hesperocyonine taxa.

The I3 is caniniform, with almost identical curvature to, and only slightly smaller size than, the canine. The I3 is more than twice the size of I1 or I2, judging from the alveoli of I1–2. There is a prominent wear facet on its posterolateral surface, and it is thus not possible to know whether the I3 has a basal lateral cusp. This facet is deep and sharp-edged, indicating very precise occlusion with the lower canine and restricted movement of the lower jaw. The canine is robust and has a distinct posterior ridge and an anteromedial ridge. The latter ridge is worn off up to the base of the canine; the wear facet faces exactly opposite to that on the I3.

The upper toothrow is significantly shortened. The upper premolars are short and stout; the length/width ratio is 1.76 for P2 as compared to 2.24 (average) in *Paraenhydrocyon wallovianus*. The P1–2 are single-cusped (single-rooted in P1 and double-rooted in P2), whereas the P3 has a small posterior cingular cusp. The crown of the P2 is slightly higher than that of the P3. There is a semicircular, sharp-edged wear facet on the anterior surfaces of P2–4 chiseled by the tips of the corresponding lower premolars. The P4 is short anteroposteriorly but broad. The protocone is posteriorly positioned, that is, slightly behind the anterior border of the paracone. A wear facet cuts deeply into the anterior cingulum between the protocone and paracone. There is a cingulum on the medial side of the P4, but none on the lateral side.

The M1 is quite small. Its lingual side is shifted anteriorly, and, together with the shortened shearing blade of P4, leaves a much reduced space for the occlusion with the trigonid of m1, which must have been short. The anterior edge of the M1 sustained considerable wear from the posterior edge of the m1 trigonid. The M1 has a larger paracone than metacone. The labial cingulum is reduced, especially near the paracone. The parastyle is small. The metastyle corner is rounded. The protocone is small, surrounded lingually by a narrow internal cingulum, which is weaker than in any other hesperocyonine. The M2 is single-rooted and is reduced to a small oval tooth. Its occlusal surface is heavily worn and individual cusps are not recognizable.

DISCUSSION: The phylogenetic relationships of *Caedocyon tedfordi* are puzzling mostly because of the incomplete knowledge of its cranial and dental anatomy and the lack of intermediate forms. Without knowledge of its basicranium, even its identity as a canid is not well established. Its extremely reduced

M2, however, makes it unlikely to be an amphicyonid. Characters that can be observed on UW 10251 are all so derived from the primitive hesperocyonine plan that homologies are difficult to establish. Four features may suggest affinity of *Caedocyon* with *Paraenhydrocyon*. (1) The presence of sharp-tipped premolars that have poorly developed accessory and cingular cusps is uniquely shared by these two genera; the premolars of *Caedocyon*, however, are considerably shortened due to the overall short toothrow. (2) The posterior palatine border of one skull of *P. josephi*, UCMP 80391, is more than 5 mm behind the posterior alveolar margin of its M2, a character only seen and further exaggerated in *Caedocyon* (19 mm behind the M2; part of this distance is obviously due to its much larger size). (3) The presence of a highly precise occlusal pattern in *Caedocyon* seems to be comparable with a similar locking mechanism in *P. wallovianus*, which has a deep trigon basin in M1–2 that limits the lateral movement of the m1 hypoconid. (4) The enlarged frontal sinus in *Caedocyon* may be a further elaboration of the modest frontal sinus seen in *P. josephi*. Except for the first feature, the second and third are not consistent (the posterior margin of palatine) or well defined (the occlusal pattern) enough to be used in the formal phylogenetic analysis. The fourth feature, the frontal sinus, is independently acquired by *Osbornodon*. The present tentative alliance of *Caedocyon* with *Paraenhydrocyon* is therefore little more than a conjecture pending verification from more complete materials.

Although the enlarged I3 of *Caedocyon* may seem to be a shared character with *Enhydrocyon*, this similarity is most likely independently derived because the I3 on *Caedocyon* is extremely caniniform (i.e., with a sharp tip) in contrast to the proportional enlargement of I3s in *Enhydrocyon*, which are columnlike and incisiform.

Ectopocynus, new genus

TYPE SPECIES: *Ectopocynus simplicidens*, new genus and species.

INCLUDED SPECIES: *Ectopocynus simplicidens*, new genus and species; *E. antiquus*, new species; and *E. intermedius*, new species.

DIAGNOSIS: *Ectopocynus* has short, blunt, and robust lower premolars with extremely reduced/absent accessory and cingular cusps (chars. 29–31). The simple cusp patterns of the premolars are easily distinguished from those of *Enhydrocyon*, which has similarly robust premolars but has well-developed accessory and cingular cusps. Except for one referred individual from the Whitneyan, all have lost their lower first premolars (char. 28). The metaconids of m1–2 are reduced even in the most primitive forms, in contrast to other lineages of hesperocyonines, which reduce their metaconids only in large-sized, highly derived forms.

DISTRIBUTION: Poleslide Member of Brule Formation, western South Dakota; Lower Arikaree Group of eastern Wyoming; and Runningwater Formation of western Nebraska. Whitneyan to Middle Hemingfordian. A long gap in the fossil record of this genus is present from Middle Arikareean through Early Hemingfordian time.

ETYMOLOGY: *ektopos*, Greek, out of place, odd, strange, unnatural; *kynos*, Greek, dog. In allusion to the unusual dental morphology of the genus.

DISCUSSION: The Frick Collection has the only six specimens representing three species of this extremely rare lineage of hesperocyonines over a geological interval of approximately 12 million years from the Whitneyan to Middle Hemingfordian. As far as I know, no specimen of *Ectopocynus* has been previously reported in the literature.

The phylogenetic relationship of *Ectopocynus* remains unsettled. The lack of knowledge about its cranial (particularly basicranial) anatomy makes it difficult to confirm its canid affinity. In fact, the musteloid *Aelurocyon*, which is contemporaneous with the Hemingfordian species *E. simplicidens*, possesses a similarly robust mandible and teeth (*E. simplicidens*, however, is distinguishable from *Aelurocyon* by a lower coronoid process, an indistinct internal ridge of angular process, a much larger M2, a lack of anterior and posterior cingula of p2–3, a longer m2, and presence of an m3). From the Hemingfordian *E. simplicidens* alone, it is especially difficult to determine the higher-level phylogenetic relationship of the genus because of its highly apomorphous status. However, the present

recognition of a single Whitneyan mandible (F:AM 63376) that is referred to *E. antiquus*, together with the intermediate form *E. intermedius*, makes it reasonably certain that *Ectopocynus* belongs to the Hesperocyoninae. The limited materials available do not permit a more precise assessment of the phylogenetic position of *Ectopocynus* within Hesperocyoninae. No synapomorphy unites it with any other particular lineage, 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 *E. antiquus* that does not yet possess these derived characters, but also because of the detailed anatomical differences between *Ectopocynus* and *Enhydrocyon*.

Ectopocynus simplicidens,
new species
Figures 55C, 56D

HOLOTYPE: F:AM 25431, complete right ramus with c1, p2–m2, and alveoli for i1–3. Collected by Theodore Galusha and AMNH party in 1964.

TYPE LOCALITY: Wood's Canyon Quarry, in Wood's Canyon, a tributary of Antelope Valley (see Galusha, 1975b: fig. 1), in SW¼, sect. 27, T. 31 N, R. 47 W, Dawes County, Nebraska. Runningwater Formation (listed as Marsland Formation in T. Galusha fieldnote, 1964. Galusha followed the definition of Schultz [1938], which included the Runningwater Formation in a more inclusive Marsland Formation; see McKenna [1965] for a summary), Middle Hemingfordian.

REFERRED SPECIMENS: From the Runningwater Formation of western Nebraska: F:AM 25426, complete mandible with left and right c1, p2–m2, and isolated right C1 and left M2, from the vicinity of the mouth of Antelope Creek, SW¼, sect. 16, T. 32 N, R. 40 W, western Cherry County, approximately 18 ft above the *Aletomeryx* Zone (Skinner and Johnson, 1984: fig. 30), Runningwater Formation, Middle Hemingfordian; F:AM 129096, nearly complete left ramus with c1, p2–m2, from Cottonwood Creek Quarry, Marshall Ranch, in Cottonwood Creek drainage system, SW¼, sect. 25, T. 30 N, R. 50 W, Dawes County, Runningwater Formation, Middle Hemingfordian.

DIAGNOSIS: *Ectopocynus simplicidens* can be differentiated from *E. antiquus* and *E. intermedius* by its robust mandibular ramus; reduced coronoid process (char. 23); massive but simple conical premolars; loss of the metaconid on m1 (char. 43); and high, conical hypoconid on m2 (char. 44). *Ectopocynus simplicidens* shares with *E. intermedius* an elongated lower carnassial (char. 34) and a loss of m3 (char. 40). In addition, *E. simplicidens* possesses a simple, reduced angular process (char. 21; this latter structure is not preserved in the two more primitive species of *Ectopocynus*, and this character may not be diagnostic at this level).

DISTRIBUTION: Runningwater Formation of western Nebraska, Middle Hemingfordian.

ETYMOLOGY: *simplex*, Latin, onefold, single, simplicity; *dens*, Latin, tooth. In reference to the simple-cusped premolars of the species.

DESCRIPTION: Three specimens, all mandibles, constitute the complete sample of this rare species. The present description of *Ectopocynus simplicidens* contrasts mainly with *Enhydrocyon* because of the many similarities independently acquired by these two lineages.

Mandible: The construction of the horizontal ramus of *Ectopocynus simplicidens* is very similar to that of *Enhydrocyon*. It is rather uniformly deep and robust, and its lower border tapers abruptly upward at the anterior end, in contrast to a slender, gradually tapering ramus in *Ectopocynus antiquus*. The lower border of the masseteric fossa is consistently more elevated than in *Enhydrocyon*. The coronoid process is high in F:AM 129096 (partially preserved), but significantly lower in F:AM 25426 and 25431. The well-preserved coronoid process in the latter two individuals has a peculiarly low, sharp-tipped outline in contrast to the broad process in *Enhydrocyon*. The posterior border of the coronoid process leans anteriorly instead of being posteriorly reclined as in most hesperocyonines.

The angular process (preserved in F:AM 25426 and 25431) is also unique in its shortened and much simplified construction. The posterior tip of the process is anterior to the posterior border of the mandibular condyle, and its round, blunt tip protrudes just slightly beyond the posterior notch beneath the mandibular condyle (fig. 61H). The internal ridge is reduced compared to most hesperocyonines except *Osbornodon fricki*. In F:AM 25426, the internal ridge is represented by a gentle ridge raised barely above the surrounding bone. The lateral surface of the angular process is smooth without distinct muscle or tendon scars.

Dentition: An isolated upper canine and a left M2, associated with the mandible of F:AM 25426, are the only upper teeth available. This upper canine has the same massive appearance as the lower ones. The isolated M2 is broader (anteroposteriorly) than that of *Ectopocynus intermedius*, and has a more quadrate appearance than the latter.

Except for the missing incisors, the lower teeth are almost completely known. The lower canines are smooth on the lateral surface and crenulated on the medial side. The p1 is suppressed, a synapomorphy for *Ectopocynus*. The p2–4 have the simple, massive construction that is characteristic of this lineage. They have a short oval outline in occlusal view and have blunt principal cusps. There is no accessory cusp except on the p4. The p4 also has anterior (not on the type) and posterior cingula. The trigonid on m1 is swollen mediolaterally. The metaconid is so reduced in all three specimens that it can be regarded as practically absent. The talonid is occupied by a single, large hypoconid, although an entoconid is variably present as a low cingulum on the lingual side. The hypoconid of *E. simplicidens* is unique in its more conical construction instead of being ridgelike as in *E. antiquus–intermedius* and other hesperocyonines. The m2 is also highly distinctive with its dominant, conical protoconid and hypoconid lacking ridges that are usually present in the rest of hesperocyonines. The paraconid is lacking. Although much smaller than the protoconid, the metaconid is still present in all individuals. The metaconid is shifted posteriorly relative to the protoconid. The m3 is lost in all individuals.

Ectopocynus antiquus, new species
Figures 55A, 56B

HOLOTYPE: F:AM 54090, partial right ramus with i3–c1, p2, p4–m3. Collected by N. J. Vaughan in 1937.

TYPE LOCALITY: From F:AM Little Muddy Creek locality, southeast of Lusk, 20 mi south of Keeline and west of Spanish Diggings, Niobrara County, Wyoming, in "middle brown sand," Lower Arikaree Group.

REFERRED SPECIMEN: From Brule Formation of South Dakota: F:AM 63376, partial right ramus with p2–m2 and broken (roots left only) c1–p1, m3, from Hay Creek, a tributary of Bear Creek, Washabaugh County, in Leptauchenia beds, Poleslide Member of Brule Formation, Whitneyan.

DIAGNOSIS: Approximately the same size as "*Mesocyon*" *temnodon* and *Paraenhydrocyon josephi*, *Ectopocynus antiquus* can be distinguished from the former two species 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 diagnostic for the genus *Ectopocynus*. In addition to its much smaller (21%) size than *E. intermedius*, *E. antiquus* also has relatively smaller and more narrow lower premolars and molars. *Ectopocynus antiquus* retains primitive characters that can be used to differentiate it from *E. simplicidens*: the presence of a small metaconid on m1 and a m3.

DISTRIBUTION: Brule Formation of western South Dakota and Lower Arikaree Group of eastern Wyoming. Whitneyan to Early Arikareean.

ETYMOLOGY: *antiquus*, Latin, of antiquity. This is the oldest and most primitive known species in the genus.

DESCRIPTION: Two partial mandibles are available. The type, F:AM 54090, has all of the derived characteristics of *Ectopocynus*, whereas the referred specimen, F:AM 63367, is more primitive and older in age.

Mandible: Mandibles of *Ectopocynus antiquus* are little different from most small, primitive hesperocyonines (such as the similar-sized "*Hesperocyon*" *coloradensis*, "*Mesocyon*" *temnodon*, and *Osbornodon renjiei*). The horizontal ramus remains primitively slender, and its anterior end tapers gradually in contrast to a more abrupt upward curve
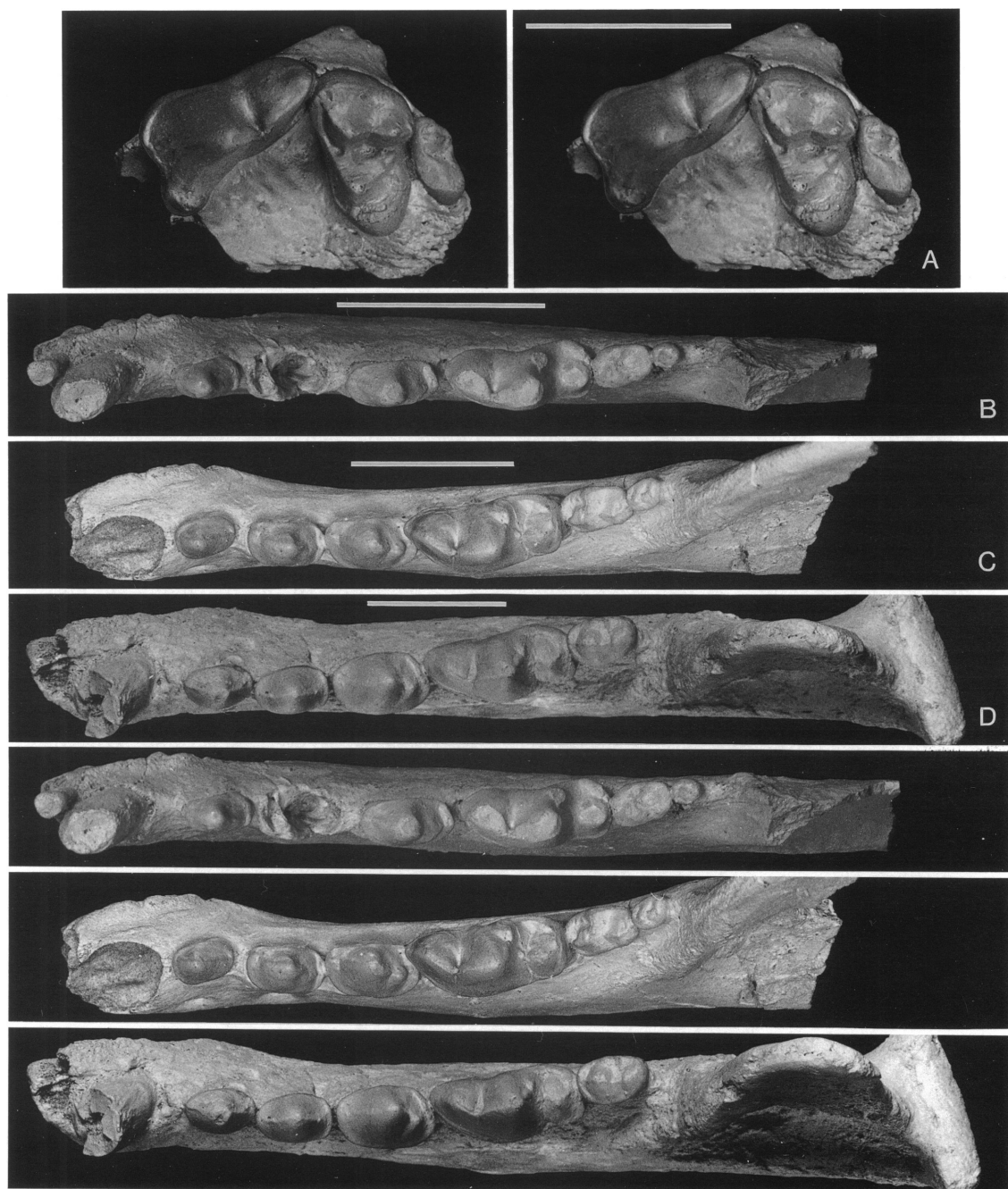
Fig. 56.   Occlusal views of **A** and **C**, *Ectopocynus intermedius*, F:AM 27580, holotype; **B**, *Ectopocynus antiquus*, F:AM 54090, holotype, reversed from right side; **D**, *E. simplicidens*, F:AM 25431, holotype, reversed from right side. All in stereo pairs. Scales = 20 mm.

←

Fig. 55.   Lateral views of **A**, *Ectopocynus antiquus*, F:AM 54090, holotype, reversed from right side; **B**, *E. intermedius*, F:AM 27580, holotype; **C**, *E. simplicidens*, F:AM 25431, holotype, reversed from right side. Scales = 20 mm.

in *E. simplicidens*. On both specimens, the coronoid process is not preserved and the masseteric fossa is broken in half; the remaining masseteric fossa indicates that it does not invade ventrally to form a pocket at its ventral border, as in *Paraenhydrocyon josephi*.

Dentition: An i3 is preserved on the type but is too worn to reveal its cusp pattern; it has a round cross section. The canine in the type is broken in half; the preserved enamel is smooth. The p1 is absent on the type and present on F:AM 63367 (with a single root only). The premolars of the type tend toward the shortened and laterally expanded proportions that are typical of *Ectopocynus*. The p2 has a length/width ratio of 1.7 as compared to 1.5 for the types of *E. intermedius* and *E. simplicidens*. The premolars of F:AM 63367, however, retain a much more slender construction (p2 length/width ratio 2.0 as compared to an average of 2.17 for *Paraenhydrocyon josephi* and 2.28 for "*Mesocyon*" *temnodon*) with less reduced posterior accessory cusps (still present on p3). The m1 of the type has a reduced metaconid although it is less reduced than in *E. simplicidens*. This is the only derived character that both the type and referred specimen have in common. The metaconid becomes a small bud at the lingual base of the protoconid and has a blunt, low tip instead of the sharp, high tip of most primitive hesperocyonines. The reduction of the metaconids is caused by the enlargement of the base of protoconid toward the lingual side at the expense of the metaconid. This relationship is more clearly demonstrated in the m2, which has a swollen protoconid. The talonid of m1 is dominated by the hypoconid, that is, a trenchant talonid. The hypoconid on F:AM 63367 is primitively ridgelike; that on the type is too worn to be ascertained. The entoconid on the type is a low, indistinct posterolingual cingulum, whereas that on F:AM 63367 is still a sharp, low, lingual ridge enclosing a nearly flat platform of approximately one-fifth the total width of the talonid. The size of m2–3 on the type is relatively reduced (relative to that of m1), but that on F:AM 63367 is not. A reduced grinding area, that is, m1 talonid through m3 (or m2 if m3 is lost), is common for all *Ectopocynus*. The base of the m2 protoconid is expanded an-

teriorly and lingually, leaving less room for the metaconid. The metaconids on both specimens are significantly smaller than the protoconids in contrast to approximately equal-sized cusps in other primitive hesperocyonines. The m2 hypoconid is low. The m3 of the type is tiny (maximum length 2.9 mm and probably single-rooted) but is unreduced on F:AM 63367 (4.6 mm, measured across the double roots).

DISCUSSION: The presence of a p1 and the primitive shape of the other lower premolars on F:AM 63367 clearly indicate its primitive status as compared to the type of *Ectopocynus antiquus*. The only character of F:AM 63367 that unambiguously identifies it with *E. antiquus* is its much reduced metaconids on m1–2. (Although reduction of metaconid has evolved a number of times, most lineages that acquired it had done so in association with a number of hypercarnivorous features, including large size and robust premolars. This reduction of the metaconid in an otherwise primitive, small canid is not seen elsewhere.) If correctly referred, F:AM 63367 offers the best evidence that *Ectopocynus* is a primitive hesperocyonine, for F:AM 63367 is little different from other small hesperocyonines, such as *Hesperocyon*, aside from this single character.

Ectopocynus intermedius, new species
Figures 55B, 56A, C

HOLOTYPE: F:AM 27580, maxillary fragments with left and right P4–M2, and partial left ramus with p2–m3. Collected by C. H. Falkenbach in 1939.

TYPE LOCALITY: F:AM Little Muddy Creek locality, southeast of Lusk, 20 mi south of Keeline and west of Spanish Diggings, Niobrara County, Wyoming. From 10 ft "below white layer" in a "low" horizon in the Little Muddy Creek locality (C. H. Falkenbach fieldnotes, 1939). Falkenbach correlated the Little Muddy Creek deposits to the Gering Formation in western Nebraska. Lower Arikaree Group.

REFERRED SPECIMEN: None.

DIAGNOSIS: Being intermediate in size, *Ectopocynus intermedius* is 21% larger than the type of *E. antiquus* and 15% smaller than that of *E. simplicidens* (length of p2–m3/2). *Ec-*

topocynus intermedius differs from *E. antiquus* in the former's relatively enlarged and more robust premolars and molars. *Ectopocynus intermedius* is more derived than *E. antiquus* in its elongated m1 (char. 34), its loss of m3 (char. 40), and its reduced metaconid on m2 (char. 43). Compared to *E. simplicidens*, *E. intermedius* primitively has a less robust ramus, a higher anterior coronoid process, less robust premolars, a small metaconid in m1, and an m3.

DISTRIBUTION: As type locality.

ETYMOLOGY: *inter*, Latin, between, among; *medius*, Latin, middle. In reference to the intermediate morphology of the species.

DESCRIPTION: The type, F:AM 27580, is the only specimen of *Ectopocynus intermedius*, and intraspecific variation cannot be assessed.

Mandible: Construction of the horizontal ramus of *Ectopocynus intermedius* is intermediate between that of the slender *E. antiquus* and that of the robust *E. simplicidens*. Due to its young age (unworn dentition), the ramus of F:AM 27580 is relatively slender as compared to its massive teeth. Although the posterior half is broken off, the remaining anterior half of the coronoid process in F:AM 27580 is relatively high, a primitive state in contrast to a low process in *E. simplicidens*.

Dentition: Except for one isolated C1 and M2 in *Ectopocynus simplicidens* (F:AM 25426), the left and right P4–M2 of F:AM 27580 are the only known upper teeth for *Ectopocynus*. For lack of comparable material in the other two species of *Ectopocynus*, the present description of the upper teeth therefore mainly compares *E. intermedius* with other genera of hesperocyonines.

The P4 is similar in size and shape to that of *Enhydrocyon pahinsintewakpa*. It is heavily built with a thick shearing blade. The protocone is small and appressed to the base of the paracone. There is a low, indistinct ridge on the anterior surface of the paracone, and an even less distinct ridge on the anterolingual side of the paracone connecting with the protocone. The anterior cingulum on P4 is poorly developed. The M1 has a rather slender appearance typical of primitive hesperocyonines. It is anteroposteriorly narrow. Its labial length is not increased and thus does not contrast with a narrow trigon width, as
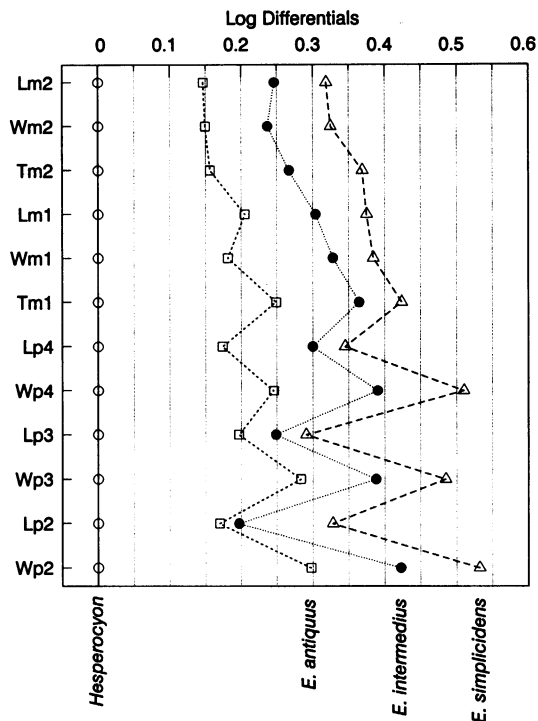
Fig. 57. Log differentials of dental measurements among species of *Ectopocynus* as compared to *Hesperocyon* as standard. *Ectopocynus* is characterized by increasing size of the first lower molars (Lm1, Wm1, Tm1) relative to the second lower molars (Lm2, Wm2, Tm2) and by short and wide premolars, that is, the contrasting log differentials of premolar lengths (Lp2, Lp3, Lp4) versus widths (Wp2, Wp3, Wp4). The primitive status of *E. antiquus* is demonstrated in its less jagged lines in the premolar (lower) portion of the diagram. Although intermediate in size, *E. intermedius* already possesses the proportions of the premolars in *E. simplicidens*. Procedures to generate the log ratios were outlined by Simpson (1941). Data points are the means of each species. Measurements on the vertical axis are defined in figure 6. See Appendix III for measurements of *Ectopocynus*.

in *Enhydrocyon* and *Paraenhydrocyon wallovianus*. The paracone is larger than the metacone, but not as much as in derived species of *Enhydrocyon*. Consequently, the parastyle of M1 is also not prominently developed. The trigon basin is less deeply excavated than in *Paraenhydrocyon*. The internal cingulum is more anteromedially positioned than in *Sunkahetanka*, but does not encircle the proto-

cone as it does in most *Enhydrocyon*. The M2 is slender and reduced in contrast to the much broader M2 of *Ectopocynus simplicidens*. This combined shortness of M1–2 corresponds to a reduced grinding area in the lower teeth (the m1 talonid through m2).

