Chapter 9

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Chapter 9

Carnivora (Mammalia, Felidae, Canidae, and Mustelidae) From the Earliest Hemphillian Screw Bean Local Fauna, Big Bend National Park, Brewster County, Texas

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ABSTRACT

The Screw Bean Local Fauna is the earliest Hemphillian fauna of the southwestern United States. The fossil remains occur in all parts of the informal Banta Shut-in formation, nowhere very fossiliferous. The formation is informally subdivided on the basis of stepwise fining and slowing deposition into Lower (least fossiliferous), Middle, and Red clay members, succeeded by the valley-filling, Bench member (most fossiliferous).

Identified Carnivora include: cf. *Pseudaelurus* sp. and cf. *Nimravides catocopis*, medium and large extinct cats; *Epicyon haydeni*, large borophagine dog; *Vulpes* sp., small fox; cf. *Eucyon* sp., extinct primitive canine; *Buisnictis chisoensis*, n. sp., extinct skunk; and *Martes* sp., marten. *B. chisoensis* may be allied with *Spilogale* on the basis of mastoid specialization. Some of the Screw Bean taxa are late survivors of the Clarendonian Chronofauna, which extended through most or all of the early Hemphillian. The early early Hemphillian, late Miocene age attributed to the fauna is based on the Screw Bean assemblage postdating oreodont and predating North American edentate occurrences, on lack of defining Hemphillian taxa, and on stage of evolution.

INTRODUCTION

NAMING AND IMPORTANCE OF THE SCREW BEAN LOCAL FAUNA: The name ''Screw Bean Local Fauna,'' Banta Shut-in formation, Trans-Pecos Texas (fig. 9.1), was introduced by Stevens and Stevens (1989: 77). The name, misprinted as Screw ''Beam'' in Janis et al. (1998b: 636), comes from ''tornillo,'' Spanish for screw, or, in local context, from the tightly coiled seedpods of the screw-bean mesquite, common along some local arroyos. To date, the Screw Bean Local Fauna contains 4 taxa of lower and 18 taxa of higher vertebrates. Considered together, the fossils indicate a late Miocene age (early early Hemphillian) that is not widely found in southwestern North America, and fill a paleobiogeographic gap. In Trans-Pecos Texas and adjacent Chihuahua and Coahuila, Mexico, they provide an age determination for postvolcanic (<18–20 Ma; Henry et al., 1998) rocks (Banta Shut-in formation; Stevens and Stevens, 1989) that contain them. Rocks of the interval between the earliest Miocene (bolsons, the Big Bend area; Stevens et al., 1969; Stevens, 1977), and the late Pliocene–early Pleistocene (Blancan bolson fills, western Trans-Pecos Texas; Strain, 1966, 1980; Akersten, 1972) were previously unknown in the region. The tectonic importance of the age and body of rock is shown in discussions of the Texas Lineament, the