Besides their much larger size, the lower teeth of *Ectopocynus intermedius* are mainly distinguished from those of *E. antiquus* by proportional differences (comparisons of lower teeth are between the types of *E. antiquus* and *E. intermedius* only). The advanced status of *E. intermedius* over *E. antiquus* is mainly reflected in its relatively enlarged teeth, which are crowded within a shorter toothrow. Thus, the maximum length of m1 is 31% longer than that of *E. antiquus*, but the toothrow is only 21% longer (p2–m3). The enlargement of the p4 is even more obvious: 37% longer than in *E. antiquus* —almost twice the elongation of the toothrow (fig. 57). To accommodate these more massive teeth, the diastemata are narrowed or closed and the premolars are imbricated (except between p2 and p3). The premolars of *E. intermedius* are also widened; the length/width ratio of p2 is 1.5 for *E. intermedius*, as compared to 1.7 for the type of *E. antiquus*. Aside from these proportional differences, the premolars between these two species are similar in their cusp morphologies. The above proportional differences are further exaggerated in *E. simplicidens*, although to a lesser degree (fig. 57).

The lower molars of *Ectopocynus intermedius* and *E. antiquus* are difficult to distinguish beyond the abovementioned en-

larged m1 in *E. intermedius*. Both retain a small metaconid on m1 and m3. As can be clearly seen on the unworn teeth of F:AM 27580, the hypoconids of m1–2 are ridgelike, that is, with anterior and posterior ridges leading down from the tip of the hypoconid, as contrasted to the rounded cusp in *E. simplicidens*. The presence of an m3 (probably single-rooted) in *E. intermedius* also demonstrates its primitive status compared to the Hemingfordian *E. simplicidens*.

DISCUSSION: The holotypes of *Ectopocynus antiquus* and *E. intermedius* are from the same locality: Little Muddy Creek. Although collected by different collectors at different times (F:AM 54090 from "middle brown sand" by N. J. Vaughan in 1937 and F:AM 27580 from "10 feet below white layer" by C. H. Falkenbach in 1939), contemporaneity for the two species is assumed (Lower Arikaree Group for both) for lack of contradictory evidence. The presumed sympatry for this species pair seems to agree with morphological evidence as well. Besides the advanced states of premolar proportions described above, *E. intermedius* is qualitatively little more advanced than the type of *E. antiquus*; for example, both still have a metaconid and a ridgelike hypoconid on m1 and retain an m3. The size difference (21%) between these two species agrees with Dayan et al.'s (1989, 1992) character displacement model in living canids of the Middle East (see Discussion of "*Hesperocyon*" *pavidus*). F:AM 27580 may be indicative of the beginning of a cladogenetic event between *E. antiquus* and *E. intermedius*.

PHYLOGENY

CHARACTER ANALYSIS

The genus *Miacis* is commonly regarded as the closest approximation to forms ancestral to canids (Matthew, 1930; Clark, 1939; Tedford, 1978; Gustafson, 1986). Indeed, the dentition of *Miacis* shows a number of initial trends that were eventually fully manifested

in canids, for example, elongation of carnassials and reduction of M3. Wang and Tedford (1994) recently attempted to put into phylogenetic perspective a few selected miacids and primitive cynoids, and to determine how they are related to primitive canids. Our cladogram (ibid.: fig. 8) in that study forms the phylogenetic framework from which out-

TABLE 5
Character Matrix of Hesperocyonines

(The 28 taxa by 46 character matrix has 14% missing data [in question marks]. Character numbers and states correspond to those listed under Character Analysis.)

Taxa	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	444444 123456
Outgroup	000000000?	0000000000	0000000000	0000000000	000000
Prohesperocyon wilsoni	1000001100	1100000000	0000??0031	0000100000	110001
Hesperocyon gregarius	0000001101	1100000000	0000000001	0101100100	010000
"Hesperocyon" pavidus	0?????????	??????????	0000??0001	0101100100	010000
"Hesperocyon" coloradensis	0000001101	1101000000	0000000000	0101100100	010000
"Mesocyon" temnodon	0000000101	1102000000	0000000001	0101100100	010000
Mesocyon brachyops	0000010101	1102100010	?000000001	0101100100	010000
Mesocyon coryphaeus	0000010111	1102100000	0000000001	0101100100	010000
Cynodesmus thooides	0000010101	1102200000	0000000001	0101100102	010000
Cynodesmus martini	0010010101	110220000?	?0?0000111	0101100102	010000
Sunkahetanka geringensis	0000010101	1102100000	0000000011	0101100100	011000
Philotrox condoni	0010010111	1102100100	0000000011	0101100100	011000
Enhydrocyon pahinsintewakpa	0110010101	1112110200	0000110111	0102110000	012000
Enhydrocyon crassidens	0110000101	1122110200	0000110111	0102111001	013000
Enhydrocyon stenocephalus	0110000111	1112110200	0000110111	0102110001	013000
Enhydrocyon basilatus	0110000111	1112120200	0000??0121	0102110001	013000
Osbornodon renjiei	0000000101	1102000000	0000000001	0101100110	010010
Osborndon sesnoni	00000?????	??????????	?0???00031	0101100110	010010
Osbornodon iamonensis	1001100121	1102101300	2000000031	0111100120	010010
Osbornodon brachypus	1001100121	1102102310	2101?00031	0111100120	010010
Osbornodon fricki	1002100121	1102102310	2000000031	0121101120	010010
Paraenhydrocyon josephi	0000000101	1100010001	0100000001	0101100100	010000
Paraenhydrocyon robustus	??????????	??????????	?1?????030	0101100100	011000
Paraenhydrocyon wallovianus	0000000101	11?0010001	21??000030	0101110100	013000
Caedocyon tedfordi	00010?????	??????????	????021010	0101100101	01????
Ectopocynus antiquus	??????????	?????????0	0000???110	1?01?????0	010000
Ectopocynus intermedius	??????????	??????????	?000???110	1102100101	011000
Ectopocynus simplicidens	??????????	?????????0	1010???110	1?02?????1	012100

groups are selected in the present analysis. Whenever material is available, *M. parvivorus*, the genotypic species, is used as the outgroup. A partial skull with nearly complete dentition (USNM 214706) of *M. parvivorus* from the Bridger Formation is the principal source of comparison. In case of missing structures, *Procynodictis vulpiceps* (AMNH 2514, CMNH 12063; = "*M.*" *gracilis* in Wang and Tedford, 1994), "*M.*" *cognitus* (TMM 40209-200), and *Vulpavus profectus* (AMNH 12626) will be used as alternative outgroups.

Some complex multistate characters (e.g., paroccipital process) are coded as separate characters to be expressed as distinct morphological trends. Numbering of the characters corresponds to numbers in the character matrix in table 5.

Skull

1. Rostrum Length: From the primitive condition of a relatively short rostrum in *Hesperocyon* and *Miacis*, the snout became elongated in *Prohesperocyon* and advanced *Osbornodon*. Associated with this elongation is the increased diastema between premolars.

Polarity: 1(0), rostrum not elongated; 1(1), rostrum elongated.

2. Anterior Process of Frontal: The lateral border of the frontal process that inserts between the maxillary and the nasal forms a smooth concave curve in the primitive hesperocyonines. In *Enhydrocyon*, this suture is pinched by a sharply cornered maxillary (fig. 58). The resulting frontal process becomes a slender tip whose lateral border forms a 90°
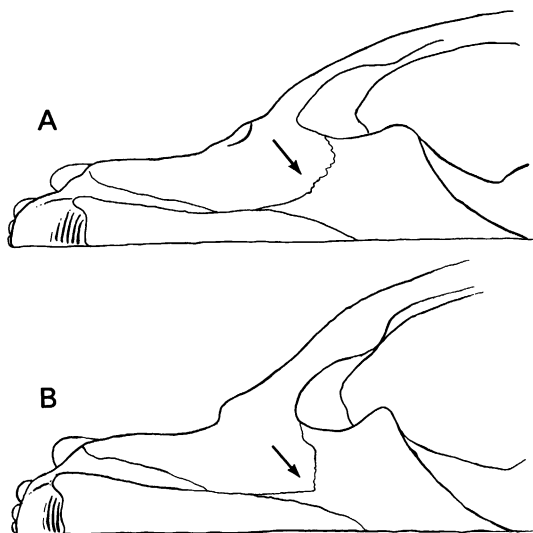
Fig. 58. Dorsal view of anterior right half skull showing different configurations of frontal/maxillary suture between primitive condition in primitive hesperocyonines (A) and derived condition in *Enhydrocyon* (B). Note also the relatively broad and short rostrum and longer distance between postorbital process and postorbital constriction in *Enhydrocyon*.

angle with the transverse segment of the frontomaxillary suture in dorsal view.

Polarity: 2(0), smoothly curved frontal process (fig. 58A); 2(1), frontal process laterally pinched with a sharp corner at its base (fig. 58B).

3. Elongation of the Orbital Section of Skull: In hypercarnivorous taxa, such as *Cynodesmus martini*, *Philotrox*, and *Enhydrocyon*, the skull is stretched in the middle portion relative to the length of the toothrow. The postorbital constriction is located well posterior of the postorbital process of the frontal. In conjunction with the elongated skull, the masseteric fossa on the lower jaw is also anteroposteriorly elongated.

Polarity: 3(0), skull not elongated in the middle; 3(1), skull elongated in the middle.

4. Frontal Sinus: In living canids, there is an air cavity or sinus between the outer and inner walls of the rostral end of frontal bone, which is usually divided into two or three compartments (Evans and Christensen, 1979). Presence of frontal sinuses in living canids has long been known and used for

classification (Huxley, 1880), although doubts had been expressed about its taxonomic importance (Matthew, 1924). Childs Frick apparently felt that this structure deserved further investigation and had a number of specimens in his collection dissected. The result clearly shows that the frontal sinus is of phylogenetic significance. For specimens not dissected, I rely on the degree of inflation of the frontal bones and a shallow depression medial to the postorbital process; the presence of the latter is correlated with the lack of frontal sinus in living canids (Tedford and Taylor, MS). A frontal sinus was variously developed, probably independently, in advanced members of all three subfamilies of the Canidae (Tedford and Taylor, MS), and has figured prominently in the phylogeny of large South American canids (Berta, 1988). Within hesperocyonines, *Caedocyon* and derived members of *Osbornodon* (especially *O. fricki*) have a well-inflated frontal sinus.

Polarity: 4(0), absence of a frontal sinus; 4(1), presence of a moderate frontal sinus; 4(2), large frontal sinus extending behind postorbital constriction.

5. Infraorbital Foramen: In the advanced species of *Osbornodon* the cross-sectional shape of the infraorbital foramen has become a vertical slit rather than being rounded or oval-shaped as in the rest of the hesperocyonines.

Polarity: 5(0), infraorbital foramen rounded or oval-shaped; 5(1), infraorbital foramen compressed into a vertical slit.

6. Fossa for Rectus Capitis Dorsalis: In contrast to the smooth surface above the occipital condyles of most primitive hesperocyonines, a pair of rounded fossae, for the insertion of the rectus capitis dorsalis muscle, are present on the supraoccipital shield in *Mesocyon* (except "*M.*" *temnodon*), *Cynodesmus*, *Sunkahetanka*, and *Philotrox*. In *Enhydrocyon*, however, this feature is lost, possibly because of its highly robust cranial construction.

Polarity: 6(0), fossa absent; 6(1), fossa present.

Basicranium

A detailed analysis of basicranial characteristics as related to the phylogeny of prim-

itive canids can be found elsewhere (Wang and Tedford, 1994), and only a brief outline is given below for these characters. Many of the basicranial characters below are assumed to be present in most taxa whose external bullar morphology suggests that of a typical canid, even though the structures inside the bulla are not exposed—a time-consuming process reserved for only a few key taxa. This is justified because, in most instances, the canid basicranial morphology remains stable throughout its history.

7. Suprameatal Fossa: In *Prohesperocyon* and *Hesperocyon* there is a small fossa in front of the mastoid process. Although the fossa is located in the same position as in some primitive arctoids, its size and depth are much smaller compared to the suprameatal fossae in some arctoids (e.g., procyonids and mustelids). In all median- to large-sized hesperocyonines, the fossa is completely lost.

Polarity: 7(0), absence of a suprameatal fossa; 7(1), presence of a small suprameatal fossa.

8. Entotympanic Bulla: No known miacid has a preserved ossified bulla. Flynn et al. (1988) and Wyss and Flynn (1993) contended that nonpreservation of the bulla could be the result of loose attachment rather than nonossification. Nonetheless, the firm attachment of an ossified entotympanic bulla still serves as a practical distinction between true canids and archaic miacids.

Polarity: 8(0), absence of an ossified entotympanic bulla; 8(1), presence of an ossified entotympanic bulla.

9. Size of Auditory Bulla: The bulla is hypertrophied in several members of the *Mesocyon–Enhydrocyon* clade. This bulla inflation seems to be particularly frequent among the middle-to-large John Day forms. In *M. coryphaeus*, this hypertrophy of the caudal entotympanic is also reflected in the unusually large septum inside the bulla (see char. 10). In *Osbornodon*, however, the bulla is anteroposteriorly shortened.

Polarity: 9(0), bulla not inflated or shortened; 9(1), bulla inflated; 9(2), bulla shortened.

10. Bulla Septum: Presence of a low septum on the inner wall of the bulla is now confirmed in *Hesperocyon*, but the septum seems to be absent in *Prohesperocyon* (Wang and Tedford, 1994). The incomplete septum inside the bulla of *Hesperocyon*, however, is formed at the suture of the caudal entotympanic and ectotympanic, instead of the rostral/caudal entotympanic suture as observed in living *Canis* by Hunt (1974). The latter condition is likely to be derived from the primitive configuration in *Hesperocyon* through expansion of the septum, and may be independently achieved in *Enhydrocyon* (Wang and Tedford, 1994). In most hesperocyonines, however, the exact configuration of the septum is not known.

Polarity: 10(0), absence of a septum; 10(1), presence of a low septum.

11. Internal Carotid Artery: Much has been said about the internal carotid artery and its related structures in regard to their relevance to carnivoran phylogeny (e.g., Flynn et al., 1988, and references therein). Within the caniform clade, all canids share the extrabullar course of the internal carotid artery and the absence of the stapedial artery, in contrast to the transpromontorial position of the internal carotid and the presence of the stapedial arteries in miacids (Wang and Tedford, 1994). In addition, the internal carotid canal in canids is embedded between the entotympanic and petrosal and is dorsally located above the basioccipital/entotympanic suture, whereas that of arctoids is embedded within the entotympanic bulla and ventrally located below the basioccipital/entotympanic suture.

Polarity: 11(0), internal carotid artery intrabullar (i.e., transpromontorial position); 11(1), internal carotid artery extrabullar, between entotympanic and petrosal.

12. Promontorium: Primitively in miacids, the promontorium is globular in shape and isolated from the surrounding bones. In *Prohesperocyon* and all more derived canids, the promontorium is flattened and in solid contact with the basioccipital and basisphenoid.

Polarity: 12(0), promontorium globular and isolated; 12(1), promontorium medially and anteriorly expanded and in contact with surrounding bones.

13. Postglenoid Foramen and Ectotympanic: In most hesperocyonines, the postglenoid foramen is enclosed posteriorly by a laterally extended lip of the ectotympanic. In *Enhy-*

pf

lpe

mp

pp

A

lpe

pf

mp

pp

B
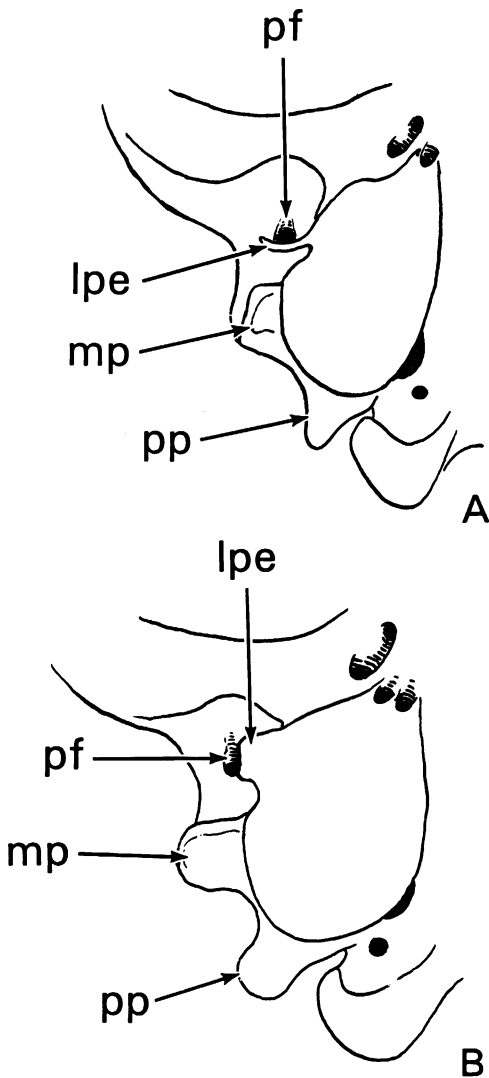
Fig. 59.   Ventral views of basicranium showing different character states of the lateral process of the ectotympanic. A, *Sunkahetanka geringensis*, UNSM 1092. The ectotympanic process forms a long, slender plate to cover the posterior wall of the postglenoid foramen. B, *Enhydrocyon basilatus*, UCMP 76749. The lateral process of the ectotympanic process stops at the postglenoid foramen. Note also the enlarged mastoid process and laterally expanded paroccipital process. Abbreviations: lpe, lateral process of ectotympanic; mp, mastoid process; pf, postglenoid foramen; pp, paroccipital process.

drocyon, the ectotympanic stops at the medial side of the postglenoid foramen, which is therefore exposed posteriorly. The ecto-

tympanic is inflated and extensively fused to the posterior surface of the postglenoid process in *E. crassidens*.

Polarity: 13(0), postglenoid foramen enclosed posteriorly by ectotympanic (fig. 59A); 13(1), postglenoid foramen not enclosed posteriorly (fig. 59B); 13(2), ectotympanic extensively fused with postglenoid process.

14. Direction of Paroccipital Process: Many authors have recognized the variation associated with the paroccipital process of the exoccipital bone (e.g., Cope, 1884; Matthew, 1924). The process serves as the site of insertion for the jugulohyoideus and digastric muscles in living *Canis*. A slender, posteriorly oriented paroccipital process, free from the posterior bulla wall, is surely the primitive condition for canids because it occurs in the miacids, *Prohesperocyon*, and *Hesperocyon*. The process progressively turns ventrally, presumably independently in the advanced members of all three subfamilies of Canidae. Correlated with this tendency toward a ventrally oriented paroccipital process is the increased amount of fusion between the caudal entotympanic and the basal part of the paroccipital process. Within the Hesperocyoninae, however, *Paraenhydrocyon* has retained the primitive condition even in the most derived species *P. wallovianus*.

Polarity: 14(0), paroccipital process posteriorly oriented and not fused with the bulla (fig. 60A); 14(1), paroccipital process turned ventrally but not fused with the bulla; 14(2), paroccipital process ventrally oriented and widely fused with the bulla (fig. 60B–E).

15. Enlargement of Paroccipital Process: From a slender, tapered tip in *Hesperocyon*, the paroccipital process tends to be elongated toward its free end and becomes more robust.

Polarity: 15(0), paroccipital process short and slender (fig. 60A–B); 15(1), paroccipital process elongated and robust (fig. 60C–D); 15(2), paroccipital process further hypertrophied and keeled posteriorly.

16. Lateral Expansion of Paroccipital Process: In *Hesperocyon*, the paroccipital process is triangular in cross section with a rounded dorsal ridge. From this primitive morphology, the process becomes laterally expanded and its cross section is flattened, as seen in *Enhydrocyon* and *Paraenhydrocyon*. In *E. basilatus*, this modification has gone to a rather extreme form, with a wide bony ex-
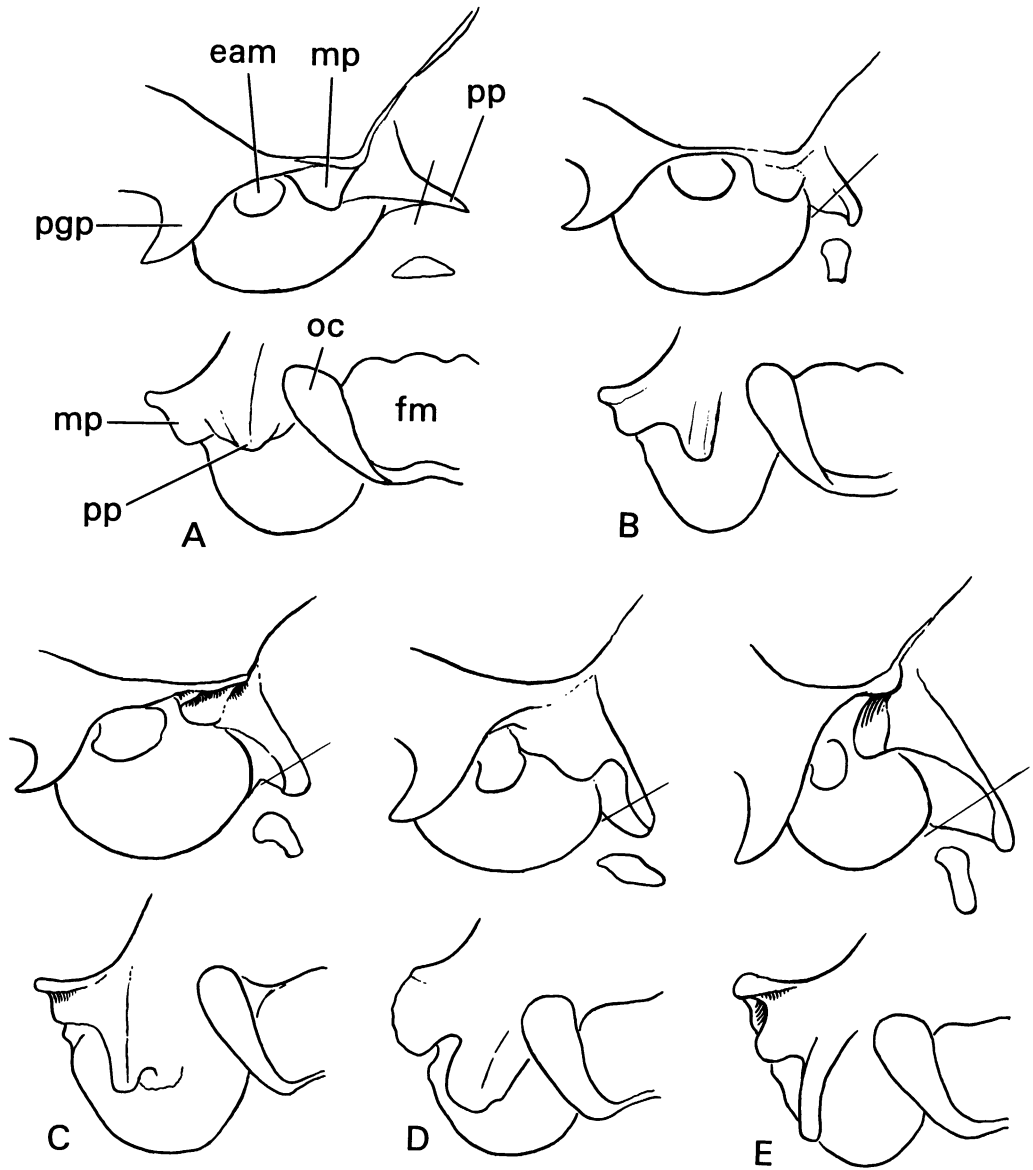
Fig. 60. Lateral (upper) and posterior (lower) views of left basicranial region showing different configurations of the paroccipital and mastoid processes. Straight lines across the paroccipital processes mark the position of the cross-section views shown below. **A**, *Paraenhydrocyon josephi*, F:AM 54106; **B**, *"Mesocyon" temnodon*, SDSM 2653; **C**, *Mesocyon coryphaeus*, AMNH 6859; **D**, *Enhydrocyon basilatus*, UCMP 76749; **E**, *Osbornodon fricki*, F:AM 67098. All are drawn to approximately the same size. Abbreviations: eam, external auditory meatus; fm, foramen magnum; mp, mastoid process; oc, occipital condyle; pgp, postglenoid process; pp, paroccipital process.

tension to the lateral edge of the paroccipital process.

Polarity: 16(0), no lateral extension of paroccipital process; 16(1), paroccipital process laterally extended (fig. 60A); 16(2), further extension into a wide blade (fig. 60D).

17. Posterior Expansion of Paroccipital Process: Within *Osbornodon*, the paroccipital process becomes posteriorly extended and thereby has a considerably enlarged lateral facet for the jugulohyoideus muscle. This posterior extension is best developed in *O*.

brachypus and *O. fricki*, in which the paroccipital process becomes a longitudinally oriented plate.

Polarity: 17(0), no posterior extension of paroccipital process; 17(1), paroccipital process posteriorly extended; 17(2), further extension of paroccipital process to form a longitudinal plate (fig. 60E).

18. Mastoid Process: Primitively the mastoid process is moderate-sized and sheltered beneath a horizontal squamosal shelf at the basal corner of the lambdoidal crest. The mastoid process is inflated beyond the squamosal shelf in *Enhydrocyon*. Independent from the above trend, the mastoid process in advanced *Osbornodon* is reduced, particularly in its posterior aspect, and is further receded beneath the squamosal shelf.

Polarity: 18(0), mastoid process uninflated and hidden beneath a horizontal shelf; 18(1), mastoid process inflated and its lateral facet at about the same level as the horizontal shelf; 18(2), mastoid process prominently inflated beyond the squamosal shelf; 18(3), mastoid process reduced.

19. Zygomatic Arch: The zygomatic arch in *Mesocyon brachyops* and some *Osbornodon* has become laterally expanded.

Polarity: 19(0), zygomatic arch not laterally expanded; 19(1), zygomatic arch laterally expanded and deepened.

Mandible

Gaspard's (1964) study of the morphology of the angular process of the mandible in living canids demonstrated that the angular process is a rather complex structure whose morphology is related to dietary habits. She divided the living canids into four morphotypes mainly on the basis of relationships of different facets for muscle attachments. Each type corresponds to a particular functional condition, which in turn relates to its ecological type (primarily sources of food). Although Gaspard did not discuss the phylogenetic implications in her study, the anatomical features are useful for systematic relationships. Many fossil canids, however, do not seem to exactly conform to her original types. The different configurations of the angular process are part of a functional complex involving the jaw mastication apparatus and are difficult to break down into discrete characters. Therefore, the following characterizations may be somewhat artificial.

20. Medial Pocket of Angular Process: In *Paraenhydrocyon*, a deep medial pocket is formed by the lateral and then the dorsal extension of the internal ridge (aréte interne; Garspard, 1964: 251, fig. 2). The internal ridge in living canids serves to divide the superior ramus of the medial pterygoideus muscle from the inferior ramus below. The pocketed angular process effectively increases the surface attachment areas for both rami. A precursor of the pocket can be seen in isolated individuals of *Hesperocyon gregarius*.

Polarity: 20(0), absence of a pocket on angular process; 20(1), presence of a medial pocket on angular process (fig. 61F–G).

21. Angular Process Size: The angular process in *Ectopocynus simplicidens* is so shortened that all that remains is a small, rounded tubercle. The angular process in *Osbornodon*, however, is deepened such that it is like a vertical blade.

Polarity: 21(0), angular process not shortened; 21(1), angular process shortened (fig. 61H); 21(2), angular process vertically expanded (fig. 61D, E).

22. Masseteric Fossa: In *Paraenhydrocyon* and also in *Osbornodon brachypus*, the masseteric fossa is deep and excavated into the ventral rim of the fossa. This ventral invasion results in a shallow pocket in the lower border of the fossa.

Polarity: 22(0), masseteric fossa shallow without ventral invasion into the lower rim; 22(1), masseteric fossa excavated into the lower rim.

23. Shape of Coronoid Process: The lateral outline of the coronoid process is unique in *Ectopocynus simplicidens*. Not only is it much lower in height, it also has a tapered upper tip unlike the rounded tops in other hesperocyonines.

Polarity: 23(0), coronoid process not reduced; 23(1), coronoid process reduced and with pointed tip.

24. Lateral Shift of Ascending Ramus: The ascending ramus of *Osbornodon brachypus* is laterally shifted relative to its basal part at the level of toothrow. Thus in anterior view,
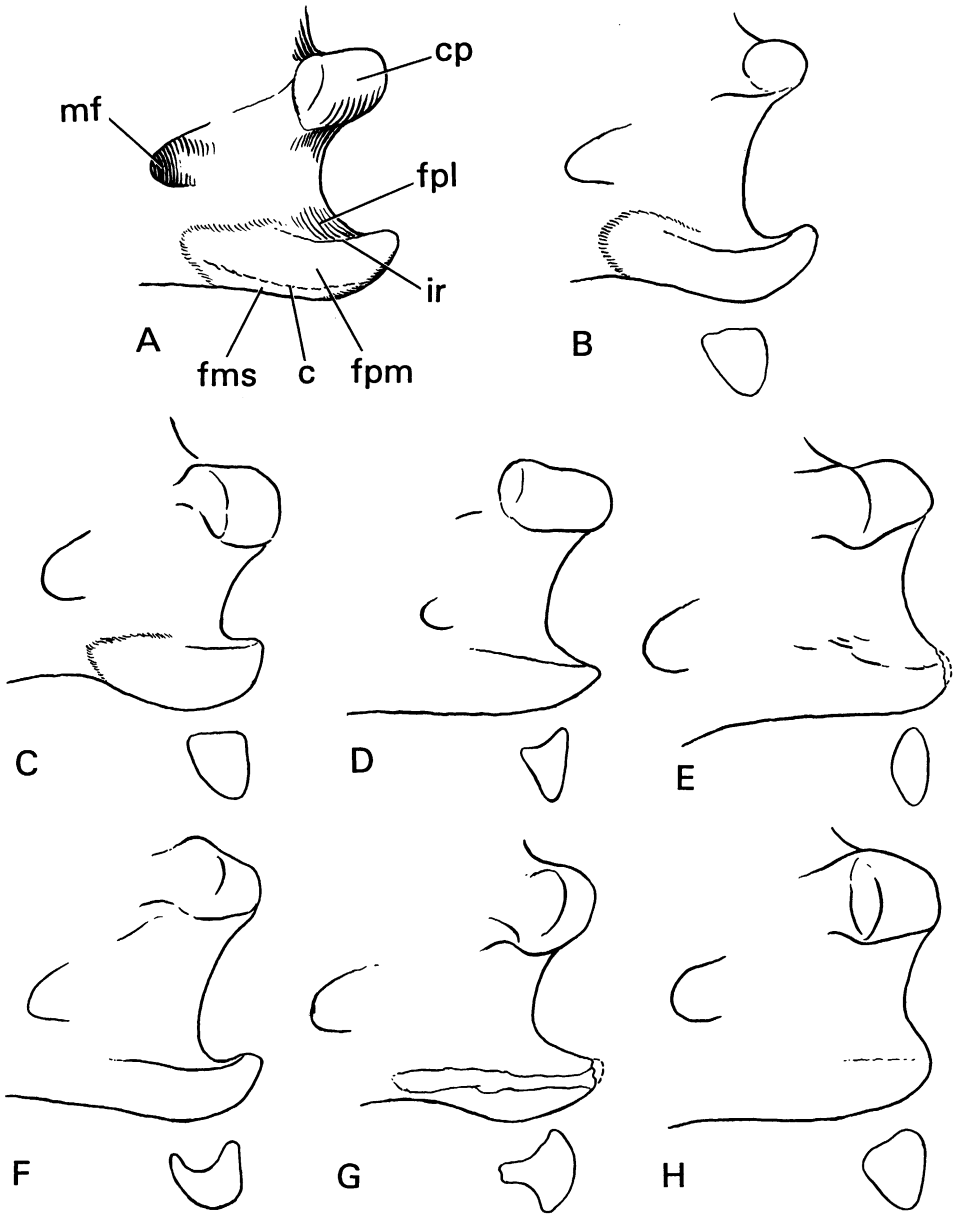
Fig. 61. Medial views and cross sections (below) of right angular processes of various hesperocyonines. A, *Cynodesmus thooides*, YPM-PU 10412, reversed from the left side; B, "*Mesocyon*" *temnodon*, F:AM 63367, reversed from the left side; C, *Enhydrocyon basilatus*, UCMP 76749; D, *Osbornodon iamonensis*, MCZ 3714, reversed from the left side; E, *O. fricki*, F:AM 54325; F, *Paraenhydrocyon josephi*, F:AM 54100; G, *P. wallovianus*, AMNH 81086; H, *Ectopocynus simplicidens*, F:AM 25431. All are scaled to approximately the same size. Abbreviations: c, crest dividing pterygoideus medialis and masseter superficialis muscles; cp, condyloid process; fms, facet for masseter superficialis muscle; fpl, facet for pterygoideus lateralis (= superior ramus of medial pterygoideus) muscle; fpm, facet for pterygoideus medialis (= inferior ramus of medial pterygoideus) muscle; ir, internal ridge; mf, mandibular foramen.
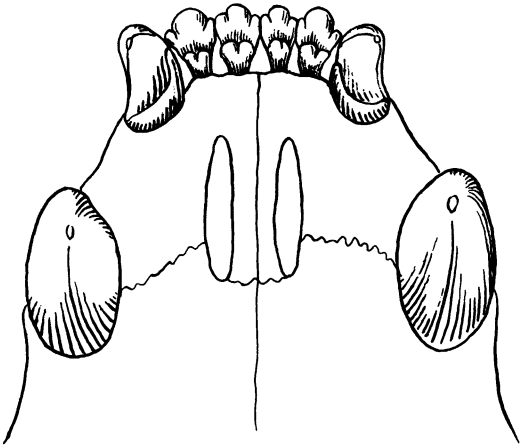
Fig. 62. Occlussal view of upper incisors and canines of YPM 12730, *Enhydrocyon stenocephalus*, showing the presence of basal internal cusps on the I1–2.

this creates a gentle sigmoid curve on the anterior border of the coronoid crest.

Polarity: 24(0), ascending ramus not shifted laterally; 24(1), ascending ramus shifted laterally.

Dentition

Some of the features discussed below are almost certainly functionally correlated to different degrees. Some are, therefore, grouped together as single characters (e.g., reduction and loss of M2 and m3). However, the discreteness of others are maintained here if they are not perfectly correlated and are assumed to retain a certain degree of independence.

25. Basal Cusps on I1-2: In *Enhydrocyon*, at the base of the first and second incisors, there are two accessory cusps on the lingual side (fig. 62).

Polarity: 25(0), absence of basal cusps (fig. 62A); 25(1), presence of basal cusps (fig. 62B).

26. Size of I3: The size of the upper third incisors in *Enhydrocyon* has been greatly increased compared to those of I1–2. This is independently evolved in *Caedocyon tedfordi*, whose I3 is shaped like a canine.

Polarity: 26(0), I3 not enlarged; 26(1), I3 enlarged; 26(2), I3 enlarged and caniniform.

27. Length of Toothrow: In *C. tedfordi*, the upper toothrow is shortened relative to the

posterior border of the palatine, a character unique to this taxon.

Polarity: 27(0), toothrow not shortened; 27(1), toothrow shortened.

28. Loss of P1 and p1: The P1 and p1 are lost in *Enhydrocyon* and *Ectopocynus*.

Polarity: 28(0), presence of P1 and p1; 28(1), absence of P1 and p1.

29. Width of Premolars: The premolars are primitively slender with sharp tips. The premolars become transversely widened in *Sunkahetanka*, *Philotrox*, *Enhydrocyon*, and *Ectopocynus*. In *Osbornodon*, however, this trend is reversed, that is, the premolars are transversely narrowed and become even more slender than in the primitive condition.

Polarity (unordered): 29(0), premolars not widened; 29(1), premolars widened; 29(2), premolars very wide and robust; 29(3), premolars narrowed.

30. Premolar Accessory and Cingular Cusps: In *Miacis*, a posterior accessory cusp is present only on p4, in contrast to most hesperocyonines and *Procynodictis*, which have an accessory cusp on P3 and p3. Associated with this acquisition of accessory cusps is the better development of cingular cusps.

Polarity: 30(0), accessory and cingular cusps on p4 only; 30(1), accessory and cingular cusps on P3 and p3 and possibly more anterior premolars.

31. Premolar Main Cusp Shape: In *Ectopocynus*, the principal cusps of the premolars become blunt, as opposed to the rather sharp tips of most other canids.

Polarity: 31(0), premolar main cusps sharp; 31(1), premolar main cusps blunt.

32. P4 Protocone: Primitively the protocone on P4 is large, anteriorly located, and thus rather isolated from the main body of the tooth. Beginning in *Hesperocyon*, the protocone becomes reduced and appressed to the anteromedial base of the paracone. Within the hesperocyonines, the size and location of the P4 protocone also vary extensively as is usually true for many carnivorans. This variation appears to be too inconsistent to be coded into discrete character states.

Polarity: 32(0), P4 protocone large and anterior to paracone; 32(1), P4 protocone reduced and medial to paracone.

33. Size of p4: In most canids, the increase

in premolar size is gradual from front to back. In derived forms of *Osbornodon*, however, the last premolar, p4, is abruptly enlarged relative to p3. This large differential between p4 and p3 is also seen in some hypercarnivorous borophagines such as *Epicyon*, *Osteoborus*, and *Borophagus*.

Polarity: 33(0), p4 not greatly enlarged relative to p3; 33(1), p4 greatly enlarged relative to p3; 33(2), p4 further enlarged and reclined toward m1.

34. Elongation of Carnassials: The carnassials in canids are significantly elongated relative to those of miacids. In the hypercarnivorous *Enhydrocyon* and some *Ectopocynus*, the P4 and m1 are further lengthened relative to the rest of the toothrow.

Polarity: 34(0), carnassials short and shearing blade forming an oblique angle to the toothrow; 34(1), carnassials elongated and shearing blade more in line with the toothrow; 34(2), carnassials further elongated relative to a shortened toothrow.

35. Parastyle on M1: A large, transversely oriented M1 parastyle occurs in almost all miacids and *Procynodictis*. Associated with this large parastyle is the development of a notch between the parastyle and paracone. The parastyle is reduced to a swollen cingulum in hesperocyonines and the notch is lost. This reduced parastyle in the hesperocyonines still varies in size and shape. Although useful for some species diagnoses, further division of the parastyle character into more states would be highly arbitrary.

Polarity: 35(0), M1 parastyle large and notch presence; 35(1), M1 parastyle reduced and notch lost.

36. M1 Paracone: In *Enhydrocyon* and *Paraenhydrocyon wallovianus*, the M1 paracone is elevated and becomes higher than the metacone, in contrast to the subequal paracones and metacones in the other taxa.

Polarity: 36(0), M1 paracone low and subequal to metacone; 36(1), M1 paracone high and larger than metacone.

37. Pseudoparastyle on P4: In *Osbornodon fricki* and some individuals of *Enhydrocyon crassidens*, there is a "parastyle" at the base of the anterior ridge of the paracone of P4. Flynn and Galiano (1982: 53) distinguished a cingular parastyle on the P4 of living feli-

form carnivorans from a so-called "pseudoparastyle" in nimravid carnivorans. They maintained that the "pseudoparastyle" in the nimravids is "positioned much higher on the flank of the paracone than would be a true cingular parastyle cusp, and it appears obvious that these two structures are not homologous."

Polarity: 37(0), absence of a pseudoparastyle in P4; 37(1), presence of a pseudoparastyle in P4.

38. Internal Cingulum of M1: Primitively in miacids, the M1 internal cingulum evenly surrounds the protocone on its anterior, medial, and posterior sides. The internal cingulum is more or less restricted to the posteromedial corner of M1 in most hesperocyonines. This restriction of the cingulum is best developed in many individuals of *Hesperocyon* in which the protocone lacks all traces of a cingulum anteriorly. In *Enhydrocyon*, this trend is reversed so that a uniform internal cingulum is seen to surround the protocone.

Polarity: 38(0), M1 internal cingulum surrounding the protocone; 38(1), M1 internal cingulum restricted to posteromedial corner.

39. Length of M1–2: Within the *Osbornodon* lineage, there is a tendency for the M1–2 to lengthen anteroposteriorly to increase the area of grinding. Correlated with this trend is the enlargement of the talonid of m1 and the entire m2.

Polarity: 39(0), M1–2 not lengthened; 39(1), M1–2 lengthened; 39(2), M1–2 further lengthened and M2 relatively enlarged.

40. Reduction and Loss of M2 and m3: Associated with the trend toward hypercarnivory, the M2 and m3 tend to be reduced or lost in the most advanced members of several hesperocyonine clades. In *Cynodesmus*, however, the M2 is transversely widened.

Polarity: 40(0), M2 and m3 not reduced; 40(1), M2 and m3 reduced or lost; 40(2), M2 widened.

41. M2 Metacone: The metacone of M2 in *Prohesperocyon* is considerably reduced relative to the paracone; this is despite the metacone in M1 not being reduced. This peculiar feature is also found in *Procynodictis vulpiceps*.

Polarity: 41(0), M2 metacone not reduced; 41(1), M2 metacone reduced.

42. M3: The absence of M3 is still a convenient character defining Canidae, although reduction of the M3 is common among miacids.

Polarity: 42(0), M3 present; 42(1), M3 absent.

43. Metaconid of m1–2: The m1–2 metaconids decrease in size in most lineages of hesperocyonines and disappear completely in a few species. The size of the m2 metaconid is more sensitive to the reduction and is easier to code. Individuals with reduced m1 metaconids also tend to have a shallower notch between the protoconid and metaconid.

Polarity: 43(0), metaconid of m1 large and that of m2 subequal to protoconid; 43(1), metaconid of m2 smaller than protoconid; 43(2), metaconid of m2 very small or vestigial; 43(3), metaconid of m1–2 completely lost.

44. Hypoconid Ridge of m1: In most hesperocyonines, the m1 hypoconid is ridgelike and oriented longitudinally. In *Ectopocynus simplicidens*, however, the hypoconid is smoothly rounded without sharp edges.

Polarity: 44(0), hypoconid of m1 ridgelike; 44(1), hypoconid of m1 conical.

45. Shape of m1 Talonid: Much has been said about this character, especially in phylogenetic discussions in the first half of this century. Matthew's (1930) bipartite division of canids, basined versus trenchant talonids, proved to be the most enduring. It is now clear that trenchant talonids probably evolved many times (Tedford and Taylor, MS). There is also the practical problem of dividing a continuum between these two extreme conditions into discrete character states. The primitive state in *Miacis* and *Hesperocyon* is fundamentally a trenchant talonid (i.e., a dominant hypoconid but with a much lower entoconid ridge), although *Hesperocyon* has been categorized as having a basined talonid in a functional analysis (Van Valkenburgh, 1991: table 1). From this primitive condition, borophagines and canines increase the entoconid and decrease the hypoconid to form a basined talonid enclosed by these two nearly equal-sized cusps, whereas most hesperocyonines tend to reduce and eventually lose the entoconid ridge so that a hypoconid is the only cusp left on the talonid, resulting in a trenchant talonid. One exception to this tendency is *Osbornodon*, which developed a basined talonid. This basined talonid tends to be correlated to more quadrate upper molars (i.e., increased grinding surface).

Polarity: 45(0), talonid of m1 trenchant; 45(1), talonid of m1 basined.

46. Size of Protoconid Versus Metaconid of m2: In large-sized hesperocyonines, the relative size of the protoconid and metaconid on m2 is generally sensitive to the corresponding development of these two cusps on m1; that is, the metaconid of m2 becomes reduced or lost if the corresponding metaconid of m1 is also reduced or lost. This general rule, however, does not apply in small canids. Thus the metaconid of m2 is extremely reduced in *Prohesperocyon* (also in *Procynodictis*), whereas its m1 metaconid is still distinctly large.

Polarity: 46(0), metaconid of m2 subequal to protoconid; 46(1), metaconid of m2 greatly reduced independent of that in m1.

ANALYSIS OF PHYLOGENY

Cladistic analysis was performed on the 28 taxa by 46 characters matrix (table 5) using HENNIG86 (version 1.5, by James S. Farris). Multistate characters were unordered (nonadditive). An initial run on the entire character matrix using the "ie-" option (generate one tree, certain to be of minimal length, by implicit enumeration) followed by the "bb*" option (generate multiple minimal length trees by extended branch-swapping to the single tree found by the "ie-") yielded 471 trees. Most of these trees involve the insertions of a few taxa with large number of unknown characters (question marks in table 5) into nearly every possible node that the limited number of known characters allow. Five species with the most missing data were then temporarily removed from the analysis: "*Hesperocyon*" *pavidus*, *Caedocyon tedfordi*, and the three species of *Ectopocynus*. From this restricted data set, 4 distinct topologies were found with an identical length of 91 and a consistency index of 62 (actually 28 trees were found by HENNIG86, but many have one or more branches without the support of at least one character and these trees often have an identical topology on CLADOS when

in the option of DICHOT = 0). The main uncertainty in these trees involves the relationship among *Hesperocyon gregarius*, "*H.*" *coloradensis*, the *Paraenhydrocyon* clade, and the *Mesocyon–Enhydrocyon–Osbornodon* clade, due to the fact that primitive members of these clades are quite similar to one another and few, if any, unique shared derived characters can be identified to link taxa to the exclusion of the others. A Nelsen's consensus tree derived from these shortest trees is shown in figure 63. The above five excluded species were then manually inserted into this consensus tree and explored with the aid of the CLADOS program (version 1.2, by Kevin C. Nixon). The resulting tree (fig. 64) is thus a combination of HENNIG's exhaustive search (on parts with good data) and CLADOS' intuitive manipulation (on parts with poor data).

Monophyly of the family Canidae is well supported by several basicranial (char. 7, 8, 11, 12) and dental (char. 30, 35, 42) synapomorphies, although some of these may have been acquired prior to *Prohesperocyon* (e.g., the presence of accessory cusps in premolars is found in primitive cynoid *Procynodictis vulpiceps* [referred to as "*Miacis*" *gracilis* in Wang and Tedford, 1994], and the expanded promontorium is seen in "*Miacis*" *cognitus*). *Prohesperocyon* is thus the most primitive canid by virtue of its possession of the above synapomorphies, and offers a good example of a transitional form still retaining some primitive features, for example, a short lower carnassial and a rather prominent parastyle in M1 (although reduced relative to that of miacids). As discussed in Wang and Tedford (1994), the low septum inside the bulla (char. 10), one of the most consistent synapomorphies of living canids, may have appeared first in *Hesperocyon* rather than in *Prohesperocyon* (the actual configuration of the septum is also different between *Hesperocyon* and later hesperocyonine canids [see Wang and Tedford, 1994]). It is only with *Hesperocyon* that the full range of canid characteristics are developed. *Prohesperocyon* has four autapomorphies in the present cladogram: an elongated rostrum (char. 1), narrowed premolars (char. 29), a subequal-sized paracone and metacone on M2 (char. 41), and an equal-

sized protoconid and metaconid on m2 (char. 46). The latter two autapomorphies, however, could have been retention of primitive characters since *Procynodictis vulpiceps*, a basal cynoid more primitive than *Prohesperocyon*, also has them (i.e., equally parsimonious solution for independent acquisitions of the characters in the two taxa, or acquisitions of the characters beginning in *Procynodictis* and reversal after *Prohesperocyon* [see Wang and Tedford, 1994]).

The next node (more derived from *Prohesperocyon*), where the Hesperocyoninae is defined, is well supported by four synapomorphies (char. 10, 32, 34, 38). However, these characters cannot be used to indicate monophyly of the subfamily because more derived subfamilies, the Borophaginae and Caninae, are not included in the present analysis. In fact, all four characters are also present in the borophagines and canines, which are presumably derived from *Hesperocyon* (Tedford, 1978). The Hesperocyoninae is thus paraphyletic not only because of the lack of a synapomorphy uniting all its members, but also because it does not include all members of its descendants (borophagines and canines).

Reflecting on the conservative nature of the primitive hesperocyonines, the species-level phylogeny shown in figure 64 is poorly resolved near the base of the tree. Most nodes are supported by few derived characters, many of which are homoplastic. The branches near the terminal part of clades, on the other hand, tend to be better supported by more characters, probably because of either missing intermediate taxa (within *Osbornodon*) or accelerated evolution (in *Enhydrocyon*). The unique combination of derived (often hypercarnivorous) characters in the terminal members has led to the recognition of 4 major clades of hesperocyonines: *Mesocyon–Enhydrocyon* clade (the original concept of the subfamily), *Osbornodon* clade, *Paraenhydrocyon* clade, and *Ectopocynus* clade. In addition, the monotypic *Caedocyon* may form a distinct clade by itself.

Hesperocyon, particularly *H. gregarius*, is clearly at the center stage of hesperocyonine diversification. No synapomorphy is found to unite its 3 species, and the genus is there-
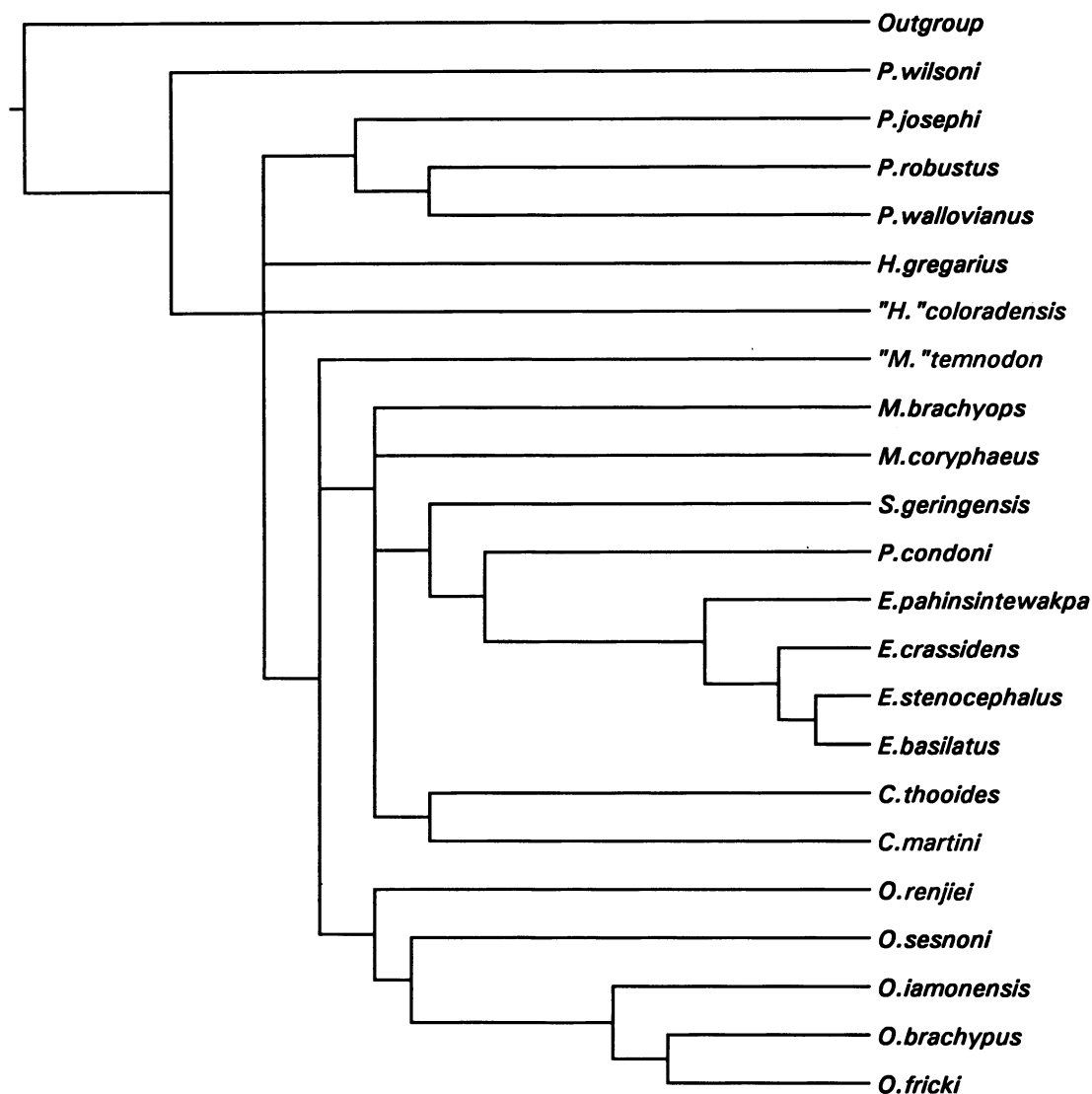
Fig. 63. Nelsen's consensus tree (HENNIG86 "nelsen" option) of 28 trees (representing 4 distinct topologies, see text) calculated on a reduced data matrix from that in table 5 ("*H.*" *pavidus*, *Caedocyon tedfordi*, and all three species of *Ectopocynus* removed). Tree statistics are: length = 92, ci = 61, ri = 78 (all calculated after the autapomorphies are removed to avoid inflation of the ci).

fore rendered paraphyletic. With the exception of its posteriorly positioned internal cingulum on M1, *H. gregarius* possesses many primitive morphologies that could be ancestral to most lineages of the Hesperocyoninae, as well as to the Borophaginae and Caninae. "*Hesperocyon*" *pavidus* appears to be derived directly from *H. gregarius*, but is unrelated to any advanced clade of hesperocyonines.

Dental features of "*H.*" *pavidus*, such as incipient development of a bicuspid talonid of m1, well-developed metaconid of m2, and reduced parastyle of M1, seem to indicate a borophagine relationship; if so, it could be the earliest and most primitive member of the subfamily.

Aside from its larger size, "*Hesperocyon*" *coloradensis* is not much different from *H.*
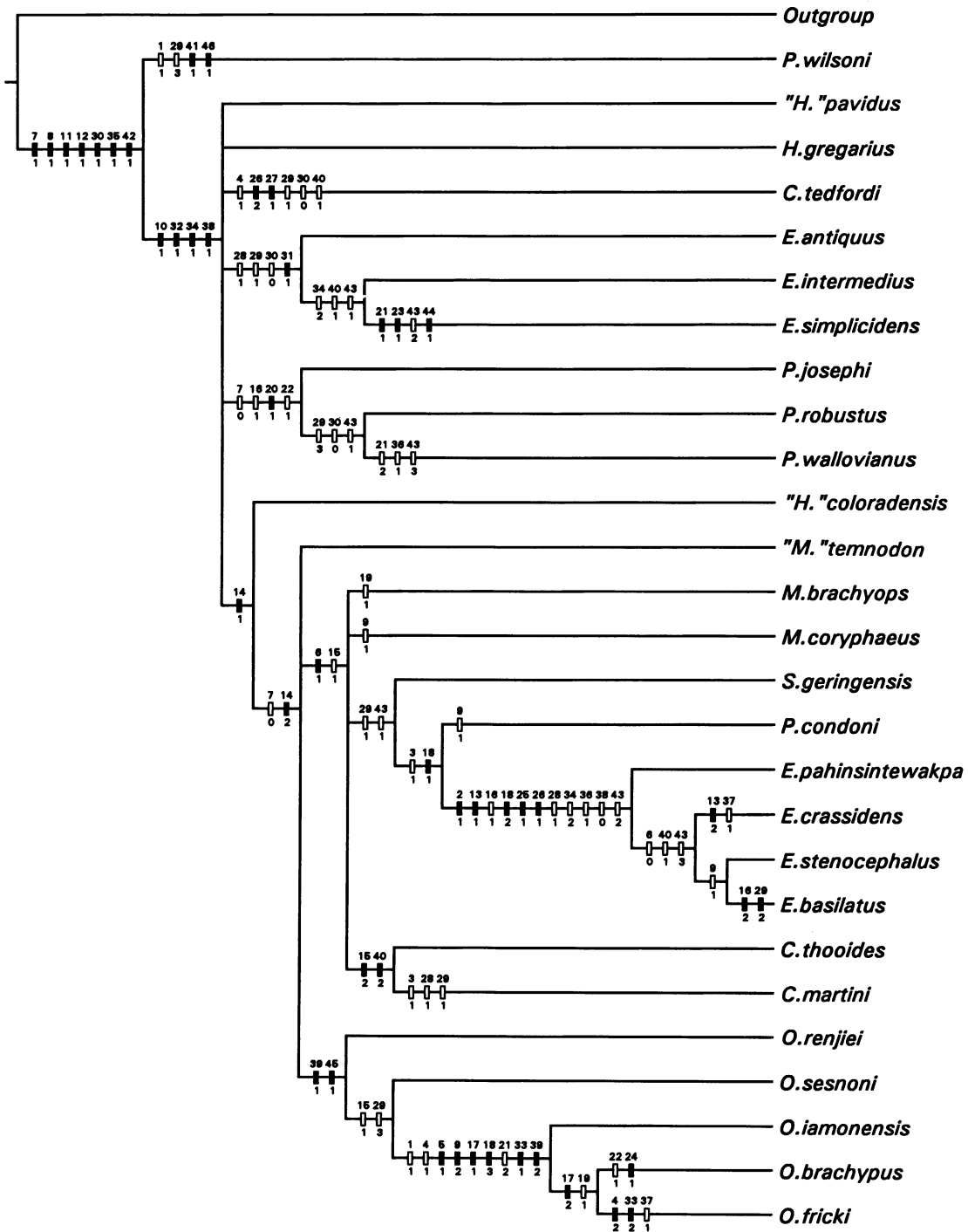
Fig. 64.   Proposed cladogram for 27 species of primitive canids. Character optimizations are carried out by CLADOS, and all characters are treated as nonadditive. Numbers above the branches are character numbers and those below are character states (all corresponding to those in table 5 and Character Analysis above). Solid bars represent synapomorphies and empty bars represent homoplasies (parallelisms and reversals). Tree statistics are: length = 106, **ci** = 55, **ri** = 74 (all calculated after the autapomorphies are removed to avoid inflation of the ci).

gregarius in the overall morphology. However, the slightly downturned paroccipital process (char. 14) in "*H.*" *coloradensis* indicates the transitional nature of the taxon and that it has acquired the initial step toward the *Mesocyon–Enhydrocyon–Osbornodon* clade. "*Mesocyon*" *temnodon* is another transitional taxon little different from the immediately more primitive and derived taxa. In fact, its overall similarity to *Hesperocyon* prompted Wortman and Matthew (1899) to refer it to the latter genus. A completely ventrally directed paroccipital process, fused with the bulla, allows the recognition of the *Mesocyon–Enhydrocyon–Osbornodon* clade. The lack of any synapomorphy at the next node above results in a multichotomy ("*M.*" *temnodon*, the *M. brachyops–Enhydrocyon* clade, and the *Osbornodon* clade), although the overall morphology of "*M.*" *temnodon* seems to be well-suited as being ancestral to *M. coryphaeus*.

The *Mesocyon–Enhydrocyon* clade, as variously formulated in early studies (Cope, 1883; Matthew, 1930 [minus *Cuon*]; Macdonald, 1963), is generally supported by the present phylogeny. *Mesocyon* and *Enhydrocyon* were also the core taxa in the original concept of hesperocyonine (Tedford, 1978). With the present addition of transitional taxa, such as *Cynodesmus*, *Sunkahetanka*, and *Philotrox*, this clade is by far the best documented and its phylogenetic relationship better understood. *Mesocyon* is the most primitive genus of this clade, and is obviously paraphyletic. No character is found to support a sister-species relationship between *M. brachyops* and *M. coryphaeus* although such may have been the case.

Between *Mesocyon* and *Enhydrocyon* stand several transitional taxa that bridge the gap between these genera. *Cynodesmus*, the most primitive of the series, forms a small clade of its own (two species), and its content is significantly restricted (see Discussion under the genus). A keeled paroccipital process (char. 15) and broad M2 (char. 6) are uniquely shared by the two species of *Cynodesmus*. Although the present cladogram (fig. 64) displays an unresolved multichotomy among two species of *Mesocyon*, the *Cynodesmus* clade, and the *Sunkahetanka–Enhydrocyon* clade, *Cynodesmus* is probably a sister-group of the *Sunkahetanka–Enhydrocyon* clade. In some continuous trends (e.g., increasingly robust premolars), *C. thooides*, the primitive species of the genus, seems to be more derived than *Mesocyon*, although such trends, subtle at this stage of their evolution, are difficult to be partitioned as discrete characters (see fig. 65, which takes such uncoded features into consideration). *Cynodesmus martini*, on the other hand, is considerably more derived. In fact, its robust construction exceeds that of *Sunkahetanka* and *Philotrox*, and parallels *Enhydrocyon* in many ways.

Two more-derived transitional monotypic genera, *Sunkahetanka* and *Philotrox*, progressively acquire skull proportions and robust dentitions that are characteristic of *Enhydrocyon* but absent in *Mesocyon* and *Cynodesmus* (except *C. martini*): widened premolars (char. 29), reduction of metaconids on m1–2 (char. 43), elongated postorbital part of skull (char. 3), and enlarged mastoid process (char. 18). In addition, *Philotrox* has an enlarged bulla that appears to be independently acquired from other taxa of the clade. The genus *Enhydrocyon* is well supported by a large number of derived characters (a total of 11; 5 of them are unique synapomorphies and the rest are homoplasies). Relationship within the genus, however, is less secure. *Enhydrocyon pahinsintewakpa* is likely the most primitive because of its less robust teeth, in contrast to forms with a highly hypercarnivorous dentition (i.e., *E. crassidens* and *E. basilatus*). The John Day taxa (*E. stenocephalus* and *E. basilatus*) form their own clade; this is, however, weakly supported by an enlarged bulla (char. 9), a character that has been independently developed at least 3 times within the hesperocyonines.

A sister-group relationship between *Osbornodon* and the *Mesocyon–Enhydrocyon* clade is mainly supported by a downturned paroccipital process (char. 14), a character also known to independently occur in borophagines and canines. *Osbornodon* is also the most caninelike genus with its elongated rostrum (char. 1) and large frontal sinus (char. 4) in the derived species, in addition to its slender premolars (char. 29) and basined talonids (char. 45), the latter being found in all species. Therefore, the present hypothesis of a sister-group relationship of *Osbornodon* and

the *Mesocyon–Enhydrocyon* group provides an interesting contrast of cranial and dental morphologies within a single clade: long rostrum and basined talonid in *Osbornodon* versus short rostrum and trenchant talonid in *Enhydrocyon*. The *Mesocyon–Enhydrocyon* clade includes the most hypercarnivorous forms, whereas the *Osbornodon* clade is composed of mesocarnivorous forms characterized by basined talonids (char. 45) on lower molars and elongated upper molars (char. 39). The most primitive species of *Osbornodon*, *Osbornodon renjiei*, is recognized based on these 2 characters. *O. sesnoni* is slightly more derived because it begins to have narrowed premolars (char. 29) and a strong paroccipital process (char. 15). Within the advanced *Osbornodon* clade (*O. iamonensis–O. fricki*), the large number of synapomorphies (totaling 9, 6 of them being unique synapomorphies) appears to result from a long hiatus in fossil record, that is, missing transitional forms (see Distribution below). The sister-species relationship between *O. brachypus* and *O. fricki* is indicated by an extremely posteriorly expanded paroccipital process (char. 17) and a laterally expanded zygomatic arch (char. 19).

Several synapomorphies (char. 7, 16, 20, 22) unite the *Paraenhydrocyon* clade, a group that has a modestly hypercarnivorous species as its terminal member (*P. wallovianus*). However, except for some parallel hypercarnivorous adaptations (such as reduction of metaconids and entoconids on lower molars), the *Paraenhydrocyon* clade lacks any character to suggest a special relationship with other clades. Its most primitive species, *P. josephi*, is almost an enlarged version of *Hesperocyon*. In fact, isolated individuals of *H. gregarius* may exhibit tendencies toward the above-derived characters, for example, pocketed angular process (char. 20). *Hesperocyon gregarius* may have directly given rise to *Paraenhydrocyon* as postulated in figure 65. *Paraenhydrocyon robustus* and *P. wallovianus*

become successively more hypercarnivorous in a rather linear fashion. At the end of the lineage, the teeth of *P. wallovianus*, especially its molars, share some similarities with those of *Enhydrocyon* (Loomis [1936] went so far as to include *P. wallovianus* in *Enhydrocyon*), for example, presence of an internal cingulum on M1 that encircles the protocone.

The remaining taxa with large numbers of missing values can be placed at many nodes with little or no support from actual characters. The enigmatic *Caedocyon* certainly falls into this category. Its peculiar cranial and dental morphologies are difficult to compare with other hesperocyonines: presence of a frontal sinus (char. 4); enlarged, caniniform I3; shortened toothrow (char. 27); widened premolar (char. 29); loss of accessory and cingular cusps on premolars (char. 30); and reduced M2 (char. 40). Its simple premolars, free of accessory and cingular cusps, may suggest affinity with *Paraenhydrocyon* (particularly *P. robustus* and *P. wallovianus*), but discovery of more complete materials or intermediate forms of *Caedocyon* is likely to change such speculation (see fig. 65).

The three species of *Ectopocynus* are another curious group whose phylogenetic position is yet to be settled. The genus clearly represents a monophyletic group held together by its uniquely blunt and featureless premolars (char. 31). Its three species form a rather continuous morphocline toward their own version of hypercarnivory; their broadened premolars, particularly those in advanced species of *Ectopocynus*, achieve the same proportions as in *Enhydrocyon*. Other than this proportional similarity, no character is found to suggest any special relationships with other clades. However, the overall morphology of the most primitive species, *Ec. antiquus*, resembles enough *Hesperocyon gregarius* to suggest another possible derivation from the latter species.

DISTRIBUTION AND ECOLOGICAL IMPLICATION

Hesperocyonines are found in all major North American terrestrial deposits of late Eocene through early Miocene age. Geologic distributions of hesperocyonines are summarized in figure 65. The temporal ranges of most hesperocyonines are in approximate correspondence with their phylogenies—a further testimony of the reasonably good geologic records of fossil canids. *Prohesperocyon wilsoni* and *Cynodesmus thooides* are the only exceptions to this correspondence in that their phylogenetic positions are inconsistent with their order of first appearance (relative to that of *Hesperocyon* and *Mesocyon*, respectively). Samples are especially good for the *Paraenhydrocyon* and *Mesocyon–Enhydrocyon* clades. In fact, the morphological continuity in the primitive members of these clades suggests that they were directly derivable from populations of *H. gregarius*.

The known ranges of most species, however, are still little more than rough estimates from isolated occurrences, except in the case of the White River records of *H. gregarius*. Even in *H. gregarius*, its record in Duchesnean is very poor (two isolated m1s and one dp4 from Saskatchewan). The same can be said of the range of *Caedocyon tedfordi*, which is represented by a single specimen (for the moment, its stratigraphy cannot be further restricted within the Lower Arikaree Group).

A major gap in the geologic record is present between *Osbornodon sesnoni* and *O. iamonensis*. The genus is almost completely unknown in the Arikareean and reappears in the Hemingfordian. This gap is also manifested by large morphological differences between these two species (i.e., a large number of synapomorphies in *O. iamonensis* relative to *O. sesnoni*; fig. 64). The advanced species of *Osbornodon* appear to enjoy the broadest distribution beyond the northern Great Plains, reflecting the geographical distribution of Hemingfordian–Barstovian deposits: *O. iamonensis* in Florida and *O. fricki* in New Mexico and California. The latter was also the last hesperocyonine to become extinct.

Records from the John Day deposits offer an interesting contrast to those from the northern Great Plains. Within the *Mesocyon–*

Enhydrocyon clade, two species pairs, of a roughly equivalent stage of evolution, have one species on one side of the continental divide and the other species on the other side: *Mesocyon coryphaeus* (John Day and California) versus *Cynodesmus thooides* (Plains), and *Enhydrocyon stenocephalus* (John Day) versus *E. pahinsintewakpa* (Plains). The John Day forms tend to have a more inflated bulla and may be derivable from those of the Plains. This limited barrier between the two sides of the continental divide seems to agree with the distribution patterns of aplodontid and geomyoid rodents. The aplodontid *Meniscomys* and geomyoid *Pleurolicus* are present in the northern Great Plains, northern Rocky Mountains, and Columbia Plateau, whereas the sister-taxa *Entoptychus–Gregorymys* are confined to one side only, that is, *Entoptychus* in John Day and *Gregorymys* in the Great Plains (Rensberger, 1971, 1973, 1981, 1983).

In the west coast, three California localities produce hesperocyonines: Otay Formation of San Diego County, Kew Quarry local fauna of Ventura County, and Barstow Formation of San Bernardino County. Among these, the Otay Formation and the Kew Quarry are probably chronologically equivalent to the early John Day Formation, that is, Turtle Cove Member (Tedford et al., 1987; Prothero, 1991). This is further corroborated by the present reference of median-sized canids from the Otay Formation to *M. coryphaeus*. The Kew Quarry median-sized canids, however, are assigned to *M. brachyops*. The geographic distribution of this pair of John Day species is now significantly expanded.

Although hesperocyonines may first appear in the Duchesnean, their undoubted presence is only seen in Chadronian deposits. The onset of initial diversification began in Orellan with five species, and the most primitive members of the *Mesocyon–Enhydrocyon* and *Osbornodon* clades were present. The hesperocyonines at this time were still more or less the size of *Hesperocyon*. By the Whitneyan, all major clades had evolved, with eight known species, and were represented for the first time by median-sized forms. Hesperocyonines achieved their maximum di-
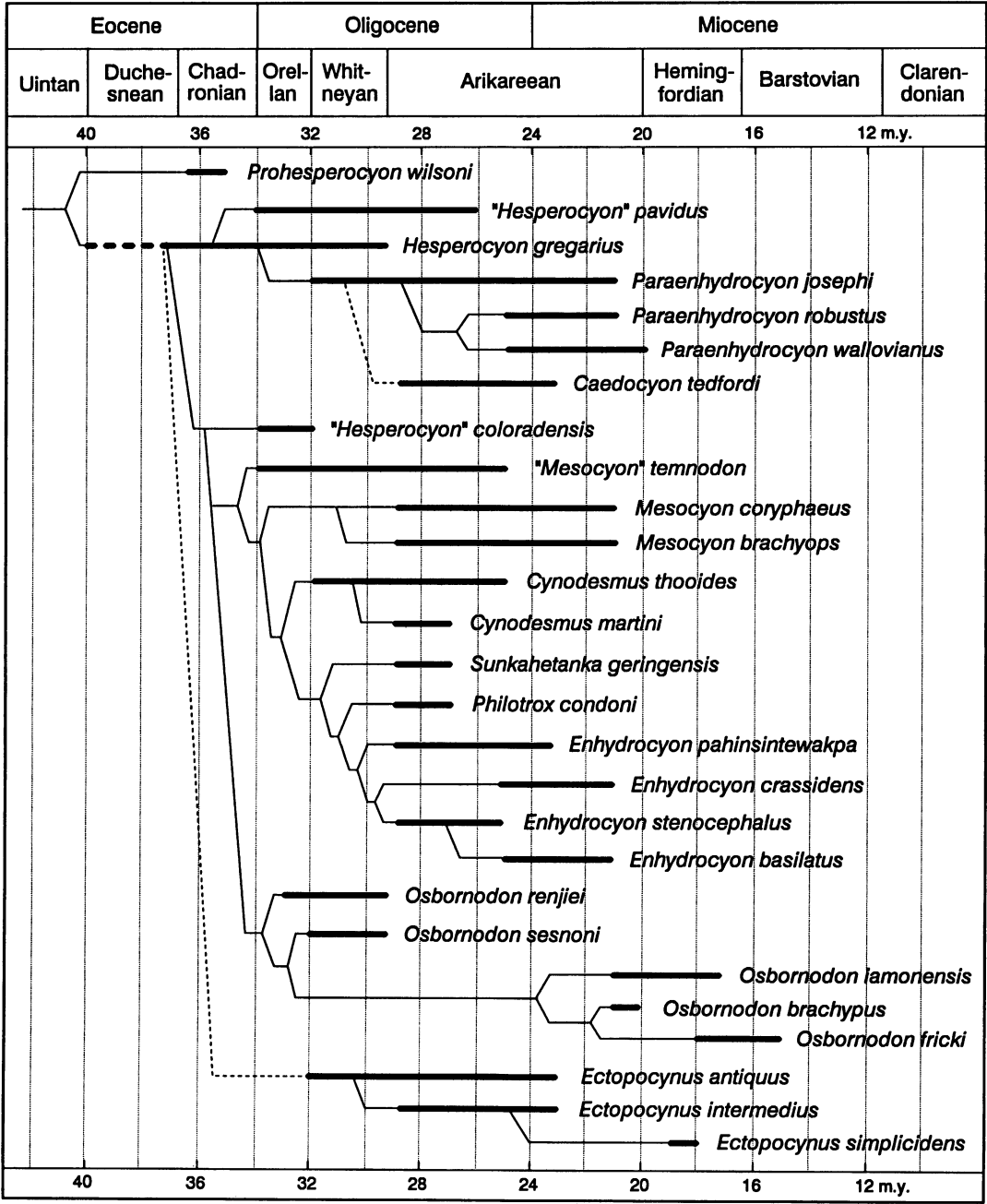
Fig. 65.   Geologic distribution and postulated phylogeny of hesperocyonines. The phylogenetic re-
lationships follow the cladogram in figure 64 where the branches are fully resolved. The multichotomies
in figure 64 are here further resolved to take into account subtle features that cannot be objectively
coded as characters. In some cases, ancestral–descendant relationships are speculated as suggested by
stratigraphic and/or morphologic continuity. Dashed lines indicate speculations without character sup-
port from the phylogenetic analysis. Stratigraphic correlations are based on Emry et al. (1987) and
Tedford et al. (1987). Calibrations of radiometric dates in the White River Group section are based on
Switsher and Prothero (1990) and Prothero and Switsher (1992).

versity of 13 species in the Early Arikareean, and acquired progressively more robust taxa, which were to give rise to the large predators that flourished from the Late Arikareean through Early Barstovian. The Late Arikareean saw the terminal members of the *Enhydrocyon* clade. Within the *Paraenhydrocyon* clade, *P. wallovianus* persisted to the end of the Arikareean, which saw the rise of derived members of *Osbornodon*. Three species are left in the late Late Arikareean and Hemingfordian, and only one is known in the Early Barstovian.

Van Valkenburgh (1991) demonstrated that repeated development of hypercarnivory occurred in all three subfamilies of Canidae. The hypercarnivorous canids tend to elongate the shearing blade of the carnassial and develop reduced or trenchant talonids to emphasize the slicing function of the cheek teeth (Crusafont-Pairó and Truyols-Santonja, 1956). In particular, this tendency was shown to be more apparent in the late Oligocene of North America and the Pleistocene of South America (Van Valkenburgh, 1991). Van Valkenburgh's (1991) high number of hypercarnivorous canids in the Oligocene is entirely due to the predominantly trenchant talonids in hesperocyonines as opposed to the mostly bicuspid talonids in the borophagines of the Mio–Pliocene. She interpreted the great di-

versity of hesperocyonines during the Arikareean as reflecting the filling of niches left by the extinction of hyaenodonts and nimravids. Van Valkenburgh's contentions seem to be generally supported by the present phylogeny, which suggests independent acquisition of hypercarnivorous dentitions by several clades of hesperocyonines: *Enhydrocyon*, *Paraenhydrocyon*, *Ectopocynus*, and *Osbornodon* (only partially).

Little is known about the ecological aspects of hesperocyonines, and the following is a summary of brief comments by various authors. The co-occurrence of abundant *Hesperocyon* and eomyid rodents has led to speculations of a predator-prey relationship (Cope, 1874; Clark et al., 1967). A premolar of *Hesperocyon* has been identified from coprolites of large-sized carnivorans (Parris and Holman, 1978). Clark et al. (1967) suggested that *Hesperocyon* may have inhabited a "riverborder forest" environment. A functional study on the limb morphology of *Hesperocyon* further indicates that it is likely to be plantigrade in posture and probably scansorial in life (Wang, 1993). Among larger-sized hesperocyonines, Stevens (1991) speculated that *Paraenhydrocyon wallovianus* may have been an ambush predator that was likely to climb trees.

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APPENDIX I
Examined Specimens of *Hesperocyon gregarius*

A Purplish (Persistent) White Layer/Ash (P.W.L.) (Upper Purplish White of Schultz and Stout, 1955) can be traced in most of the type and adjacent areas of the Brule Formation in western Nebraska through eastern Wyoming, and is used as a marker bed to separate the Chadron Formation and the Orella Member of the Brule Formation. Mammalian faunas from these respective strata roughly correspond to the Chadronian/Orellan mammal ages; that is, specimens found below the P.W.L. belong to Chadronian and those from above to Orellan (see Emry et al. [1987: 139] for discussions of the problems with this usage). Such a convenient marker bed, however, is less readily identifiable in other areas (e.g., South Dakota and North Dakota).

Less precise and more confusing is "Oreodon beds" used by earlier collectors or where the P.W.L. cannot be readily identified. Essentially following Osborn (1907) and Wanless (1923), M. F. Skinner and other Frick collectors divided the Brule Formation in the Big Badlands area of South Dakota and localities in other states into Lower ("Metamynodon beds" of early AMNH collections) and Middle beds to represent their concept of Lower Brule, and the Upper Oreodon beds and Protoceras–Leptauchenia beds on top to represent the Upper Brule. The Orellan age, as currently understood, is approximately equivalent to the Orella/Scenic Member, which includes the Lower and Middle Oreodon beds only (Emry et al., 1987: fig. 5.1). A few of the stratigraphic sections of Skinner were published in Prothero and Swisher (1992: fig. 2.7).

For detailed physical stratigraphy of the Frick collection, the AMNH archives should be consulted. Other peculiarities of particular collections are noted at the beginning of each respective listings.

COLORADO

E. D. Cope collection from Cedar Creek Member of White River Formation, Logan and Weld Counties, Orellan (detailed stratigraphy is unknown): — AMNH 5298, left ramus fragment with c1, p3–m1; AMNH 5299, left ramus fragment with p4–m2; AMNH 5300, right ramus fragment with p2–m2; AMNH 5301, left ramus fragment with m1–2; AMNH 5302, left ramus fragment with m1; AMNH 5303, left ramus fragment with m1–2; AMNH 5304, left ramus fragment with p3–m1; AMNH 5307, left ramus fragment with m1; AMNH 5308, left ramus fragment with p3–4; AMNH 5309, right ramus fragment with p3;

AMNH 5311, right ramus fragment with p3–4; AMNH 5313, left ramus fragment with m1–2; AMNH 5315, left ramus fragment with p1, m1; AMNH 8758, right ramus fragment with p4–m2; AMNH 8759, right ramus fragment with m1–2; AMNH 8760, left ramus fragment with p2–m1; AMNH 8761, right ramus fragment with p4–m3; AMNH 8772, right ramus fragment with p1 and erupting p2, p4–m2; AMNH 8774, skull and mandible with nearly complete skeleton; AMNH 9313, maxillary and mandible fragments with right P2–M2, left c1–m2, right c1–m3, and isolated skeletal parts; AMNH 9314, left ramus fragment with p2–m2.

C. Frick collection from northeast Colorado (stratigraphy of the specimens below are mostly unclear): — F:AM 50304, right ramus fragment with p4–m1, 6–12 mi east of Highway 85; F:AM 50305, right ramus fragment with m1–2, below Pawnee Quarry, 2.5 mi southeast of Ubanks Sheep Camp, head of Pawnee Creek; F:AM 50308, left ramus fragment with p4–m2, 6–12 mi east of Highway 85; F:AM 50309, nearly complete mandible with left p1–m2 and right c1–m3, 3 mi north of Grover, one-third way down in the exposed section; F:AM 50310, left ramus fragment with p4–m1, 6 mi east of Pawnee Pit, Grover; F:AM 50311, maxillary fragment with P4–M2 and right ramus fragment with p3–4; F:AM 50312, crushed skull with left M1–2 and right P2–M2, near Pawnee Buttes locality.

KUVP collection from Cedar Creek Member of White River Formation, Orellan (letters and numbers following the specimen description are KUVP locality numbers, e.g., KU-CO-008):

Clyde Ward Ranch, SW¼, sect. 12, T. 11 N, R. 54 W, Weld County. — KUVP 8177, left m2, level 3; KUVP 8178, right m1, level 6; KUVP 8180, left p4.

Jack Casement Ranch, Chimney Canyon, E½, sect. 3, T. 11 N, R. 54 W, Logan County. (see section VII of Galbreath, 1953: 24). — KUVP 8185, left p4–m1; KUVP 8186, ramal fragment with p4–m1; KUVP 8187, left ramus with c1–p1, p4–m3; KUVP 8188, right ramus with p4–m2.

Micro Locality, W½, sect. 7, T. 11 N, R. 54 W, Logan County. (see section IX of Galbreath, 1953: 24). — KUVP 8182, ramal fragment with p4–m1, level 12; KUVP 8183, partial skull with M1; KUVP 8184, right M1; KUVP 8192, M2; KUVP 8193, left p4–m1; KUVP 8194, right p4–m2; KUVP 8195, right ramus with dp3–dp4; KUVP 10659, right P4; KUVP 10799, right M1; KUVP 11069, right ramus with p4–m1.

Beaver Locality, SW¼, sect. 21, T. 11 N, R. 53 W, Logan County.— KUVP 8190, right p4, below olive band; KUVP 10955, left mandible; KUVP 11046, left m1.

Other isolated KUVP collections from Cedar Creek Member of Colorado.— KUVP 134, left ramus, KU-CO-014, Chimney Rock, Yuma County; KUVP 5046, left ramus with m2, KU-CO-008; KUVP 8179, ramal fragment with left p4–m2, KU-CO-075, Deadman's Draw, N½, sect. 33, T. 11 N, R. 53 W, Weld County; KUVP 8181, left m1, level 1, SE¼, sect. 7, T. 11 N, R. 53 W, Logan County; KUVP 8189, left m1, Oscar Olander Ranch, sect. 35, T. 11 N, R. 57 W, Weld County; KUVP 11093, crushed skull; KUVP 14308, right ramus fragment with m3; KUVP 14473, left ramus with m1, KU-CO-033; KUVP 14483, right ramus with m1, KU-CO-038; KUVP 14807, m1, KU-CO-042; KUVP 28699, left ramus with m1–3, KU-CO-006; KUVP 69134, left ramus, KU-CO-004; KUVP 69144, partial skull and mandible, KU-CO-011; KUVP 69145, left ramus, KU-CO-004; KUVP 99367, M1–3, KU-CO-046.

KUVP collection from Horsetail Creek Member of White River Formation, Chadronian:

Two Miles Creek, KU-CO-071, NE¼, sect. 31, T. 11 N, R. 56 W, Weld County.— KUVP 8174, right ramus fragment with p4–m1; KUVP 8175, left ramus fragment with p4–m3; KUVP 8176, left ramus fragment with m1–2.

Peevy Ranch, George Creek, KU-CO-088, Logan County.— KUVP 83514, left m1–2; KUVP 83516, right m1–2.

MONTANA

Middle Renova Formation, Pipestone Local Fauna, Jefferson County, Middle Chadronian: — AMNH 9614, right ramus fragment with m1–2; AMNH 9616, partial left ramus with p3 (broken), m1–3; AMNH 9617, left ramus fragment with p4–m1; AMNH 9618, partial left ramus with p3–m2; AMNH 9619, left c1, p4 (?), m2; AMNH 9622, right ramus fragment with p4; AMNH 9722, left P4, from Thomson's Creek; F:AM 50230, partial right ramus with p4–m3; F:AM 50233, fragment of right maxillary with P2–4; F:AM 50235, left P4; F:AM 50236, partial mandible with left and right p3–m1, from north Pipestone; KUVP 88185, partial left ramus with p3–m2; USNM 19074, maxillary and ramus fragments with P2, P4–M1 and m2; USNM 361256, right ramus fragment with m1; USNM 361257, right maxillary fragment with M1; USNM 361448, right M1 and left m2, in Little Pipestone; USNM 361494, left m1.

Canyon Ferry Locality, Lewis and Clark County,

Chadronian (see White [1954] for descriptions of localities): —USNM 18895, left ramus fragment with p2–3, m1–3, 24BW18/5; USNM 18896, left ramus fragment with m1–2, 24BW18/5; USNM 18897, right ramus fragment with m1–3, 24LC16/24; USNM 18911, nearly complete skull and mandible with articulated partial skeleton, 24LC16/27, from 1 mi north of Canyon Ferry.

NEBRASKA

1. Plunkett-Parson's locality, 8 mi north of Harrison, in E½ of sect. 34, sect. 35, S½ of sect. 36, T. 36 N, R. 56 W, and N½ sect. 1, T. 32 N, R. 56 W, Sioux County, mostly Orella Member of Brule Formation (Early Frick collections from this locality, labeled as "10 miles north of Harrison, west end," were assigned to the Lower Oreodon beds, here interpreted as lower Orella Member; later additions [most of the list below] placed the specimens in a more detailed stratigraphy adopted from field observations by M. R. Skinner, which divided the Orella Member into three [upper, middle, and lower] banded layers):

F:AM 50315, partial skull with left P4–M2, right M1–2, and right p4–m1, in lower Orella Member; F:AM 50316, crushed skull and mandible and a right humerus, in lower Orella Member; F:AM 50317, right ramus fragment with m1–2; F:AM 50318, left ramus fragment with p4–m1, lower Orella Member; F:AM 63871, left maxillary fragment with P4–M2, lower to middle banded layers; F:AM 63872, right P4–M2, left c1, p3–m1, right p4–m1, and right bulla, 5 ft below upper banded layer; F:AM 63873, maxillary fragments with left and right P4–M2, between lower and middle banded layer; F:AM 63874, right m1, between middle and upper banded layers; F:AM 63875, right ramus fragment with p4–m2, between middle and upper banded layers; F:AM 63876, right ramus fragment with p4–m2, between lower and middle banded layers; F:AM 63877, ramus fragments with left m1–2 and right m1, 15 ft above upper banded layer; F:AM 63878, right ramus fragment with p3–m1, between lower and middle banded layers; F:AM 63879, left ramus fragment with m1–2, between lower and middle banded layers; F:AM 63880, right ramus fragment with m1, 10 ft below middle banded layer; F:AM 63881, left ramus fragment with m1, 20 ft below upper banded layer; F:AM 63882, right ramus fragment with m1, between lower and middle banded layers; F:AM 63883, left ramus fragment with p4–m1, between lower and middle banded layers; F:AM 63884, right ramus with p3–m1, below upper banded layer; F:AM 63885, complete skull and mandible with partial skeleton, 10 ft below middle banded layer; F:AM 63886, nearly complete skull, 8 ft below

middle banded layer; F:AM 63887, anterior half skull and mandible and skeleton fragments, 10 ft below middle banded layer; F:AM 63888, skull fragments with left P4–M2, between lower and middle banded layers; F:AM 63889, crushed skull, 15 ft below upper banded layer; F:AM 63973, left and right P4–M1, right p4–m1, in lower Orella Member; F:AM 63974, right ramus fragment with m1–2, in lower Orella Member; F:AM 63974a, right ramus fragment with m1–3, in lower Orella Member; F:AM 63977, left M1–2, below first Whitneyan ash layer, Whitneyan.

2. Ten mi north of Harrison, east end, Sioux County, in lower Orella Member (Lower Oreodon beds):

F:AM 50319, right ramus fragment with m1–2; F:AM 50320, right ramus fragment with m1; F:AM 50321, skull and skeleton fragments with left and right P3–M2; F:AM 50323, anterior half skull and mandible; F:AM 50324, partial skull and mandible; F:AM 63972, left maxillary fragment with P3–M1.

3. Herb Geike Ranch, north side of Warbonnet Creek, 9 mi north and 3 mi west of Harrison, in S½ of sect. 17, SE¼ of sect.18, and E½ of sects. 19 and 20, T. 33 N, R. 56 W, Sioux County:

F:AM 63966, left ramus fragment with m1–2, 110 ft above P.W.L.; F:AM 63968, right ramus with c1, p2–m1, 90 ft above P.W.L.; F:AM 63997, crushed skull and mandible with partial skeleton, 110 ft above P.W.L.; F:AM 63998, cranial and skeletal fragments with left P4–M2 and p4–m2, 45 ft above P.W.L. and 5 ft above a local sandstone channel; F:AM 63999, maxillary and mandible fragments with left and right P4–M2, p3–m3, 60 ft above P.W.L.; F:AM 76518, skull and mandible and cervical vertebrae, 90 ft above P.W.L.; F:AM 76520, partial skull, 60 ft above P.W.L.; F:AM 76521, left P4, 30 ft above P.W.L.; F:AM 76522, right P4, 60 ft above P.W.L.; F:AM 76523, right ramus fragment with m1–2, 70 ft above P.W.L.; F:AM 76528, skull fragment with left P2–M2 and right P4–M2, 55 ft above P.W.L.

4. Walter Brecht Ranch, 4 mi west and 4.5 mi south of Chadron, in sect. 9, T. 32 N, R. 49 W, Dawes County (M. F. Skinner used a White Marker clay with brown spots as a data plane for field stratigraphy. It is tentatively used as the Chadron/Brule boundary; 35 ft above this clay is a Blue Ash, which was also used in the field stratigraphy below):

F:AM 63979, left ramus with p2, p4–m3, 25–30 ft above White Marker Zone; F:AM 63981, partial mandible with left and right c1–m1, in White Marker Zone, lower Orella Member; F:AM 63982, right ramus fragment with p4–m3, 25–30 ft above White Marker Zone; F:AM 63982a, left

m2, 25–30 ft above White Marker Zone; F:AM 63983, left ramus fragment with p3–m1, 25–30 ft above White Marker Zone; F:AM 63985, partial skull and mandible, 25–30 ft above White Marker Zone; F:AM 63988, left ramus fragment with p3–m1, 10 ft below Blue Ash in massive pink clay, lower Orella Member; F:AM 63989, right ramus fragment with m1, 30 ft above basal White Marker Zone; KUVP 84777, mandible with left c1–m1 and right p3–m1, KU-NE-083, Chadronian.

5. Other miscellaneous Frick collections (except the last specimen) from Chadron–Brule Formation of Dawes, Scotts Bluff, Sheridan, and Sioux Counties (similar stratigraphic terms have been used as in above lists of Frick localities):

F:AM 50314, left m1, north of Harrison, east end, in lower Orella Member; F:AM 50322, partial skull with left P1–M2 and right P2–M1, Cedar Creek, Hat Creek Basin, northwest of Crawford, in Green Caliche zone, in lower Orella Member; F:AM 50325, nearly complete skull, 4 mi northeast of Chadron, Orellan; F:AM 50326, partial mandible with left p1, p3–m1 and right c1–p1, p3–m2, north of Chadron, Orellan; F:AM 50327, maxillary and mandible fragments with right P2–M2, 2.5 mi northwest of Chadron, 7 ft below Blue Ash, Orellan; F:AM 50328, right ramus with p3–m2, north of Chadron, Orellan; F:AM 50332, right ramus with p1–m2, 2.5 mi northwest of Chadron, 6 ft below Blue Ash, Orellan; F:AM 50339, left m1–2, 4 mi northeast of Chadron, Orellan; F:AM 50340, left ramus with p3–m2, north end of Beaver Wall, 20 ft below upper white layer, Whitneyan; F:AM 50341, right P3–M2, northeast of Crow Butte, north of road, 5 ft below green layer, Whitneyan (?); F:AM 63957, left maxillary fragment with P4–M2, 2.5 mi north of Chadron, 6 ft below Blue Ash, Orellan; F:AM 63958, left ramus fragment with m1–2, 4 mi west and 4 mi south of Chadron, in NW¼, sect. 9, T. 32 N, R. 49 W, just below Blue Ash, Orellan; F:AM 63959, right ramus fragment with m1–2, west of Hall Ranch, in E½, sect. 31, T. 33 N, R. 55 W, 80–90 ft above P.W.L., Orellan; F:AM 63967, mandible fragment with left p1–m1 and right p4–m3, R. H. Schmechel Ranch, 0.75 mi southeast of Pancake Butte, 30 ft above White Marker Zone, lower Orella Member; F:AM 63975, right ramus fragment with m1–2, Hat Creek Basin (?); F:AM 63978, partial skull and mandible and a fragment of baculum, north face of Scotts Bluff Monument, 147 ft above North Platte River in massive gray siltstone, Orellan; F:AM 63984, right ramus with p1–m3, 2 mi northeast of Trunk Butte and 1 mi west of Pancake Butte, 7 ft below White Marker Zone, Chadronian; F:AM 63991, right ramus fragment with m2, 0.5 mi north of Pancake Butte, 4 mi west and 1 mi

south of Chadron, 6 ft below gray nodular zone in lower Orella Member; F:AM 63995, left ramus fragment with p4–m3, 4 mi west and 4 mi south of Chadron (see F:AM 63958), just below Blue Ash, Orellan; F:AM 63995a, left ramus with p1–m2, Bartlet Ranch, 2 mi north of Chadron, 120 ft above Blue Ash, Orellan; F:AM 76519, right maxillary fragment with P4–M2, 1 mi south of Clarence Dout Ranch, 55 ft above P.W.L., Orellan; F:AM 76524, left ramus fragment with p3–m3, 1.5 mi southwest of Clarence Dout Ranch, 60 above P.W.L., Orellan; F:AM 76525, right ramus fragment with p4–m2, 1 mi west of Clarence Dout Ranch, 60 ft above P.W.L., Orellan; F:AM 76526, right ramus fragment with p4–m1, 1 mi south of Clarence Dout Ranch, 55 ft above P.W.L., Orellan; AMNH 89718, right m1, Arner Ranch, micro locality, late Chadronian.

6. H. J. Cook collection from Dawes, Scotts Bluff, and Sioux Counties, Nebraska (Insufficient field data are associated with Cook's specimens [Cook, 1912: 33]. Most of them were roughly placed in a framework of Chadronian, "Lower Brule" [approximately Orellan], and "Upper Brule" [approximately Whitneyan] as outlined in Cook [1912], who basically followed Matthew [1899].):

AMNH 81038, skull and mandible fragments with left p3–m2 and right P3–M2 and p2–m2, Robert's Draw, Hat Creek Basin, 6–7 mi northeast of Harrison, in nodular layer, early Orellan; AMNH 82411, right ramus fragment with p4–m1; AMNH 82412, right ramus fragment with m1–2; AMNH 82915, right ramus fragment with m1–3, Lampsilus locality, Chadronian; AMNH 82916, juvenile left ramus fragment with m1 and erupting p3–4, Chadronian Pocket, NW¼, sect. 36, T. 33 N, R. 52 W (Ostrander, 1985), late Chadronian; AMNH 82918, maxillary and ramus fragments with left M1 and m1–2, Chadronian Pocket (see above); AMNH 83193, right ramus fragment with m1–2; AMNH 83323, left ramus fragment with m1–2, Schaeffer Place, 15 mi northeast of Harrison; AMNH 85855, left ramus with p3–m3, Robert's Draw, 50 ft below top of Brule Formation, Whitneyan (?); AMNH 85856, right ramus fragment with m1, Robert's Draw, level as above; AMNH 85857, right ramus fragment with p3–m1, Robert's Draw, level as above; AMNH 85858, mandible fragment with left c1–m2 and right p4, m2–3, Robert's Draw, level as above; AMNH 85869, right ramus fragment with m1, Robert's Draw, Upper Brule; AMNH 85876, right ramus fragment with m1, Robert's Draw; AMNH 85879, left ramus fragment with a broken m1, Robert's Draw, Upper Brule; AMNH 85881, left ramus fragment with a broken m1, Robert's Draw, Upper Brule; AMNH 85882, left ramus with m1, Rob-

ert's Draw, Upper Brule; AMNH 85883, left ramus fragment with p3–m1, Robert's Draw, Upper Brule; AMNH 85884, right ramus fragment with p3–m1, north end of Scotts Bluff, Upper Brule; AMNH 85885, left ramus fragment with p4–m3, north base of Scotts Bluff, 100 ft below the level of AMNH 85884, Upper Brule; AMNH 85888, partial skull with broken left and right P1–M2, Robert's Draw, middle Brule; AMNH 85889, left ramus with p2–m3, 7 mi southwest of Chadron, Lower Brule; AMNH 85890, left ramus with p2–m3, 7 mi southwest of Chadron, Lower Brule; AMNH 85891, right ramus fragment with m1–2, 7 mi southwest of Chadron, Lower Brule; AMNH 85892, left maxillary fragment with P4–M2, 7 mi southwest of Chadron, Lower Brule; AMNH 85893, right ramus fragment with m1–2, 7 mi southwest of Chadron, Lower Brule; AMNH 86196, left ramus fragment with m1–2, 15 mi north of Harrison.

7. UNSM collection from mostly Brule Formation in northwestern Nebraska (Toadstool Park, Scotts Bluff Monument areas, etc.) in Dawes, Scotts Bluff, and Sioux Counties (Four lithostratigraphic units, Orella A, B, C, and D, were recognized by UNSM collectors in type Orella and adjacent strata, as divided by Schultz and Stout [1955]. The Orella A+B+C were interpreted to be equivalent to the Lower Oreodon beds and Orella D to Middle Oreodon beds in the Big Badlands of South Dakota [Emry et al., 1987: 140]. Letters and numbers following description of specimens represent University of Nebraska locality numbers. For details of the localities, the locality cards in the UNSM should be consulted.):

UNSM 25000, right ramus with m1, Sx-26, Orella ?; UNSM 25013, left M1, Sx-26, Orella A; UNSM 25014, left maxilla with M1–2, Sx-26, Orella A; UNSM 25022, right ramus with p3–m2, Sx-6, Orella C; UNSM 25023, left ramus with p2–m1, Sx-5, Orella C; UNSM 25024, right ramus with p2–m1, Sx-5, Orella C; UNSM 25034, right ramus with p4–m1, Sx-1, Orella C; UNSM 25036, right ramus with p1–m3, Sx-26, Orella A; UNSM 25039, right ramus with m1, Sx-17; UNSM 25041, right ramus with p4, m2, Sx-37, Orella C; UNSM 25045, right maxilla with P4, Sx-39, Orella A; UNSM 25059, right maxilla with M1, Sx-39, Orella A; UNSM 25061, left maxilla with M1–2, Sx-13, Orella C; UNSM 25063, right ramus fragment with p4–m2, Sx-1, Whitneyan; UNSM 25071, right ramus with p4–m1, Sf-101, Orella B; UNSM 25075, left ramus with m1, Sx-26, Orella A; UNSM 25076, right ramus fragment with m1, Sx-17, Orella B; UNSM 25077, left ramus fragment with m1, Sx-0, Orella A; UNSM 25080, left maxilla with P4–M1, Sx-4, Orella B; UNSM 25095, left

ramus with m1–3, Sx-26; UNSM 25096, left ra-
mus with m1–2, Sx-26, Orella A; UNSM 25098,
left ramus fragment with m2, Sx-26; UNSM 25000,
right ramus fragment with m1, Sx-26, Orella A;
UNSM 25102, left maxilla with P4, Sx-26, Orella
A; UNSM 25103, right maxilla fragment with M2,
Sx-26, Orella A; UNSM 25104, left M1, Sx-26,
Orella A; UNSM 25106, right ramus with m1–2,
Sx-23, Orella B; UNSM 25108, left maxilla frag-
ment with P4, Sx-0, Orella A; UNSM 25110, left
maxilla with M1–2, Sx-0, Orella A; UNSM 25112,
right ramus with m1–2, Sx-0, Orella A; UNSM
25114, right maxilla with M1–2, Sx-13, Orella A;
UNSM 25115, left ramus with p2–4, Sx-26, Orella
A; UNSM 25116, left m1, Sx-26, Orella A; UNSM
25117, right ramus with m1–3, Sx-26, Orella A;
UNSM 25122, left P4, Sx-4; UNSM 25123, left
ramus with m1–2, Sx-4, Orella B; UNSM 25127,
left ramus with p4–m3, Sx-39, Orella A; UNSM
25128, right ramus with m1–2, Sx-39, Orella A;
UNSM 25130, right ramus with p2, p4–m1, Sx-
38, Orella A; UNSM 25132, right ramus with m1,
Sx-14, Orella C (?); UNSM 25135, left ramus with
p4–m1, Sx-0, Orella B; UNSM 25139, left maxilla
with P2–M2, Sx-19, Orella C; UNSM 25159, right
maxilla with P4–M1, Sx-2, Orella C; UNSM 25169,
right ramus fragment with m1–2, Sx-17; UNSM
25171, left ramus with p2, p4–m2, Sx-38, Orella
A; UNSM 25178, right ramus with m1, Sx-37,
Orella B; UNSM 25180, left maxilla with P4, Sx-
17, Orella B; UNSM 25183, right maxilla with P4,
Sx-0, Orella A; UNSM 25184, left maxilla with
M1–2, Sx-0, Orella A; UNSM 25189, right ramus
with m1, Sx-0, Orella A; UNSM 25195, left ramus
with m1, Sx-0, Orella A; UNSM 25196, left ramus
with m1, Sx-0, Orella A; UNSM 25209, left max-
illa with P4–M1, Sx-26, Orella A; UNSM 25219,
left ramus with m1, Sx-0, Orella A; UNSM 25220,
left ramus with p3, m1, Sx-0, Orella A; UNSM
25222, right ramus with p2, m1, Sx-0, Orella A;
UNSM 25226, left ramus with m1–2, Sx-6, Orella
C; UNSM 25228, left ramus with p3–m2, Sx-6,
Orella B; UNSM 25230, left ramus with p4–m1,
Sx-4, Orella C; UNSM 25231, right ramus with
p4–m2, Sx-0, Orella A; UNSM 25232, right ramus
with p4–m2, Sx-26, Orella A; UNSM 25234, right
ramus with p2–m2, Sx-6, Orella C; UNSM 25238,
left ramus with p2–m1, Sx-1, Orella C; UNSM
25239, left ramus with p3–m2, Sx-0, Orella A;
UNSM 25243, right ramus with p2, m1–2, Sx-11,
Orella A; UNSM 25247, left ramus with m1, Sx-
43, Orella A or B; UNSM 25251, left ramus with
m1–2, Sx-11, Orella B; UNSM 25272, left maxilla
with P4–M1, Sx-0, Orella A; UNSM 25273, left
ramus with m1, Sx-0; UNSM 25275, right ramus
with m1–2, Sx-0, Orella A; UNSM 25277, left
ramus with p4–m1, Sx-6, Orella B or C; UNSM
25283, left maxilla with P4–M1, Sx-1, Orella C;

UNSM 25302, left and right m1–2, Sx-6, Orella
C; UNSM 25306, right ramus with m1, Sx-25,
Orella A; UNSM 25307, left ramus with p4–m2,
Sx-25, Orella A; UNSM 25332, left maxilla with
P4–M2, Sx-37, Orella C; UNSM 25344, right
maxilla with P4–M1, Sx-6, Orella C; UNSM 25353,
right ramus with p4–m2, Sx-38, Orellan; UNSM
25363, right ramus with m2, Sx-26, Orella A;
UNSM 25367, left ramus with m1, Sx-26, Orella
A; UNSM 25372, left ramus with p4–m1, Sx-26,
Orella A; UNSM 25373, left ramus with p2–m2,
Sx-26, Orella A; UNSM 25374, partial skull and
mandible with left and right P3–M2, left p1–m3,
right p2–m3, Sx-17, Orella A; UNSM 25376, left
ramus with p1–m3, Sf-0, Orella B or C; UNSM
25378, left ramus with m1–3, Sx-20; UNSM
25384, maxillae with left P4–M2 and right P4–
M1, Sx-6, Orella C; UNSM 25385A, left maxilla
with M1–2 and right maxilla with P4–M2, Sx-6,
Orella B; UNSM 25378, left ramus fragment with
m1–3, Sx-20, Orella D; UNSM 25387, left ramus
with p1–m2, Sf-0, Orella C; UNSM 25401, left
maxilla with P4–M2, left ramus with p4–m2, and
right ramus with p3, Sx-6, Orella B; UNSM 25701,
mandible with left and right p1–m3, Sf-101, Or-
ellan; UNSM 25703, left ramus with m1–2, Sf-
102, Orella B; UNSM 25704, crushed skull and
mandible with left C1, P2, P4–M2, right I3, P1–
M3, left p3–m3, right p2–m2, Dw-104, Orella A
(?); UNSM 25706, left maxilla with P3–M2, Sf-
102; UNSM 26094, mandible with left p2–m1 and
right p3–m2, Dawes County, 16 ft above Purple
White Layer, Orella A; UNSM 50788, right ramus
fragment with p4–m1, Sx-35, 10 ft below P.W.L.,
late Chadronian.

8. Specimens from institutions other than AMNH
and UNSM:

From Cedar Creek or Antelope Creek, Hat Creek
Basin, Orella Members of Brule Formation, Sioux
County, Nebraska: FMNH UC495, skull, man-
dible, and skeleton; FMNH UC496, skull and
mandible; FMNH UC497, skull, mandible, and
vertebrae; FMNH UC1405, skull and mandible;
FMNH UC1417, skull and mandible.

KUVP 12498, p4–m2; KUVP 32526, ramus
with p1–m3, KU-NE-034, Roundhouse Rock,
Morrill County, Whitneyan; KUVP 84207, right
m1, KU-NE-077, Norman Ranch, Sioux County,
Chadronian.

USNM 15937, complete skull, 9 mi north of
Harrison, Sioux County; USNM 15957, partial
skull and mandible and skeleton, 8 mi northeast
of Harrison, Sioux County; USNM 450583, ramus
fragment with m1, Munson Ranch, 7–8 mi north
of Harrison (probably equal to Plunkett-Parson's
locality of F:AM collection).

North Dakota

Skinner's (1951) field guide is followed for correlations of physical stratigraphy in North Dakota; his field terminologies were preserved to correspond to his correlation chart (p. 57). Skinner's Whitneyan (Upper Oreodon Zone), thus, is probably Orellan as is the case in the Badlands of South Dakota (Emry et al., 1987).

1. Jean Hough collection from Leo Fitterer Ranch, 13 mi south and 8 mi west of Dickinson, SE¼, sect. 7, T. 137 N, R. 97 W, Stark County, from level 2B of basal clay in Skinner (1951), early Orellan (late Chadronian?):

AMNH 80214, ramal fragments with left and right m2; AMNH 80215, left m1; AMNH 80232, right P4; AMNH 80235, partial mandible with left and right m1–2; AMNH 82036, left ramus fragment with m1; AMNH 80237, left ramus fragment with m1–2; AMNH 80239, partial right ramus with m1–2; AMNH 80240, left m2; AMNH 80243, right ramus fragment with p4–m1; AMNH 80246, left m2; AMNH 80248, left ramus fragment with p3–4.

2. Childs Frick collection from Leo Fitterer Ranch (see above), Orellan:

F:AM 50373, partial left ramus with p3–m1, above nodular zone in channel, Orellan; F:AM 50374, left ramus fragment with m1, above nodular zone, Orellan; F:AM 50377, nearly complete skull with left dC1, P1, dP2–dP3, P4–M2 and right P1–2, dP3, P4–M2, 20 ft above base of channel and 8 ft above White Marker zone; F:AM 50380, right ramus with p2–m3, 15 ft above base of channel; F:AM 50381, left ramus fragment with p4–m2 and fragments of skeletons, 10 ft above base of channel; F:AM 50382, right ramus with i2–m3, 15 ft above base of channel; F:AM 50383, right m1, 15 ft above base of channel; F:AM 50387, left ramus fragment with p3–4, 15 ft above base of channel; F:AM 50388, right ramus fragment with p4–m1, 15 ft above base of channel; F:AM 50395, left ramus fragment with p4–m3, 15 ft above base of channel; F:AM 50396, left ramus fragment with p4–m1, 15 ft above base of channel; F:AM 50397, right ramus with c1–m2, 15 ft above base of channel; F:AM 50399, left ramus fragment with p1–m1 and skeleton fragments, 20 ft above base of channel; F:AM 72500, partial mandible with left p3–m1 and right m1–3, in base of nodular layer; F:AM 72504, left P4 and right m1–2, 15 ft above base of channel; F:AM 72505, maxillary fragments with left P3–4 and right P2, P4–M2, 15 ft above base of channel; F:AM 72506, left ramus fragment with p3–m1, 15 ft above base of channel; F:AM 72506a, right m1, 15 ft above base of channel; F:AM 72506b, left ramus fragment with m1–2, 15

ft above base of channel; F:AM 72506c, left ramus with c1–m2, 15 ft above base of channel; F:AM 72506d, right ramus with c1–m1, 15 ft above base of channel; F:AM 72506e, right m1, 15 ft above base of channel; F:AM 72506f, left ramus fragment with p4–m2, 15 ft above base of channel; F:AM 72506g, left ramus fragment with p4–m1, 15 ft above base of channel; F:AM 72506h, right ramus fragment with m1–2, 15 ft above base of channel; F:AM 72506i, right ramus fragment with m1, 15 ft above base of channel; F:AM 72506j, right ramus fragment with p1–4, 15 ft above base of channel; F:AM 72507, left ramus fragment with m1–2, 15 ft above base of channel; F:AM 72507a, left m1, 15 ft above base of channel; F:AM 72507b, left m1, 15 ft above base of channel; F:AM 72507c, right m1, 15 ft above base of channel; F:AM 72507d, left ramus fragment with m1–2, 15 ft above base of channel; F:AM 72507e, left ramus fragment with p3–m1, 15 ft above base of channel; F:AM 72507f, left m1, 15 ft above base of channel; F:AM 72507g, left m1, 15 ft above base of channel; F:AM 72507h, right ramus with m1–3, 15 ft above base of channel; F:AM 72508, right m1, 15 ft above base of channel; F:AM 72509, right ramus fragment with p2, p4–m1, 50 ft above base of banded zone; F:AM 72510, left and right m1, 50 ft above base of banded zone; F:AM 72520, right ramus with p3, m1, in base of channel; F:AM 72523, maxillary fragment with P2, P4–M2, in Fitterer Channel; F:AM 126898, right ramus fragment with dp3, in Fitterer Channel.

3. Frank Kostelecky Ranch, 10 mi south and 8 mi west of Dickinson, Stark County, Orellan:

F:AM 50376, left P4–M1, 12 ft above the White Marker Zone; F:AM 72502, maxillar and mandible fragments with right P3–M1 and m2, 15 ft below the White Marker Zone.

4. Little Badlands, 7 mi south of South Heart, sects. 13 and 14, T. 138 N, R. 98 W, Stark County, Orellan:

F:AM 50370, left ramus with p3–m2, 10 ft above base of nodules; F:AM 50371, right ramus fragment with p4–m2, in talus of nodules; F:AM 50372, left ramus with p2–m2, 10 ft above base of nodules; F:AM 50375, left ramus fragment with p3–4, in talus of nodules; F:AM 50385, right ramus with p3–m3, 5–10 ft above base of nodules; F:AM 50386, right M1, 10 ft above base of the White Marker Layer in channel; F:AM 50394, rostral part of skull, in basal or middle of nodules; F:AM 50398, left ramus with p3–m2, 15–20 ft above top of nodules; F:AM 72503, left ramus fragment with m1, 4 ft above the White Marker Layer; F:AM 72503a, right ramus fragment with m1–2, 4 ft above the White Marker Layer; F:AM 72511, par-

tial cranium, 50 ft above top of nodules; F:AM 72515, nearly complete skull with right P1, P3–M2; F:AM 72516, rostral part of skull and partial mandible; F:AM 72517, crushed skull and mandible with skeleton fragments, 10 ft above base of nodules; F:AM 72518, left ramus with p4–m2, at base of the nodules; F:AM 72519, right ramus fragment with m1–2, 10 ft above base of nodules; F:AM 72522, nearly complete skull and mandible, in lower part of nodules.

5. East of Little Badlands localities, Stark County, Orellan (?):

AMNH 80208, left ramus fragment with p4–m1, in SE¼, sect. 18, T. 138 N., R. 97 W, from Clay Ball conglomerate; AMNH 80220, left m1, in sect. 29, T. 138 N, R. 97 W, 25 ft below a green sandstone.

6. Meduna Ranch, 1.5 mi west of Little Badlands area, NE¼, NE¼, sect. 28, T. 138 N, R. 98 W, Stark County:

F:AM 72521, right ramus fragment with m1–3, in base of nodular zone, Orellan.

7. Southeastern corner of White (Chalky) Buttes, south of Amidon, Slope County:

F:AM 50378, right P4, in talus of nodules, Orellan; F:AM 50379, right m1, upper 10 ft of nodules, Orellan; F:AM 50384, left ramus fragment with m1–2, in a channel, Whitneyan (?); F:AM 50389, left ramus fragment with m1–3, in talus of nodules, Orellan; F:AM 50390, right p4–m1, in talus of nodules, Orellan; AMNH 80203, left ramus fragment with broken p4; AMNH 80208, left m2, in a block of dark bentonite from west side of Chalking Buttes, Chadronian (?); AMNH 80225, left ramus with p2–m3; AMNH 80227, right P3–4, Orellan; AMNH 80229, right m1.

SOUTH DAKOTA

Field documents are on file in the archives of the AMNH. For a brief outline of the stratigraphic correlations and field terminologies, such as Middle Oreodon beds, etc., see Prothero and Swisher (1992: fig. 2.7).

1. Eight mi north of Rocky Ford, east side of highway, sect. 24, T. 42 N, R. 44 W, in Pine Ridge Indian Reservation:

F:AM 50363, mandible fragments with left p4–m1 and right p4–m3 plus skeleton fragments, in base of Middle Oreodon beds; F:AM 50364, mandible fragments with left and right p4–m1, in top of Middle Oreodon beds; F:AM 50365, right ramus fragment with p4–m1, in top of Middle Oreodon beds; F:AM 50366, right ramus fragment with m1–2, in top of Middle Oreodon beds; F:AM

50367, left ramus fragment with p4–m1, in top of Middle Oreodon beds; F:AM 50368, mandible fragments with left p1–2 and right m1, in top of Middle Oreodon beds; F:AM 50369, left ramus with p1–m3, in top of Middle Oreodon beds; F:AM 63357, cranial and skeletal fragments with left P2–M1, left p2, M1–2, and right p3, m1, in top of Middle Oreodon beds; F:AM 63358, left ramus fragment with m1–3, in top of Middle Oreodon beds; F:AM 63359, cranial fragments and partial skeleton with right M1–2, left m1–3, and right m1, in top of Middle Oreodon beds; F:AM 63362, right ramus fragment with p4–m1, in top of Middle Oreodon beds; F:AM 63853, right ramus with m1–3, in top of Middle Oreodon beds; F:AM 63855, right ramus fragment with p4–m1, in top of Middle Oreodon beds; F:AM 63856, left ramus fragment with p4–m1, in top of Middle Oreodon beds; F:AM 63857, right ramus fragment with m1, in top of Middle Oreodon beds; F:AM 63858, right m1, in top of Middle Oreodon beds; F:AM 63861, right maxillary and ramus fragments with M1–2 and m1, in top of Middle Oreodon beds.

2. Seven mi north of Rocky Ford:

F:AM 50347, maxillary and mandible fragments with left P4–M2, right P3–M2, and right p4–m1, on east side of Scenic–Rocky Ford road, in top of Middle Oreodon beds; F:AM 50354, right ramus with p2–m2, in top of Middle Oreodon beds.

3. Cottonwood Pass areas, in Big Corral drainage, 3 mi southwest of Sheep Mountain, NE¼, sect. 1 or 2, T. 42 N, R. 45 W, Washington County:

F:AM 50351, nearly complete skull and mandible, 1 mi north of Cottonwood Pass, east side of Big Corral Draw, 4 ft above base of lower nodules, in Lower Oreodon beds; F:AM 50353, right ramus with c1–m1, 0.75 mi south of eastern end of Cottonwood Pass, in top of Lower Oreodon beds; F:AM 50357, left maxillary fragment with P4–M2 and right ramus fragment with p4–m1, south side of Cottonwood Pass, in upper part of Middle Oreodon beds.

4. Sheep Mountain areas, Shannon County:

F:AM 50343, partial skull and mandible with left I1–P4, right I2–M2, and left p2, m1–2, Harney Springs range, southeast of Sheep Mountain, 10 ft below upper nodules, in middle Oreodon beds; F:AM 50346, left maxillary with M1–2, Harney Springs range, southeast of Sheep Mountain, in middle of Middle Oreodon beds; F:AM 50352, mandible with left p2, p4–m3 and right c1, p2, p4–m2, 1 mi north of Sheep Mountain road, in Middle Oreodon beds; F:AM 50359, left P4, east side of Harney Springs range, from base of Middle Oreodon beds; F:AM 63860, partial mandible with

left c1–p2 and right m1, head of Spring Creek, Harney Spring Basin, NW¼, sect. 34, T. 43 N, R. 44 W, in Upper Nodules of Middle Oreodon beds; F:AM 63862, right maxillary fragment with P4–M2, head of Spring Creek (see F:AM 63860), in top of Middle Oreodon beds.

5. Near Indian Stronghold, on north side of Cuny Table, SW¼, NE¼, sect. 22, T. 42 N, R. 45 W, Shannon County:

F:AM 50345, complete skull and mandible, Quinn Draw, north and northwest side of Indian Stronghold, near top of lower nodulars, in Lower Oreodon beds; F:AM 50355, left ramus with p4–m2, near head of Quinn Draw, in base of lower nodules, in Lower Oreodon beds; F:AM 50362, right M1–2, northeast of Indian Stronghold, east of head of West Big Corral Draw, 4 mi south of Sheep Mountain, in Protoceras channel, Whitneyan.

6. Miller Basin, Cain Creek Drainage, 6 mi west of Imlay and 1.5 mi north of the road to Scenic, Pennington County:

F:AM 50360, left ramus fragment with m1, in base of Lower Oreodon beds; F:AM 50361, left ramus fragment with m1–3, in base of Lower Oreodon beds;

7. Other isolated Frick collections from Brule Formation in Big Badlands area (most of the following specimens, except as otherwise noted, are within lithostratigraphic units containing fauna of Orellan age):

F:AM 50350, left ramus fragment with p3–m1, southeast end of Hart Table, southwest of Scenic, in lower part of Middle Oreodon beds; F:AM 63850, nearly complete skull and mandible, 2 mi west of Fancher Ranch, south side of Cuny Table, south of Swallow Springs, sect. 3, T. 41 N, R. 47 W, in Lower Oreodon beds; F:AM 63851, edentulous skull, south Arrow Wound Table, on west side of Pine Ridge Indian Reservation, in Lower Oreodon beds; F:AM 63854, right ramus with c1, p2–m3, 1 mi north of Pete Crow Ranch buildings, west-central side of Red Shirt Table, sect. 3, T. 41 N, R. 47 W, in top of Lower Oreodon beds; F:AM 63859, right ramus fragment with p4–m2, Saddle Horse Pass, north end of Sheep Mountain, in Upper Oreodon beds, early Whitneyan.

8. Early American Museum collection from the Big Badlands (Besides the general lack of detailed locality descriptions [often labeled as Cheyenne River], problems also arise with the term Oreodon beds, which includes part of the Poleslide Member [part of Upper Oreodon beds, see Emry et al., 1987]. Thus, unless labeled as Lower Oreodon beds [i.e., definite Orellan], the rest of the Oreodon beds

or Upper Oreodon beds are here treated as within the Brule Formation.):

AMNH 1004, partial rami with left c1–m1 and right p1–m3, Cheyenne River, in Lower Oreodon beds; AMNH 1383, rostral part of skull and mandible with skeleton fragments, Cheyenne River, in Lower Oreodon beds; AMNH 1384, rostral part of skull and mandible, Cheyenne River, in Oreodon beds; AMNH 1389, partial crushed skull with left P4, M2 and right P4–M2, Cottonwood Draw, in Lower Oreodon beds; AMNH 1408, partial edentulous skull, left ramus, and left tarsus and metatarsus, in Oreodon beds; AMNH 1472, partial skull and mandible, Cheyenne River, in Oreodon beds; AMNH 1487, skull and mandible fragments with left I1–C1, right I1–M2, left i1–p3, m1–3, and right i2, p2–3, m1–3, Cheyenne River, in Oreodon beds; AMNH 1794, left ramus fragment with p4–m2; AMNH 1795a, left ramus fragment with p3–m1, near Scenic, in Oreodon beds; AMNH 1795b, right ramus fragment with p4–m2, near Scenic, in Oreodon beds; AMNH 12350, posterior half skull, Silas Ranch, Cheyenne River, in Upper Oreodon beds; AMNH 38815, left ramus fragment with m1–2, south of Scenic, in Lower Oreodon beds; AMNH 38817, skull and skeleton fragments with left and right P3–M2, left p1, p4–m2, right p2–m2; AMNH 38819, partial palate with left and right P4–M2, south of Scenic, in Lower Oreodon beds; AMNH 38820, partial skull with left M1–2 and right P4–M1, 6 mi south of Scenic, in Lower Oreodon beds; AMNH 38821a, left ramus fragment with p3–m1, south of Scenic, in Lower Oreodon beds; AMNH 38821b, left ramus fragment with m1, south of Scenic, in Lower Oreodon beds; AMNH 38822, maxillary, ramus, and skeleton fragments with left P4–M1 and right m1–2, 6 mi south of Scenic, in Lower Oreodon beds; AMNH 38824, right ramus fragment with p3–m1, south of Scenic, in Lower Oreodon beds; AMNH 38949, right ramus fragment with p4–m2, south of Scenic; AMNH 38988, right ramus with p3–m3, from Scenic, in Oreodon beds; AMNH 39096, crushed skull and mandible with partial forelimbs, from Scenic, in Oreodon beds; AMNH 39097, left ramus fragment with p3–m2, from Scenic, in Oreodon beds; AMNH 39442, nearly complete skull, south of Scenic; AMNH 90279a, left ramus fragment with m1, south of Scenic, in Lower Oreodon beds; AMNH 90307, partial right ramus with dp3–dp4 and erupting c1 and m1, south of Scenic; AMNH 90329, right ramus fragment with p4–m2, south of Scenic; AMNH 90330, right ramus fragment with p4–m1, south of Scenic; AMNH 96696, right maxillary fragment with P4–M2, Cedar Draw, in Oreodon beds; AMNH 96697a, right ramus fragment with p4–m1, south of Scenic, in Lower Oreodon beds; AMNH 96697b,

left m1, south of Scenic, in Lower Oreodon beds; AMNH 96697c, left m1, south of Scenic, in Lower Oreodon beds; AMNH 96697d, left M1, south of Scenic, in Lower Oreodon beds; AMNH 96698, right maxillary fragment with P4–M2, Cedar Draw, in Oreodon Beds; AMNH 96701, right maxillary fragment with P4–M2, 7 mi south of Scenic, in Lower Oreodon beds.

9. Slim Buttes area, Harding County:
    AMNH 39095, left ramus fragment with p2–m1, southeast of Ralph Waugh's Ranch, Oreodon beds; AMNH 96700a, right maxillary fragment with P4–M1; F:AM 63361, left P4, Tepee Canyon, south of Ralph Waugh's Ranch and south Reva Gap, just below gray channel-like sands, in Middle or Upper Oreodon beds.

WYOMING

1. Chadronian of Bates Hole area, Natrona County (detailed stratigraphy of the Flagstaff Rim area can be found in Emry [1973, 1992]; the letter designations of the ashes in Emry's work are followed below):
    Six mi northwest of Alcova.— F:AM 50231b, partial left ramus with m1; F:AM 50231c, left ramus fragment with m1–2; F:AM 50232, left maxillary fragment with P4–M2.
    Three mi northwest of Alcova.— F:AM 50231a, right ramus fragment with m1.
    North fork of Lone Tree Gulch, 1 mi west and 4–6 mi north of 1957 Alcova Post Office, SE¼ of sect. 22, SW¼ of sect. 23, and NE¼ of sect. 27, T. 31 N, R. 83 W.— F:AM 63934, left P4–M2 and alveolus of M3, in Ash D; F:AM 63940, right M1, in Ash D; F:AM 63946, right ramus fragment with p4–m2, 15 ft above Ash D; F:AM 63951, right m1, in Ash F; USNM 22974.
    Middle fork of Lone Tree Gulch.— F:AM 63942, complete skull, 10 ft above Ash F; F:AM 63944, left ramus fragment with p4–m1, 30 ft above Ash D; F:AM 63948, left ramus fragment with p4–m1, 35 ft below Ash D.
    South fork of Lone Tree Gulch, 2 mi west and 4 mi north of Alcova 1957 Post Office, SW¼ of sect. 26 and S1½ of sect. 27, T. 31 N, R. 83 W.— F:AM 63941, right P4–M1, 20 ft above Ash D; F:AM 63945, right ramus fragment with m1–3, 30 ft below Ash G; F:AM 63947, right ramus fragment with p4–m2, 35 ft below Ash G; F:AM 63950, left ramus fragment with p4–m1, in Titanothere channel (laterally replaced by Ash F).
    Main fork of Lone Tree Gulch.— F:AM 63943, partial crushed skull with left and right P2–M3, 6 ft above Ash D.
    Little Lone Tree Gulch, NE¼ of sect. 22 and N¼ of sect. 23, T. 31 N, R. 83 W.— F:AM 63949,

left ramus fragment with p4–m2, 10 ft above Ash D.
    Trail Fork of Blue Gulch, 2–3 mi west and 3–4 mi north of 1957 Alcova Post Office, SE¼, NW¼, sect. 34, T. 31 N, R. 83 W.— F:AM 63939, right P4–M2, 40 ft below Ash D.

2. Shirley Basin, SW½, sect. 15, T. 29 N, R. 80 W, Natrona County, Chadronian:
    USNM 22974, right ramus fragment with p3–m2.

3. Chadronian to Orellan of Seaman Hill area, Niobrara County:
    Shack Draw.— F:AM 50276, complete skull and mandible and atlas–axis; F:AM 50277, nearly complete skull, from upper end of Shack Draw.
    Upper Spring Draw, Indian Creek area, Hat Creek Basin.— F:AM 50245, right ramus fragment with m1, Orellan; F:AM 50246, partial maxillaries with left M1–2 and right P4–M2, Orellan; F:AM 50250, right ramus fragment with m1, F:AM 50251, left m1, from south of road, Chadronian; F:AM 50252, left ramus fragment with p3–m1; F:AM 50247, left ramus fragment with p3–m2, from Indian Creek area, Chadronian; F:AM 50288, left ramus with p4–m2.
    Piper Ranch, Spring Draw.— F:AM 63902, left ramus fragment with p4–m2, 75 ft above P.W.L., early Orellan; F:AM 63915, right P4, 35 ft above P.W.L., early Orellan; F:AM 63911, left ramus with p4–m2, 15 ft above P.W.L., early Orellan.
    Southeast end of Hat Creek Basin.— F:AM 50249, left ramus fragment with p4–m1, Chadronian; F:AM 50254, left ramus fragment with m1–2.
    Five mi north and 1 mi east of Hat Creek Store.— F:AM 50244, right ramus fragment with p4–m1, above (?) P.W.L., early Orellan; F:AM 50256, left ramus with p4–m3.
    North of Node Road.— F:AM 50278, partial skull, mandible, and skeletons, 20 ft below a channel; F:AM 50279, left ramus with p4–m1.
    Boner Brothers Ranch, in the Pass area, N½ of sect. 14 and S½ of sect. 11, T. 35 N, R. 62 W.— F:AM 63901, left ramus with p3–m1, 10 ft above P.W.L., early Orellan; F:AM 63904, right ramus with p4–m3, 35 ft above P.W.L., early Orellan; F:AM 63914, left maxillary fragment with P4–M2, 30 ft above P.W.L., early Orellan; F:AM 76178, right ramus fragment with p4–m2, southeast of Pass area, 20 ft above P.W.L., early Orellan; F:AM 76179, left ramus fragment with p4–m1, 10 ft above P.W.L., early Orellan; F:AM 76187, complete skull and partial skeletons, north side of Pass area, 30 ft above P.W.L., early Orellan.
    Jim Christian Hills, on south side of Indian Creek, southeast of Seaman Hills, N½ of sects. 3 and 4 and S½ of sects. 9 and 10, T. 34 N, R. 61

W.— F:AM 63907, right ramus with p3–m2, 70 ft above P.W.L., early Orellan; F:AM 63912, left ramus fragment with p4–m1, 2.5 mi southeast of Jim Christian Hills on west side of S-Bar Creek, 35 ft above P.W.L., early Orellan; F:AM 63920, right ramus with p1–m1, 0.5 mi south of Jim Christian Hills, 60 ft above P.W.L., early Orellan; F:AM 63919, right m1, 0.5 mi south of Jim Christian Hills, 60 ft above P.W.L., early Orellan.

DeGerring Ranch, in northwestern corner of Seaman Hills, sect. 3, T. 35 N, R. 62 W, and S½, sect. 34, T. 36 N, R. 62 W.— F:AM 63903, right ramus fragment with m1–2, 30–35 ft above P.W.L., early Orellan; F:AM 63906, right m1, 30–35 ft above P.W.L., early Orellan.

Kraft Ranch area, on west side of Plum Creek, southcentral part of sect. 23, T. 34 N, R. 61 W.— F:AM 63910, left ramus fragment with p4–m1, south of Kraft Ranch, 15 ft above P.W.L., early Orellan; F:AM 63913, right ramus with p4–m1, south of Kraft Ranch, 15 ft above P.W.L., early Orellan; F:AM 63918, left ramus with p2–m1, southwest of Kraft Ranch, 30 ft above P.W.L., early Orellan; F:AM 128064, crushed skull and mandible and skeletal fragments, west side of S-Bar Creek, 80 ft above P.W.L., Orellan; USNM 450582, skull and ramus fragments with left P3–M2 and m1–2.

Ant Hill Locality, southeastern end of Seaman Hills, NW¼, SE½, sect. 28, T. 35 N, R. 61.— F:AM 63905, left ramus fragment with m1–2, west of Ant Hill Locality, 40 ft above P.W.L., early Orellan; F:AM 63908, right m1, 25–30 ft above P.W.L., early Orellan.

Spring Draw, 1.5 mi west of Ant Hill, E½ of sect. 30 and all sect. 29, T. 35 N, R. 61 W.— F:AM 50248, left ramus fragment with p4–m1, West Spring Draw, 18 ft below channel sandstone, Chadronian; F:AM 63909, left ramus with p4–m2, 70 ft above P.W.L., early Orellan.

Southwestern end of Seaman Hills.— F:AM 50242, left ramus fragment with m1, above P.W.L., Orellan; F:AM 50257, left ramus with p4–m3, between channels, above P.W.L., early Orellan; F:AM 63925, partial right ramus with p2–m3, below P.W.L.; F:AM 63929, partial maxillaries with left P4–M2 and right M1–2, 30 ft above P.W.L., early Orellan; F:AM 63930, maxillar and ramal fragments with left P4–M2, left p4, m2, and right c1–p2, m2, 20 ft above P.W.L., early Orellan; F:AM 63936, right ramus fragment with m1–3, from southwestern side of Seaman Hills, 15 ft below P.W.L. in pink clay, late Chadronian.

Southeastern end of Seaman Hills.— F:AM 50258, left ramus with p1–m3, below P.W.L., late Chadronian; F:AM 63926, posterior half of cranium, 45 ft above P.W.L., early Orellan; F:AM 63931, right maxillary with P4–M2, early Orellan.

Northwestern end of Seaman Hills.— F:AM 63928, right ramus with c1–m3, in a channel 50 ft below P.W.L., late Chadronian; F:AM 63932, left ramus fragment with p3–m1, 15 ft below P.W.L., late Chadronian; F:AM 63932a, right p4–m1, 20 ft below P.W.L. in green clay, late Chadronian.

Road Stop locality.— F:AM 62900, skull fragments with left P4–M2 and right P4, 20 ft above P.W.L., early Orellan; F:AM 63916, left ramus fragment with m1, 20 ft above P.W.L., early Orellan.

Other localities in Seaman Hills area.— F:AM 50243, left ramus fragment with p4–m1, on the road (south side) to north Indian Creek; F:AM 50255, right ramus fragment with p4–m1, 2 mi northeast of Whitman Post Office, above P.W.L., early Orellan; F:AM 50275, partial cranium, from Indian Creek, south of road; F:AM 50281, left ramus with p4–m2, 2 mi northwest of Whitman, 30 ft below P.W.L., late Chadronian; F:AM 63917, left ramus with p4–m2, from Keel Ranch, 45 ft above P.W.L., early Orellan; F:AM 63927, left m1, in north end of saddle in Seaman Hills, in the base of a Channel which cuts through P.W.L., Orellan; F:AM 63932b, left ramus fragment with p4–m2, from southeast side of the saddle of Seaman Hills, 15 ft below P.W.L. in brown clay, late Chadronian; F:AM 63935, right ramus fragment with p4–m1, Channel Quarry, southeast end of Seaman Hills, Chadronian (?); F:AM 63937, right ramus fragment with m1–2, from southwestern side of saddle in Seaman Hills, 15 ft below P.W.L., late Chadronian; F:AM 63938, right m1, in a channel quarry, Chadronian (?).

4. Douglas area, Converse County, late Chadronian to early Orellan (The local stratigraphy in the Douglas area contains a 50–70 ft nodular layer in which many of the specimens listed below are found. The nodules are bound on top by a White Ash [Marker] zone and at bottom by a Black Ash. The last occurrence of titanothere materials is approximately 25 ft above the White Ash. Following the same convention as discussed at the beginning of this appendix, the White Marker bed is here designated as an arbitrary Chadronian/Orellan boundary, that is, the Nodular Layer belongs to Orellan age.):

Eight mi southeast of Douglas, approximately ⅙ mi to the south of U.S. Highway 20: —F:AM 50259, anterior half skull and mandible with skeletal fragments; F:AM 50264, partial skeleton without cranial material; F:AM 50270, left ramus fragment with m1–2, in top of nodular layer; F:AM 50271, left ramus with p3–m2; F:AM 50272, right ramus fragment with p4–m1, in top of nodular layer; F:AM 50273, left ramus fragment with p4–

m1; F:AM 50280, right ramus fragment with m1; F:AM 50284, maxillary and mandible fragments with left P4–M2 and m1–2; F:AM 50285, right maxillary fragment with P3–M2, in lower part of nodular layer; F:AM 50286, left m1; F:AM 50287, left m1, in lower nodular layer.

Six mi southeast of Douglas: —F:AM 50260, skull and mandible; F:AM 50261, anterior skull and mandible with nearly entire teeth, in nodular layer; F:AM 50262, skull fragment with right P2–M2, in nodular layer; F:AM 50266, crushed partial skull and mandible with left I1–dC1, dP3–dP4, M1–2, right dP3, P4–M1, left i1–dc1, p1, dp2, dp4, m1–2, and right p1–m2, in nodular layer; F:AM 50267, right ramus fragment with p3–m2, in nodular layer; F:AM 50268, left ramus with p2–m3, 50 ft above nodular layer.

Reno Ranch, 5–6 mi southeast of Douglas on south side of Highways 20 and 87, sect. 32, T. 32 N, R. 70 W, Converse County: —F:AM 76156, right P4–M1, 10–20 ft below Black Ash; F:AM 76158, partial skull and mandible with skeleton fragments, in middle part of nodular layer; F:AM 76159, right M1–2, 10–20 ft below Black Ash; F:AM 76164, right maxillary with P4–M2, 35 ft below Black Ash; F:AM 76167, left m1, 20 ft above White Marker zone; F:AM 76168, right m1–2, 20 ft above White Marker zone.

Reno Ranch, south of Tower area, W½, SE¼, sect. 31, T. 32 N, R. 70 W, 5 mi southeast of Douglas, Converse County: —F:AM 76157, anterior half skull, 60 ft above Black Ash; F:AM 76161, partial palate and mandible with most cheek teeth, 30 ft above White Marker; F:AM 76166, nearly complete skull and mandible, in upper part of nodular layer; F:AM 76172, left m1, in upper part of nodular layer; F:AM 76175, left ramus with p2–m2, in middle part of nodular layer.

Reno Ranch east area, E½ of sect. 32 and SW¼ of sect. 33, T. 32 N, R. 70 W, 6.5 mi southeast of Douglas, Converse County: —F:AM 76169, left ramus with i3–c1, p2–m2, 3 ft below Black Ash.

Reno Ranch reservoir area, 5 mi southeast of Douglas, NE¼ of sect. 31 and W½ of sect. 32, T. 32 N, R. 70 W, Converse County: —F:AM 76181, right m1, in middle part of nodular layer; F:AM 76184, right ramus fragment with p4–m1, in middle part of nodular layer; F:AM 76185, right ramus with p4–m2, in middle part of nodular layer.

W. R. Silver Ranch, E½ of sect. 28, S½ of sect. 27, SW¼ of sect. 26, NW¼ of sect. 35, T. 32 N, R. 71 W, 2 mi south to 3.5 mi southeast of Douglas, Converse County.— F:AM 76162, anterior half skull, 30 ft below Black Ash; F:AM 76163, in middle part of nodules.

H. Wulff Ranch, sect. 36, T. 32 N, R. 71 W, 3.5 mi southeast of Douglas, on north side of Platte River, Converse County: —F:AM 76160, poste-

rior half skull, in middle part of nodular layer; F:AM 76170, left ramus with c1–m3, in upper part of nodular layer; F:AM 76171, right ramus fragment with m1–2, in middle part of nodular layer; F:AM 76173, left ramus fragment with p3–m1, in upper part of nodular layer; F:AM 76176, left ramus fragment with p4–m1, in middle part of nodular layer; F:AM 76177, crushed skull and nearly complete mandible with most teeth; F:AM 76180, anterior half skull and mandible and isolated skeletal fragments, in top part of nodular layer; F:AM 76182, right ramus fragment with p3–m1, in top part of nodular layer; F:AM 76183, maxillary and mandible fragments with right P4–M2 and m1, in middle part of nodular layer; F:AM 76186, left ramus fragment with p4–m2, in top part of nodular layer; F:AM 76188, anterior half skull, in middle part of nodular layer; F:AM 76189, crushed anterior half skull and mandible, in upper part of nodular layer; F:AM 76190, right ramus fragment with p4–m2, in middle part of nodular layer; F:AM 76191, left ramus with p2–m2, in upper part of nodular layer; F:AM 76192, nearly complete skull and mandible with partial skeleton, in lower part of nodular layer, 20 ft above White Marker; USNM 437888, complete skull and mandible, 55 ft above White Marker; USNM 450576, complete skull and right ramus, 20 ft above White Marker; USNM 450577, mandible fragments with left p1–m2 and right p2–m3, 55 ft above White Marker; USNM 450578, right maxillary fragment with P4–M2, 55 ft above White Marker; USNM 450579, right ramus fragment with p2–m1, 25 ft above White Marker; USNM 450580, left ramus fragment with p4–m2, 30 ft above White Marker; USNM 450581, right maxillary fragment with M1–2, 15 ft above White Marker.

Other localities near Douglas: —F:AM 50263, crushed skull and mandible with five cervical vertebrae, 6.5 mi southeast of Douglas, in nodular layer; F:AM 50265, fragmentary skull and skeleton, 7 mi southwest of Douglas; F:AM 50269, right m1, 8 mi southeast of Douglas, on north side of U.S. Highway 20, in top of nodular layer; F:AM 76165, complete skull and mandible with partial skeleton, 25 ft above base of Indian Hill channel; F:AM 76174, right p4–m1, 6–7 mi southeast of Douglas, in nodular layer; FMNH P15427, skull, Orellan; FMNH P15428, skull, mandible, and partial skeleton, Orellan; KUVP 13569, left ramus with p4–m1, KU-WY-057, Whitneyan; USNM 17892, skull, 8 mi east of Douglas; USNM 450585, crushed skull with partial skeleton, Douglas.

SASKATCHEWAN, CANADA

Specimens from Cypress Hills localities described by Lambe (1908) and Russell (1934, 1972)

were broadly referred to the Lower Oligocene (i.e., Chadronian), although the Cypress Hills strata clearly cover a much more extensive geologic record, both earlier and later than Chadronian (Storer, 1975a, b, 1984). Part of Lambe's original collection as well as a few representative specimens of those more recently collected (Bryant, 1992, 1993) were examined in the present study. Except for the Lac Pelletier Lower Fauna, the majority of *Hesperocyon* specimens were probably Chadronian in age (Storer, personal commun. 1992).

Lac Pelletier Lower Fauna, Cypress Hills Formation, Duchesnean (Bryant, 1992).— SMNH P1899.5, right m1; SMNH P1899.6, right m1; SMNH P1899.1428, left dp4.

Russell Hill locality, sect. 4, T. 8, R. 22, West Third Meridian.— NMC 9127, right M1; NMC 9130, left m2; ROM 1818, right M2.

Calf Creek, opposite to Hunter Quarry, sect. 7, T. 8, R. 22, West Third Meridian (Bryant, 1993).— ROM 6334, right P4, Calf Creek West; ROM 6335, left M1; ROM 6344, left m2; ROM 6388, right m1; SMNH P166.1689, left P4; SMNH P661.1546, left m1; SMNH P661.1555, left ramus fragment with m1–2; SMNH P661.1690, right P4; SMNH P661.1693, left M1; SMNH P661.1694, left M1; SMNH P661.1698, right M1; SMNH 1017.27, left P4.

Other Cypress Hills localities.— NMC 6501, left p3, from Bone Conlee; NMC 6502, left p4; NMC 6503, left p4; NMC 9202, fragment of right ramus with m2; NMC 9353, left P4 (referred to Cf. *Hyaenodon*? *minutus* (Douglass) Russell, 1972: 47, fig. 13F–G); NMC 9354, right P4; ROM 1812, left dP4 (type of *Nanodelphys*? *mcgrewi* Russell, 1972: 7, fig. 1F); ROM 6338, right M1, Herman Pirsson's Hill, SE¼, SE¼, sect. 4, T. 8, R. 22; ROM 6339, right M2, Rodent Hill, SE¼, NE¼, sect. 9, T. 8, R. 22; ROM 6340, right M2, NW¼, sect. 33, T. 7, R. 22; ROM 6341, right m1, road cut in NW¼, sect. 33, T. 7, R. 22; ROM 6343 left m2, Hanson Ranch, in north edge of sect. 32, T. 7, T. 22 and south edge of sect. 5, T. 8, R. 32.

APPENDIX II

Cranial Measurements of Hesperocyonines

(See Method section for definition of the measurements. Units are in millimeters. Asterisks indicate estimates.)

	1 WBR	2 WZA	3 WPC	4 WFS	5 LNI	6 HTO	7 DJG	8 LPS
Prohesperocyon wilsoni								
TMM 40504-126	27.9		13.5	15.8	88.1*			64.2
Hesperocyon gregarius								
AMNH 39096	30.4	50.1	11.2	18.1	82.9	11.4	6.9	65.4
FMNH UC495	29.4	48.8	11.6	16.7	79.0	10.2	5.8	61.6
F:AM 39442	25.4		12.0	15.7				57.0
F:AM 50260	27.9					10.0	5.7	61.6
F:AM 50276	26.4			15.8*	75.5	9.4	5.6	59.3
F:AM 50325			11.6	19.0	83.9	12.3	7.1	67.0
F:AM 50345	29.6	52.0*	13.2	18.1	84.9	10.5	5.7	
F:AM 50351	29.4			17.4	86.7	11.1		66.5
F:AM 63850	28.4		11.3	18.5		11.4		
F:AM 63885					83.9	11.5	5.8	65.2
F:AM 63886	27.9		12.0	14.5		10.9	6.1	62.5
F:AM 72515	31.6	52.6*	12.1	18.8	92.7	12.6	5.7	71.1
F:AM 76187		48.9	11.1	17.5	87.7	12.1	6.6	67.8
F:AM 76518	27.2				75.4	9.5		61.6
USNM 437888	27.0	42.0*	13.1	15.3	75.7	8.7	5.7	58.9
"Hesperocyon" coloradensis								
KUVP 85067	32.6		11.5	19.1		11.0	7.1	70.1
"Mesocyon" temnodon								
F:AM 63367	40.4	79.2*	17.4	28.4		14.4	9.2	
SDSM 2653	41.8		13.7	27.2	135.4			
Mesocyon coryphaeus								
AMNH 6859	49.6	89.0	19.5	34.4	149.6	20.3	9.9	114.1
AMNH 6860				37.9		18.6	12.0	115.8
AMNH 6862			20.5	36.6		19.5		
AMNH 6909	52.2	104.0*	24.5	37.1	148.5	21.1	10.7	118.4
AMNH 6920	52.0				155.4	21.8		
JODA 153	49.8	98.5	21.5	38.9	158.0	19.1	11.3	
UCMP 75500	50.1		20.6	33.9		21.3		112.5
Mesocyon brachyops								
AMNH 6921	49.0	91.0*	20.0	32.6		17.4	10.0	
JODA 2399	49.6		22.2	35.2	139.9	18.9		105.4
JODA 3082		74.4	19.8	34.1	139.4	19.8	11.0	101.8
UCMP 1692	43.9		22.6	30.6		15.8	8.5	100.9
Cynodesmus thooides								
BHI 1965	50.5	93.0*	22.0	33.5	146.6	18.4	9.8	112.6
CMNH 792	47.8	84.4*	22.6	33.0		20.4	10.4	
F:AM 63382	45.7		19.1	31.3	135.2	18.4	9.0	103.3
F:AM 63386	46.0		19.2			18.6		
LACM 17076			19.5*	32.7				
YPM-PU 10412	49.9	101.4*	21.2	35.0		18.4	11.1	
Cynodesmus martini								
UNSM 25796			29.1	44.2	167.7*	25.3	17.6	112.3

APPENDIX II (*Continued: cranial measurements 1--8*)

	1 WBR	2 WZA	3 WPC	4 WFS	5 LNI	6 HTO	7 DJG	8 LPS
Sunkahetanka geringensis								
UNSM 1092	53.0	100.4	23.6	33.0	142.2	18.7	12.3	114.9
Philotrox condoni								
F:AM 63383	55.6	104.0			173.8			123.3
LACM 15910	54.1		22.5	38.3		21.4	12.3	124.8
UCMP 76712	55.6		22.5	37.1	163.1	23.9	13.5	128.2
Enhydrocyon pahinsintewakpa								
CMNH 13588	61.3	117.4*	24.7	42.2	175.3	27.7	16.8	
F:AM 27579	57.4	110.2*	24.9	37.6	168.8	22.7	16.9	124.2
SDSM 53320	59.6		25.7	45.0	170.0	28.1	14.5	135.3
Enhydrocyon crassidens								
AMNH 12886	59.0		28.7		175.0	22.4	17.7	130.4
F:AM 27560		117.0	30.2	40.7	167.1	23.4	18.9	132.5
Enhydrocyon stenocephalus								
AMNH 6901	60.2	111.4*	24.3	41.1	167.9	27.0	15.5	129.7
USNM 7745	65.0		31.0*	49.4	171.2	29.2		135.4
YPM 12730			28.0	36.2		19.5		
Enhydrocyon basilatus								
UCMP 76749	63.2		30.1	43.8		24.4	19.4	135.0
Osbornodon renjiei								
AMNH 1382					126.9			95.5
AMNH 1386	44.5	69.4*	21.2*	28.2*	123.4	16.5	9.0	
Osbornodon iamonensis								
F:AM 128763	59.3		28.3	43.5	178.8	23.3		134.0
UM 528		98.2*			161.1	25.6	13.5	128.1
Osbornodon brachypus								
AMNH 8140	55.5						13.0	136.7
Osbornodon fricki								
F:AM 27563	64.0	150.2	32.0	48.9	207.4	32.5	21.9	149.4
F:AM 67098	82.0	170.0*	44.6	65.4*	223.2*	33.0	22.5	163.4
Paraenhydrocyon josephi								
AMNH 6861	47.5		19.0*			17.3		110.5
AMNH 6910	46.0	91.5	18.6	30.0		17.0	9.4	107.7
F:AM 54097					141.1	17.7	9.9	108.7*
F:AM 54106	42.9		19.3	27.5	132.7	18.3	8.8	101.3
F:AM 54107	46.3	83.0*	21.2	29.7	140.6	17.4	7.7	104.5
F:AM 54108	45.0	88.2*	19.3	32.5		20.3	10.0	
F:AM 54115	44.2	79.1	16.5	26.6	126.1	18.6	9.6	97.4
JODA 761		83.2*			138.0*	17.1	9.7	99.8
MCZ 2102	43.2	82.6	18.0	30.3		16.9	9.5	99.1
UCMP 80391					138.3	18.6	8.7	105.2
YPM 12702	48.1	90.3	26.5*	31.8	145.3	15.9	8.3	108.6
Paraenhydrocyon wallovianus								
AMNH 81086	58.6	105.8*	24.1					127.4
TMM 40879-9				37.6*	157.4*	21.0	11.0	124.4

APPENDIX II   (*Continued: cranial measurements 9--16*)

	9 LCO	10 LBS	11 LDS	12 LMO	13 LMT	14 LCT	15 WUT	16 WAC
Prohesperocyon wilsoni								
TMM 40504-126	88.3	93.6	95.8*	47.5	33.8	41.0	26.6	
Hesperocyon gregarius								
AMNH 39096	83.8	90.5	89.9	46.8	31.5	37.0	27.4	14.3
FMNH UC495	79.7	84.4	86.7	44.1	29.4	34.5	28.8	14.0
F:AM 39442	72.9			41.7	26.2	30.1	23.8	
F:AM 50260	80.5	85.5		44.5	30.1	35.8	27.5	13.1
F:AM 50276	76.2	81.1	81.1	42.1	30.0	35.0	25.9	12.2
F:AM 50325	85.6	90.1	92.1	48.8	31.1	36.8		17.6
F:AM 50345			91.3		32.0	38.8	29.6	14.9
F:AM 50351	87.0	90.5*		48.2	32.5	38.6	29.2	14.6
F:AM 63850			90.7		32.6	37.6	28.7	16.3
F:AM 63885	83.6	91.0	90.8	49.5	29.6	35.4	25.5	
F:AM 63886	81.0	87.8	88.5	45.0	32.0	37.0	29.2	14.1
F:AM 72515	91.0	96.6	99.2	51.1	34.5	40.1	33.0*	16.0
F:AM 76187	87.5	92.6	93.5	50.0	32.9	38.3	27.6	14.6
F:AM 76518	76.3	82.4	81.7	44.1	29.4	34.0	24.6	13.6
USNM 437888	76.7	81.1	82.0	41.8	29.9	35.6	26.7	13.0
"Hesperocyon" coloradensis								
KUVP 85067	96.8	104.1		55.1*	34.9*	41.8*	30.8	17.1
"Mesocyon" temnodon								
F:AM 102381					44.0	53.0		
F:AM 63367					40.0*	50.0	39.3	24.5
SDSM 2653			147.0		46.6			26.1
Mesocyon coryphaeus								
AMNH 6859	148.9	158.7	165.6	85.7	53.5	63.9	51.4	31.7
AMNH 6860	154.7	165.4		85.7	56.5	69.4	50.5	34.7
AMNH 6862					49.2	59.6	55.1	35.0
AMNH 6909	152.8	162.3	168.1	88.1	53.3	65.0	54.7	34.8
AMNH 6911					46.0	55.6	48.1	29.2
AMNH 6920			167.5		49.2	60.5		33.5
JODA 153			172.0		52.5	63.2		34.3
UCMP 75500	147.6	157.6	161.7	83.9	52.3	63.5	48.1	32.0
Mesocyon brachyops								
AMNH 6921					45.5	54.2	46.6	29.5
JODA 2399	138.6	149.0	153.4	80.2	47.5	57.1	51.3	30.1
JODA 3082	136.4			82.3*	44.3*	54.7	51.4	
UCMP 1692	128.5	134.8		74.3	45.7	54.0	48.3	29.3
Cynodesmus thooides								
BHI 1965	143.4	152.4	157.0	82.5	49.6	60.2	49.4	30.3
CMNH 792					49.6	61.0	47.0	30.8
F:AM 63382	134.8			75.8	49.1	59.8	48.1	29.5
F:AM 63386					49.5	58.8	52.7	
LACM 17076					50.6	59.7	50.5	
YPM-PU 10412					51.1	61.4	51.0	31.4
Cynodesmus martini								
UNSM 25796	162.5	175.4	183.4	96.5	53.7	68.4	62.8*	45.2

APPENDIX II *(Continued: cranial measurements 9--16)*

	9 LCO	10 LBS	11 LDS	12 LMO	13 LMT	14 LCT	15 WUT	16 WAC
Sunkahetanka geringensis								
UNSM 1092	143.9	154.7	153.8	82.6	50.5	62.1	53.3	34.4
Philotrox condoni								
F:AM 63383	161.4	172.0	181.2	95.5	53.2	63.9	59.7	37.5
LACM 15910	160.1	169.5	175.0	97.1	51.9	64.5	56.3	37.4
UCMP 76712	158.8	172.0	177.5	95.3	53.5	65.1	57.4	38.9
Enhydrocyon pahinsintewakpa								
CMNH 13588					53.0	67.9		
F:AM 27579	153.7	164.2	176.4	91.2	48.7	63.7	58.6	
F:AM 54062					51.6	65.5		
SDSM 53320	168.7	179.8	190.0	101.8	52.5	67.3	61.1	42.1
Enhydrocyon crassidens								
AMNH 12886	165.7	183.0	188.1	97.5		69.4		
F:AM 27560	166.1	178.8	181.5	98.3	53.8	67.6	66.5	·43.4
Enhydrocyon stenocephalus								
AMNH 6901	161.5	172.2	189.0	95.7	51.8	66.1		39.6
USNM 7745	166.2			99.1	50.4	67.0		
YPM 12730					47.2	61.4	62.5	37.7
Enhydrocyon basilatus								
UCMP 76749	164.5			95.9	56.6	68.6	74.5	
Osbornodon renjiei								
AMNH 1382	123.8	130.6	136.6	70.0	44.4	53.7		
AMNH 1386					44.8	52.2	36.7	22.4
Osbornodon sesnoni								
LACM 17039					48.3	58.0	45.6	
Osbornodon iamonensis								
F:AM 128763	175.9	188.4	198.0	95.5	65.7	80.0	69.0*	37.8
UM 528	164.8	174.0	175.8	96.4	57.0	69.4		
Osbornodon brachypus								
AMNH 8140	187.8	195.7		100.7	68.0*	85.0		
Osbornodon fricki								
F:AM 27563	201.5	215.8	233.9	103.5	78.0	97.8	81.2*	46.7
F:AM 67098	222.0	238.1	247.1	113.8	83.9	107.3	75.4*	52.5
Paraenhydrocyon josephi								
AMNH 6861	148.8	157.4					47.8*	
AMNH 6878					48.4	59.2	42.9	26.1
AMNH 6910	143.8			88.9	51.7	64.6	46.3	27.5
F:AM 54097	142.3*	149.6*	152.8	79.2*	52.3	63.1		
F:AM 54106	132.4	141.0	144.9	73.3	47.7	58.1		
F:AM 54107	138.6	148.0	151.4	76.9	51.4	61.2	41.2	
F:AM 54108					49.5	61.6	44.9	30.9
F:AM 54115	127.6			68.7	47.5	58.2	41.3	25.5
JODA 761	142.5	149.5	158.0*					
MCZ 2102	130.1	137.4	143.8	73.8	46.6	57.6	41.1	26.7
UCMP 80391	137.9	145.7	150.6	78.5	49.1	60.0		
YPM 12702	143.3	152.4	155.9	89.3	52.8	63.4	46.0	29.1

APPENDIX II (*Continued: cranial measurements 9–16*)

	9 LCO	10 LBS	11 LDS	12 LMO	13 LMT	14 LCT	15 WUT	16 WAC
Paraenhydrocyon robustus								
F:AM 27554					55.7	67.4		
Paraenhydrocyon wallovianus								
AMNH 81086				93.7	60.2		56.7	
TMM 40879-9	163.4	173.8	172.4*	91.3	61.1	72.7		37.3
Caedocyon tedfordi								
UW 10251					57.4	71.2	57.5*	46.2

APPENDIX II (*Continued: cranial measurements 17–24*)

	17 WPP	18 LBC	19 LMF	20 HCC	21 HCP	22 LLT	23 LHR	24 DHR
Prohesperocyon wilsoni								
TMM 40504-126		25.9	16.3		25.6*	35.9*		8.6
Hesperocyon gregarius								
AMNH 39096	10.0*	27.0	18.4	16.1	30.0*	35.8	61.0	10.1
FMNH UC495		24.0	15.8	11.7	24.0	34.9	55.9	8.6
F:AM 39442	8.2							
F:AM 50260	8.9	25.3	17.2			35.5	58.3	9.5
F:AM 50276		23.4	15.1	12.2		33.5	54.6	9.1
F:AM 50325	10.6	25.5						
F:AM 50345	9.9		17.6	13.6		37.1	61.3	10.6
F:AM 50351	10.1	25.5	17.5		26.9	35.6		10.4
F:AM 63850			17.3			36.0	59.5	9.6
F:AM 63885		27.7	18.4	14.1	28.4	35.5	58.3	9.6
F:AM 63886		27.5						
F:AM 72515	10.4	28.8						
F:AM 76187			20.0	15.1	28.6	34.5	63.0	10.0
F:AM 76518		24.0	15.6	12.1	23.7	32.9*	54.1	9.0
USNM 437888	8.7	23.5	15.0	11.0	23.3	33.8	50.3	8.6
"Hesperocyon" coloradensis								
KUVP 85067	9.1	27.5	21.0	15.1	31.5	41.8	70.0	11.5
"Mesocyon" temnodon								
AMNH 8753			28.6			49.6	88.8	15.3
F:AM 102381						54.1		
F:AM 63367	15.0		31.7	20.6	46.0	49.7		17.7
F:AM 63962						56.3		17.0
KUVP 46767						54.2		17.5
SDSM 2653	15.1							
UNSM 25690						52.5		18.5
Mesocyon coryphaeus								
AMNH 6859	18.9	42.6						
AMNH 6860	21.0				45.4	64.4		20.3
AMNH 6862	19.4							
AMNH 6909	23.3*	42.9						

APPENDIX II   *(Continued: cranial measurements 17–24)*

	17 WPP	18 LBC	19 LMF	20 HCC	21 HCP	22 LLT	23 LHR	24 DHR
Mesocyon coryphaeus (continued)								
AMNH 6911	17.4							
AMNH 6920	19.9							
JODA 153			40.9	25.2*	54.2	60.0*	116.3	
UCMP 75500	18.1	42.7						
Mesocyon brachyops								
AMNH 6921	17.2							
JODA 2399	18.1	39.6						
JODA 3082		39.5*	34.9	21.8	51.3	54.5*		18.8
UCMP 1692	18.2	36.6						
Cynodesmus thooides								
BHI 1965	17.6	41.1	37.0	23.3	50.8	59.8		
CMNH 792	16.6							
F:AM 63382			32.2	22.0*	43.5	57.6	102.0	
F:AM 63385			37.0			59.4		19.6
F:AM 63386		38.2						
LACM 17003						58.9*		
LACM 17076	18.5					62.0*		19.0
YPM-PU 10412	18.1		36.1	24.8	51.9	61.0	111.2	21.2
Cynodesmus martini								
UNSM 25796	21.8*	37.6	45.4	33.9	72.9	63.9	124.7	27.3
Sunkahetanka geringensis								
UNSM 1092	17.7	41.2	34.6	26.3	57.1	62.2	111.0	20.9
YPM-PU 13602			36.0	26.5	58.6	58.1	107.9	21.9
Philotrox condoni								
LACM 15910	21.2	46.9						
UCMP 89						61.1		20.0
UCMP 76712	19.7	43.6	44.6			63.2	120.1	24.6
Enhydrocyon pahinsintewakpa								
ACM 7645			43.3	30.5		58.5	115.5	
CMNH 13588	23.3					63.5		
F:AM 27579	20.0	41.3						
F:AM 54062						66.1		27.5
F:AM 54065			45.5	30.9		63.0	127.7	32.1
LACM 9193			54.3	35.0		63.2	136.3	29.6
SDSM 53320	23.6	48.4						
SDSM 53325			48.8	40.0	74.9	68.8	135.3	28.9
Enhydrocyon crassidens								
AMNH 12886		47.9	49.3	31.0	67.6	65.5	132.3	26.5
F:AM 27560	25.0	50.9						
F:AM 54073			51.1	33.2	73.5			
Enhydrocyon stenocephalus								
AMNH 6901	20.5	48.6						
USNM 7745		48.5						
Enhydrocyon basilatus								
F:AM 54072			46.0	30.5		68.7	132.5	30.0
UCMP 76749	20.8	48.9	44.9	33.6		68.9		29.3

APPENDIX II   (*Continued: cranial measurements 17--24*)

	17 WPP	18 LBC	19 LMF	20 HCC	21 HCP	22 LLT	23 LHR	24 DHR
Osbornodon renjiei								
AMNH 1382		39.4						
AMNH 1386	14.2							
Osbornodon sesnoni								
LACM 17039	15.6							
Osbornodon iamonensis								
F:AM 128763	23.2	44.3						
Osbornodon brachypus								
AMNH 8140		42.2	57.4	27.3	59.6	81.4	153.5*	31.4
Osbornodon fricki								
F:AM 27563	21.9	44.4	56.1	37.5		95.3	176.1	37.2
F:AM 54325			56.8	37.5	75.5	101.2	185.7	36.6
F:AM 67098	26.7	46.3						
Paraenhydrocyon josephi								
AMNH 6861		41.6						
AMNH 6878	15.2							
AMNH 6910	16.7	37.0						
F:AM 54097		40.4*	35.6	20.0		56.9	106.1	20.5
F:AM 54106		38.2	35.4	20.4	40.0	57.1	98.6	17.3
F:AM 54107	15.5	38.6						
F:AM 54108	16.6							
F:AM 54115	14.4	34.4	31.5	18.3	41.7	54.3	97.0	15.5
JODA 761		30.7*		19.5			109.2	18.9
MCZ 2102	14.7	36.6	32.6	18.0		54.6	99.2	18.0
UCMP 80391		38.5	34.1	19.3	48.4	58.5	102.7	16.7
YPM 12702	17.2	40.7	34.3	20.4*	40.9	60.8	107.9	17.0
Paraenhydrocyon robustus								
AMNH 12884						58.1		16.3
F:AM 27554			38.9			66.6	118.8	18.6
F:AM 27557				19.5		59.1	111.4	19.6
Paraenhydrocyon wallovianus								
AMNH 81086	27.1	43.6	44.4	23.5		71.2	132.4	26.0
F:AM 54050			51.2	26.8		75.3	143.0	30.1
F:AM 54110			42.6	26.0		67.5	128.8	22.6
TMM 40879-9	23.0	43.6						
Caedocyon tedfordi								
UW 10251	26.1							
Ectopocynus antiquus								
F:AM 54090						49.8		17.1
F:AM 63376						55.3		16.5
Ectopocynus intermedius								
F:AM 27580						60.7		21.7
Ectopocynus simplicidens								
F:AM 128742						71.2		32.4
F:AM 25426			52.5	31.9	60.5	61.5	137.9	30.5
F:AM 25431			43.5	26.5	58.5	66.0	133.7	28.0

APPENDIX III
Summary Statistics of Dental Measurements of Hesperocyonines
(See Method section for definition of the measurements. Units are in millimeters)

	LM2	WM2	MM2	LM1	WM1	MM1	LP4	WP4	MP4
Prohesperocyon wilsoni									
Mean (N = 1)	2.9	4.8	5.2	6.7	7.9	9.6	9.1	5.7	11.0
Hesperocyon gregarius									
Mean	3.56	4.96	5.88	6.51	7.72	9.35	8.73	5.38	10.00
Standard Deviation	0.43	0.55	0.62	0.48	0.63	0.66	0.56	0.47	0.65
Maximum	5.0	6.5	7.6	7.9	9.7	11.6	10.7	6.7	11.9
Minimum	2.6	3.6	4.4	5.2	6.3	7.7	7.6	4.3	8.4
Number	120	116	117	159	151	146	143	127	125
"Hesperocyon" pavidus									
Mean	3.17	4.50	5.30	5.23	6.25	7.62	6.77	4.00	7.10
Standard Deviation	0.17	0.14	0.08	0.19	0.25	0.27	0.60	0.00	0.30
Maximum	3.4	4.7	5.4	5.5	6.6	7.9	7.6	4.0	7.4
Minimum	3.0	4.4	5.2	5.1	6.0	7.3	6.2	4.0	6.8
Number	3	3	3	3	3	3	3	1	2
"Hesperocyon" coloradensis									
Mean	4.35	5.75	6.75	7.37	8.90	10.70	10.10	6.45	11.45
Standard Deviation	0.05	0.15	0.05	0.26	0.14	0.22	0.20	0.15	0.25
Maximum	4.4	5.9	6.8	7.6	9.0	11.0	10.3	6.6	11.7
Minimum	4.3	5.6	6.7	7.0	8.7	10.5	9.9	6.3	11.2
Number	2	2	2	3	3	3	2	2	2
"Mesocyon" temnodon									
Mean	5.50	7.44	8.80	9.67	11.20	13.53	12.50	7.67	14.08
Standard Deviation	0.32	0.59	0.51	0.67	0.85	0.99	0.83	0.52	0.89
Maximum	6.1	8.4	9.3	10.5	12.8	15.4	14.2	8.5	15.5
Minimum	5.0	6.3	7.8	8.6	9.7	11.8	11.4	6.8	13.0
Number	9	9	9	11	10	10	10	9	10
Mesocyon coryphaeus									
Mean	5.52	7.71	9.26	10.83	11.94	14.72	14.99	9.31	15.79
Standard Deviation	0.61	0.80	0.77	0.43	2.81	3.75	0.77	0.56	3.73
Maximum	6.6	8.7	10.3	11.7	14.2	16.8	16.0	10.6	18.3
Minimum	4.5	6.3	7.7	10.0	0.0	0.0	13.3	8.3	0.0
Number	14	14	14	21	20	17	21	19	20
Mesocyon brachyops									
Mean	5.37	6.90	8.48	9.99	11.80	14.92	13.82	8.86	15.60
Standard Deviation	0.49	0.53	0.66	0.49	0.60	0.76	0.79	0.68	0.84
Maximum	6.1	7.6	9.4	10.7	12.7	16.2	15.7	9.8	17.1
Minimum	4.7	6.1	7.7	9.1	10.6	13.4	12.5	7.6	14.2
Number	7	5	5	13	11	10	15	11	10
Cynodesmus thooides									
Mean	6.09	8.29	9.85	10.53	13.38	15.84	14.54	9.33	16.19
Standard Deviation	0.45	0.51	0.52	0.52	0.81	1.00	0.73	0.69	1.00
Maximum	7.0	9.0	10.9	11.4	15.2	18.0	15.4	10.6	18.0
Minimum	5.4	7.4	8.9	9.6	12.3	14.6	13.1	8.4	14.5
Number	10	11	11	11	11	11	12	12	11
Cynodesmus martini									
Mean (N = 1)	6.7	10.3	11.6	12.7	17.1	19.5	19.2	13.6	22.0

APPENDIX III (*Continued: upper teeth measurements*)

	LM2	WM2	MM2	LM1	WM1	MM1	LP4	WP4	MP4
Sunkahetanka geringensis									
Mean (N = 1)	5.30	8.30	8.90	11.50	13.50	16.60	16.00	10.30	17.20
Philotrox condoni									
Mean	5.27	7.97	9.27	10.67	13.78	16.80	16.90	10.94	18.90
Standard Deviation	0.74	1.33	2.03	0.56	0.74	0.97	0.89	0.71	0.98
Maximum	6.1	9.1	10.7	11.5	15.0	18.9	18.6	11.8	20.2
Minimum	4.3	6.1	6.4	10.0	12.7	15.9	15.4	9.8	17.1
Number	3	3	3	6	6	6	7	7	7
Enhydrocyon pahinsintewakpa									
Mean	4.97	8.02	8.88	11.39	15.46	18.54	19.34	12.48	20.43
Standard Deviation	0.46	0.98	1.15	0.83	0.96	1.43	0.94	1.21	4.06
Maximum	5.8	9.5	10.5	12.5	17.7	21.5	21.5	14.9	24.2
Minimum	4.4	6.8	7.1	9.8	14.5	16.9	18.1	10.9	10.1
Number	6	6	6	10	10	9	8	8	8
Enhydrocyon crassidens									
Mean	2.90	4.40	4.50	11.78	16.53	20.10	22.55	13.35	24.13
Standard Deviation	0.00	0.00	0.00	0.35	0.70	0.10	0.66	0.68	0.64
Maximum	2.9	4.4	4.5	12.2	17.6	20.2	23.6	14.4	25.0
Minimum	2.9	4.4	4.5	11.3	15.7	20.0	21.9	12.7	23.3
Number	1	1	1	4	4	4	4	4	4
Enhydrocyon stenocephalus									
Mean	4.00	5.30	5.60	10.15	14.40	18.10	19.30	13.00	20.30
Standard Deviation	0.00	0.00	0.00	0.45	0.50	1.50	0.00	1.50	0.00
Maximum	4.0	5.3	5.6	10.6	14.9	19.6	19.3	14.5	20.3
Minimum	4.0	5.3	5.6	9.7	13.9	16.6	19.3	11.5	20.3
Number	1	1	1	2	2	2	1	2	1
Enhydrocyon basilatus									
Mean	4.40	7.70	7.60	12.10	16.50	20.70	23.40	14.80	25.45
Standard Deviation	0.00	0.00	0.00	0.00	0.00	0.00	0.80	0.50	0.75
Maximum	4.4	7.7	7.6	12.1	16.5	20.7	24.2	15.3	26.2
Minimum	4.4	7.7	7.6	12.1	16.5	20.7	22.6	14.3	24.7
Number	1	1	1	1	1	1	2	2	2
Osbornodon renjiei									
Mean	5.73	7.00	8.45	8.54	10.20	12.10	11.24	7.50	12.70
Standard Deviation	0.45	0.34	0.70	0.21	0.67	0.70	0.39	0.42	0.65
Maximum	6.1	7.4	9.1	8.9	11.2	13.1	11.8	7.9	13.7
Minimum	5.0	6.5	7.3	8.3	9.3	11.1	10.8	6.6	12.0
Number	4	4	4	5	5	5	5	6	5
Osbornodon sesnoni									
Mean	6.05	8.30	9.85	10.10	11.60	13.60	13.35	8.60	15.40
Standard Deviation	0.25	0.30	0.45	0.00	0.00	0.00	0.35	0.00	0.00
Maximum	6.3	8.6	10.3	10.1	11.6	13.6	13.7	8.6	15.4
Minimum	5.8	8.0	9.4	10.1	11.6	13.6	13.0	8.6	15.4
Number	2	2	2	1	1	1	2	1	1

APPENDIX III *(Continued: upper teeth measurements)*

	LM2	WM2	MM2	LM1	WM1	MM1	LP4	WP4	MP4
Osbornodon iamonensis									
Mean	7.01	9.66	11.01	11.94	14.43	16.93	18.03	10.37	19.44
Standard Deviation	0.60	1.01	1.22	0.98	1.01	1.34	1.36	1.07	1.59
Maximum	8.0	12.0	13.0	13.3	16.2	18.7	19.6	12.2	21.8
Minimum	5.6	7.9	8.7	10.0	12.2	13.7	14.6	8.5	15.7
Number	16	16	15	16	15	15	14	14	14
Osbornodon fricki									
Mean	9.24	12.41	14.54	16.48	19.98	22.43	25.52	14.04	26.76
Standard Deviation	0.67	1.10	1.22	0.99	1.27	1.11	0.70	0.43	0.77
Maximum	10.0	14.0	16.0	18.0	22.0	24.8	26.6	14.9	28.0
Minimum	8.0	11.0	11.9	14.5	17.3	20.7	24.3	13.4	25.5
Number	7	7	7	14	14	13	10	10	10
Paraenhydrocyon josephi									
Mean	5.25	7.50	8.76	9.65	11.51	14.03	13.24	7.95	14.66
Standard Deviation	0.43	0.51	0.66	0.51	0.55	0.74	0.63	0.57	0.82
Maximum	5.9	8.3	9.9	10.5	12.4	15.6	14.4	9.1	15.6
Minimum	4.5	6.5	7.4	8.8	10.7	12.9	12.3	7.0	13.1
Number	11	11	11	13	12	12	12	11	11
Paraenhydrocyon robustus									
Mean (N = 1)	5.00	7.90	8.90	11.60	13.00	16.20	15.60	9.70	17.50
Paraenhydrocyon wallovianus									
Mean	5.68	8.78	9.85	12.26	14.58	17.64	17.58	10.76	19.28
Standard Deviation	0.38	0.25	0.21	0.60	0.62	0.71	0.78	0.45	0.65
Maximum	6.1	9.2	10.0	12.7	15.6	18.8	18.2	11.6	20.4
Minimum	5.1	8.6	9.5	11.1	14.0	16.6	16.1	10.3	18.6
Number	4	4	4	5	5	5	5	5	5
Caedocyon tedfordi									
Mean (N = 1)	4.00	6.10	6.10	10.40	14.30	15.10	17.10	11.50	17.70
Ectopocynus intermedius									
Mean (N = 1)	4.40	6.90	8.60	10.90	13.70	17.30	18.20	12.20	19.70

APPENDIX III (*Continued: lower teeth measurements*)

	Lm3	Wm3	Lm2	Wm2	Tm2	Lm1	Wm1	Tm1
Prohesperocyon wilsoni								
Mean (N = 1)	2.0	1.6	4.5	2.6	2.8	9.1	4.6	6.0
Hesperocyon gregarius								
Mean	2.61	2.04	4.92	3.28	2.73	9.37	4.24	6.27
Standard Deviation	0.37	0.25	0.42	0.31	0.27	0.64	0.32	0.49
Maximum	3.2	2.8	6.2	4.4	3.7	11.3	5.7	7.6
Minimum	1.6	1.5	3.1	1.9	2.0	7.7	3.3	5.1
Number	55	55	280	273	273	415	412	408
"Hesperocyon" pavidus								
Mean	2.15	1.75	4.14	2.81	2.14	7.29	3.25	4.81
Standard Deviation	0.05	0.15	0.29	0.17	0.24	0.42	0.21	0.31
Maximum	2.2	1.9	4.7	3.1	2.5	7.8	3.6	5.2
Minimum	2.1	1.6	3.8	2.6	1.8	6.7	3.0	4.2
Number	2	2	9	8	8	7	6	7
"Hesperocyon" coloradensis								
Mean			5.93	3.85	3.05	11.04	5.07	7.06
Standard Deviation			0.16	0.13	0.18	0.42	0.19	0.19
Maximum			6.2	4.0	3.4	11.5	5.3	7.2
Minimum			5.8	3.7	2.8	10.4	4.8	6.7
Number			6	6	6	5	6	5
"Mesocyon" temnodon								
Mean	4.17	3.09	7.23	4.68	3.78	13.78	6.01	9.34
Standard Deviation	0.39	0.37	0.61	0.23	0.38	0.61	0.35	0.51
Maximum	4.7	3.7	8.5	5.1	4.4	14.8	6.6	10.6
Minimum	3.7	2.5	6.6	4.2	3.1	12.2	5.2	8.4
Number	7	7	12	12	12	17	17	16
Mesocyon coryphaeus								
Mean	4.90	3.85	7.65	5.52	4.60	16.75	7.35	11.73
Standard Deviation	0.37	0.23	0.50	0.24	0.28	0.82	0.37	0.66
Maximum	5.2	4.2	8.6	5.8	5.0	18.4	7.9	12.8
Minimum	4.3	3.6	7.0	5.1	4.2	15.5	6.7	10.9
Number	4	4	6	6	6	10	11	10
Mesocyon brachyops								
Mean	4.46	3.35	7.10	4.88	4.02	14.63	6.44	10.37
Standard Deviation	0.19	0.15	0.33	0.25	0.15	0.76	0.36	0.50
Maximum	4.6	3.5	7.7	5.2	4.1	16.1	7.0	11.3
Minimum	4.1	3.2	6.7	4.5	3.7	13.6	5.8	9.6
Number	5	4	7	6	6	8	10	10
Cynodesmus thooides								
Mean	4.84	3.62	8.04	5.60	4.63	15.97	6.94	10.98
Standard Deviation	0.34	0.20	0.46	0.21	0.10	0.77	0.39	0.70
Maximum	5.2	3.9	8.9	5.8	4.8	17.2	7.4	12.2
Minimum	4.4	3.3	7.6	5.2	4.5	14.6	6.1	9.8
Number	5	5	7	8	7	9	10	9
Cynodesmus martini								
Mean (N = 1)	6.2	4.7	9.1	6.3	4.6	20.1	9.0	15.5

APPENDIX III (*Continued: lower teeth measurements*)

	Lm3	Wm3	Lm2	Wm2	Tm2	Lm1	Wm1	Tm1
Sunkahetanka geringensis								
Mean	4.87	3.87	8.57	5.47	5.37	17.63	8.05	13.08
Standard Deviation	0.26	0.41	0.29	0.21	0.26	0.38	0.17	0.44
Maximum	5.1	4.4	8.9	5.7	5.6	18.0	8.3	13.5
Minimum	4.5	3.4	8.2	5.2	5.0	17.0	7.9	12.5
Number	3	3	3	3	3	4	4	4
Philotrox condoni								
Mean	3.95	8.50	5.45	5.35	18.28	8.07	13.40	
Standard Deviation	0.05	0.50	0.05	0.25	0.73	0.33	0.27	
Maximum	4.0	9.0	5.5	5.6	19.0	8.5	13.7	
Minimum	3.9	8.0	5.4	5.1	17.2	7.7	13.0	
Number	2	2	2	2	4	3	4	
Enhydrocyon pahinsintewakpa								
Mean	4.31	3.61	8.00	5.90	4.52	20.62	9.25	15.45
Standard Deviation	0.55	0.42	0.45	0.25	0.41	1.00	0.58	0.90
Maximum	5.2	4.4	8.8	6.3	5.2	22.1	10.7	17.0
Minimum	3.7	3.1	7.1	5.4	3.7	18.6	8.1	13.8
Number	8	8	10	10	10	13	13	13
Enhydrocyon crassidens								
Mean			7.83	5.73	4.43	23.25	9.84	17.82
Standard Deviation			0.71	0.33	0.17	1.16	0.31	1.41
Maximum			8.8	6.1	4.6	25.6	10.3	20.3
Minimum			7.1	5.3	4.2	21.9	9.5	15.9
Number			3	4	3	6	5	5
Enhydrocyon stenocephalus								
Mean (N = 1)				6.30	5.40	20.00	10.30	15.50
Enhydrocyon basilatus								
Mean	4.00	4.20	8.95	6.55	4.95	24.50	10.80	19.10
Standard Deviation	0.00	0.00	0.55	0.15	0.25	0.90	0.10	0.40
Maximum	4.0	4.2	9.5	6.7	5.2	25.4	10.9	19.5
Minimum	4.0	4.2	8.4	6.4	4.7	23.6	10.7	18.7
Number	1	1	2	2	2	2	2	2
Osbornodon renjiei								
Mean	3.50	2.70	6.35	4.40	3.30	12.33	5.75	8.23
Standard Deviation	0.00	0.00	0.35	0.10	0.10	0.66	0.17	0.38
Maximum	3.5	2.7	6.7	4.5	3.4	12.9	6.0	8.5
Minimum	3.5	2.7	6.0	4.3	3.2	11.4	5.6	7.7
Number	1	1	2	2	2	3	4	3
Osbornodon sesnoni								
Mean	4.70	4.00	8.20	4.85	4.50	14.97	6.53	10.13
Standard Deviation	0.00	0.00	0.10	0.05	0.00	0.34	0.33	0.24
Maximum	4.7	4.0	8.3	4.9	4.5	15.3	6.9	10.3
Minimum	4.7	4.0	8.1	4.8	4.5	14.5	6.2	9.8
Number	1	1	2	2	1	3	4	3

APPENDIX III (*Continued: lower teeth measurements*)

	Lm3	Wm3	Lm2	Wm2	Tm2	Lm1	Wm1	Tm1
Osbornodon iamonensis								
Mean			9.94	6.27	5.47	19.93	8.36	13.58
Standard Deviation			0.75	0.39	0.47	1.06	0.37	0.71
Maximum			11.5	7.0	6.3	21.5	9.0	14.6
Minimum			8.8	5.7	4.8	17.4	7.5	12.3
Number			10	9	9	11	11	11
Osbornodon fricki								
Mean	7.00	5.88	12.79	8.23	7.11	27.88	11.69	20.23
Standard Deviation	0.54	0.36	0.68	0.52	0.56	1.11	0.63	0.97
Maximum	7.8	6.5	14.1	8.9	8.4	29.7	12.9	21.8
Minimum	6.3	5.6	11.5	7.4	6.3	26.0	10.6	19.0
Number	4	4	16	15	14	16	16	16
Paraenhydrocyon josephi								
Mean	4.45	3.37	7.26	4.75	4.29	14.57	6.23	10.01
Standard Deviation	0.47	0.30	0.54	0.40	0.37	1.01	0.54	0.77
Maximum	5.5	4.1	8.1	5.5	5.1	16.5	7.3	11.1
Minimum	3.9	3.0	6.3	4.1	3.8	13.0	5.4	8.8
Number	13	13	11	12	11	15	16	15
Paraenhydrocyon robustus								
Mean	4.30	3.30	7.40	4.90	4.40	15.80	6.70	11.10
Standard Deviation	0.50	0.43	0.65	0.45	0.50	1.59	0.51	1.02
Maximum	4.7	3.7	8.0	5.4	5.1	18.0	7.4	12.5
Minimum	3.6	2.7	6.5	4.3	4.0	14.3	6.2	10.1
Number	3	3	3	3	3	3	3	3
Paraenhydrocyon wallovianus								
Mean	5.45	4.25	8.45	5.78	5.70	19.83	8.53	14.07
Standard Deviation	0.45	0.45	0.65	0.33	0.14	1.25	0.18	0.68
Maximum	5.9	4.7	9.2	6.3	5.9	21.0	8.7	14.6
Minimum	5.0	3.8	7.4	5.4	5.6	18.1	8.3	13.1
Number	2	2	4	4	3	3	4	3
Ectopocynus antiquus								
Mean	3.00	2.50	7.00	4.50	3.80	14.90	6.35	10.65
Standard Deviation	0.00	0.00	0.90	0.40	0.90	0.60	0.25	0.05
Maximum	3.0	2.5	7.9	4.9	4.7	15.5	6.6	10.7
Minimum	3.0	2.5	6.1	4.1	2.9	14.3	6.1	10.6
Number	1	1	2	2	2	2	2	2
Ectopocynus intermedius								
Mean (N = 1)	4.60	3.80	8.80	5.50	4.90	18.70	8.90	13.90
Ectopocynus simplicidens								
Mean			10.40	6.73	6.20	22.03	10.13	15.93
Standard Deviation			0.64	0.33	0.08	1.41	0.86	1.43
Maximum			11.3	7.1	6.3	23.9	11.2	17.4
Minimum			9.9	6.3	6.1	20.5	9.1	14.0
Number			3	3	3	3	3	3

APPENDIX III   (*Continued: lower teeth measurements*)

	Lp4	Wp4	Lp3	Wp3	Lp2	Wp2	Lc1	Wc1
Prohesperocyon wilsoni								
Mean (N = 1)	6.8	2.6	6.2	2.2	4.8	1.7		
Hesperocyon gregarius								
Mean	6.19	2.75	5.51	2.34	4.71	1.95	3.91	2.77
Standard Deviation	0.44	0.25	0.41	0.21	0.40	0.18	0.39	0.30
Maximum	7.8	3.5	6.5	3.0	5.8	2.4	4.5	3.5
Minimum	5.1	2.3	4.2	1.8	4.0	1.6	3.2	2.2
Number	247	238	130	120	87	82	35	33
"Hesperocyon" pavidus								
Mean	5.21	2.23	4.63	1.90	3.85	1.56	2.70	2.15
Standard Deviation	0.63	0.13	0.58	0.10	0.30	0.04	0.20	0.15
Maximum	6.1	2.4	5.5	2.0	4.2	1.6	2.9	2.3
Minimum	4.5	2.1	4.1	1.8	3.5	1.5	2.5	2.0
Number	4	5	4	4	4	4	2	2
"Hesperocyon" coloradensis								
Mean	7.22	3.34	6.25	2.77	5.75	2.35	5.50	3.90
Standard Deviation	0.43	0.19	0.05	0.12	0.45	0.15	0.60	0.20
Maximum	7.8	3.5	6.3	2.9	6.2	2.5	6.1	4.1
Minimum	6.6	3.0	6.2	2.6	5.3	2.2	4.9	3.7
Number	5	5	2	3	2	2	2	2
"Mesocyon" temnodon								
Mean	9.11	4.17	8.06	3.69	7.11	3.11	6.98	4.84
Standard Deviation	0.41	0.25	0.61	0.22	0.51	0.28	0.81	0.55
Maximum	10.1	4.5	8.5	4.0	7.8	3.5	8.2	5.7
Minimum	8.3	3.7	6.6	3.2	6.1	2.6	6.2	4.2
Number	15	15	8	8	9	9	4	5
Mesocyon coryphaeus								
Mean	10.45	5.30	9.43	4.60	8.03	3.93	9.30	6.60
Standard Deviation	0.54	0.31	0.60	0.16	0.33	0.25	0.71	0.49
Maximum	11.1	5.7	9.9	4.8	8.4	4.2	10.3	7.2
Minimum	9.7	4.8	8.4	4.4	7.6	3.6	8.7	6.0
Number	6	7	4	3	3	3	3	3
Mesocyon brachyops								
Mean	9.55	4.77	7.93	4.22	6.95	3.62	8.43	5.63
Standard Deviation	0.36	0.30	0.32	0.17	0.49	0.17	0.89	0.34
Maximum	10.0	5.4	8.5	4.5	7.7	3.8	9.9	6.1
Minimum	8.9	4.2	7.5	4.0	6.3	3.3	7.6	5.3
Number	10	11	6	5	6	5	6	6
Cynodesmus thooides								
Mean	10.06	5.21	8.79	4.74	7.73	3.99	8.45	6.05
Standard Deviation	0.51	0.41	0.26	0.29	0.48	0.19	0.45	0.35
Maximum	11.0	6.0	9.4	5.1	8.3	4.2	8.9	6.4
Minimum	9.4	4.6	8.6	4.3	6.9	3.6	8.0	5.7
Number	9	7	7	7	6	7	2	2
Cynodesmus martini								
Mean (N = 1)	12.0	7.2					13.2	9.8

APPENDIX III (*Continued: lower teeth measurements*)

	Lp4	Wp4	Lp3	Wp3	Lp2	Wp2	Lc1	Wc1
Sunkahetanka geringensis								
Mean	11.0	6.13	9.27	5.40	8.15	5.00	10.15	7.40
Standard Deviation	0.57	0.31	0.76	0.22	0.15	0.40	0.25	0.10
Maximum	11.5	6.6	10.3	5.6	8.3	5.4	10.4	7.5
Minimum	10.2	5.8	8.5	5.1	8.0	4.6	9.9	7.3
Number	3	4	3	3	2	2	2	2
Philotrox condoni								
Mean	11.24	6.48	9.63	5.68	8.65	5.15	11.20	8.03
Standard Deviation	0.21	0.30	0.28	0.15	0.05	0.05	0.51	0.12
Maximum	11.6	6.9	10.1	5.9	8.7	5.2	11.7	8.2
Minimum	11.0	6.1	9.4	5.5	8.6	5.1	10.5	7.9
Number	5	4	4	4	2	2	3	3
Enhydrocyon pahinsintewakpa								
Mean	12.47	7.29	10.17	6.35	8.31	5.14	12.46	9.03
Standard Deviation	0.66	0.51	0.50	0.59	0.47	0.31	0.75	0.43
Maximum	13.5	8.0	11.0	7.2	9.0	5.7	13.9	9.7
Minimum	11.0	6.0	9.3	5.5	7.6	4.7	11.5	8.3
Number	13	13	10	10	10	11	7	7
Enhydrocyon crassidens								
Mean	13.97	8.13	10.90	6.67	7.70	4.50	13.20	9.95
Standard Deviation	0.31	0.09	0.29	0.49	0.00	0.00	0.50	0.25
Maximum	14.4	8.2	11.3	7.3	7.7	4.5	13.7	10.2
Minimum	13.7	8.0	10.6	6.1	7.7	4.5	12.7	9.7
Number	3	3	3	3	1	1	2	2
Enhydrocyon stenocephalus								
Mean (N = 1)	13.4	7.3	10.3	6.1				
Enhydrocyon basilatus								
Mean	16.60	9.55	12.57	7.77	9.47	5.70	14.55	11.00
Standard Deviation	0.50	0.35	0.50	0.12	0.74	0.37	0.15	0.20
Maximum	17.1	9.9	13.1	7.9	10.4	6.2	14.7	11.2
Minimum	16.1	9.2	11.9	7.6	8.6	5.3	14.4	10.8
Number	2	2	3	3	3	3	2	2
Osbornodon renjiei								
Mean	8.30	3.80	7.23	3.18	6.37	2.73	6.25	4.35
Standard Deviation	0.57	0.25	0.59	0.23	0.40	0.12	0.35	0.35
Maximum	9.0	4.1	7.7	3.4	6.7	2.9	6.6	4.7
Minimum	7.6	3.5	6.4	2.9	5.8	2.6	5.9	4.0
Number	4	4	3	4	3	3	2	2
Osbornodon sesnoni								
Mean	10.05	4.70	8.35	3.60	7.45	2.70	8.40	
Standard Deviation	0.25	0.28	0.05	0.14	0.35	0.20	0.00	
Maximum	10.3	5.1	8.4	3.8	7.8	2.9	8.4	
Minimum	9.8	4.5	8.3	3.5	7.1	2.5	8.4	
Number	2	3	2	3	2	2	1	

APPENDIX III (*Continued: lower teeth measurements*)

	Lp4	Wp4	Lp3	Wp3	Lp2	Wp2	Lc1	Wc1
Osbornodon iamonensis								
Mean	11.87	6.32	10.01	5.07	8.68	4.43	9.20	6.80
Standard Deviation	0.51	0.46	0.94	0.69	0.33	0.47	0.00	0.00
Maximum	12.5	7.0	12.2	6.5	9.0	5.1	9.2	6.8
Minimum	10.9	5.4	9.2	4.3	8.3	3.9	9.2	6.8
Number	10	10	7	7	4	4	1	1
Osbornodon fricki								
Mean	16.61	8.99	12.30	6.86	12.11	6.80	16.06	11.80
Standard Deviation	0.84	0.53	1.06	0.37	0.73	0.51	1.43	0.68
Maximum	17.8	9.9	14.4	7.6	13.1	7.5	18.5	13.1
Minimum	14.9	8.1	11.2	6.3	11.1	6.1	14.1	11.2
Number	16	15	8	8	7	7	5	5
Paraenhydrocyon josephi								
Mean	9.81	4.49	8.53	4.11	7.51	3.43	8.00	5.84
Standard Deviation	0.53	0.37	0.63	0.40	0.44	0.30	0.61	0.40
Maximum	11.1	5.2	9.7	4.8	8.2	4.1	9.3	6.5
Minimum	8.9	3.8	7.1	3.5	6.9	3.0	7.3	5.4
Number	15	16	12	12	12	12	8	8
Paraenhydrocyon robustus								
Mean	10.27	4.97	8.70	4.77	7.97	3.97	9.57	6.90
Standard Deviation	0.79	0.34	0.59	0.53	0.45	0.29	0.45	0.29
Maximum	11.1	5.3	9.5	5.4	8.5	4.3	10.2	7.2
Minimum	9.2	4.5	8.1	4.1	7.4	3.6	9.2	6.5
Number	3	3	3	3	3	3	3	3
Paraenhydrocyon wallovianus								
Mean	12.70	6.27	10.85	5.70	9.20	4.50	5.85	4.05
Standard Deviation	0.22	0.53	0.15	0.86	0.41	0.70	0.85	0.95
Maximum	13.0	6.9	11.0	6.9	9.8	5.6	6.7	5.0
Minimum	12.5	5.6	10.7	4.9	8.7	3.7	5.0	3.1
Number	3	3	2	3	4	4	2	2
Ectopocynus antiquus								
Mean	9.35	4.80	8.70	4.40	6.95	3.75	7.50	5.30
Standard Deviation	0.25	0.00	0.00	0.00	0.45	0.05	0.00	0.00
Maximum	9.6	4.8	8.7	4.4	7.4	3.8	7.5	5.3
Minimum	9.1	4.8	8.7	4.4	6.5	3.7	7.5	5.3
Number	2	2	1	1	2	2	1	1
Ectopocynus intermedius								
Mean (N = 1)	12.50	6.70	9.80	5.60	7.40	5.00		
Ectopocynus simplicidens								
Mean	13.87	8.83	10.80	7.00	10.00	6.43	13.53	10.00
Standard Deviation	0.83	1.11	0.14	0.75	0.28	0.52	2.03	0.57
Maximum	14.6	10.1	10.9	7.8	10.2	6.9	16.4	10.5
Minimum	12.7	7.4	10.6	6.0	9.6	5.7	12.1	9.2
Number	3	3	3	3	3	3	3	3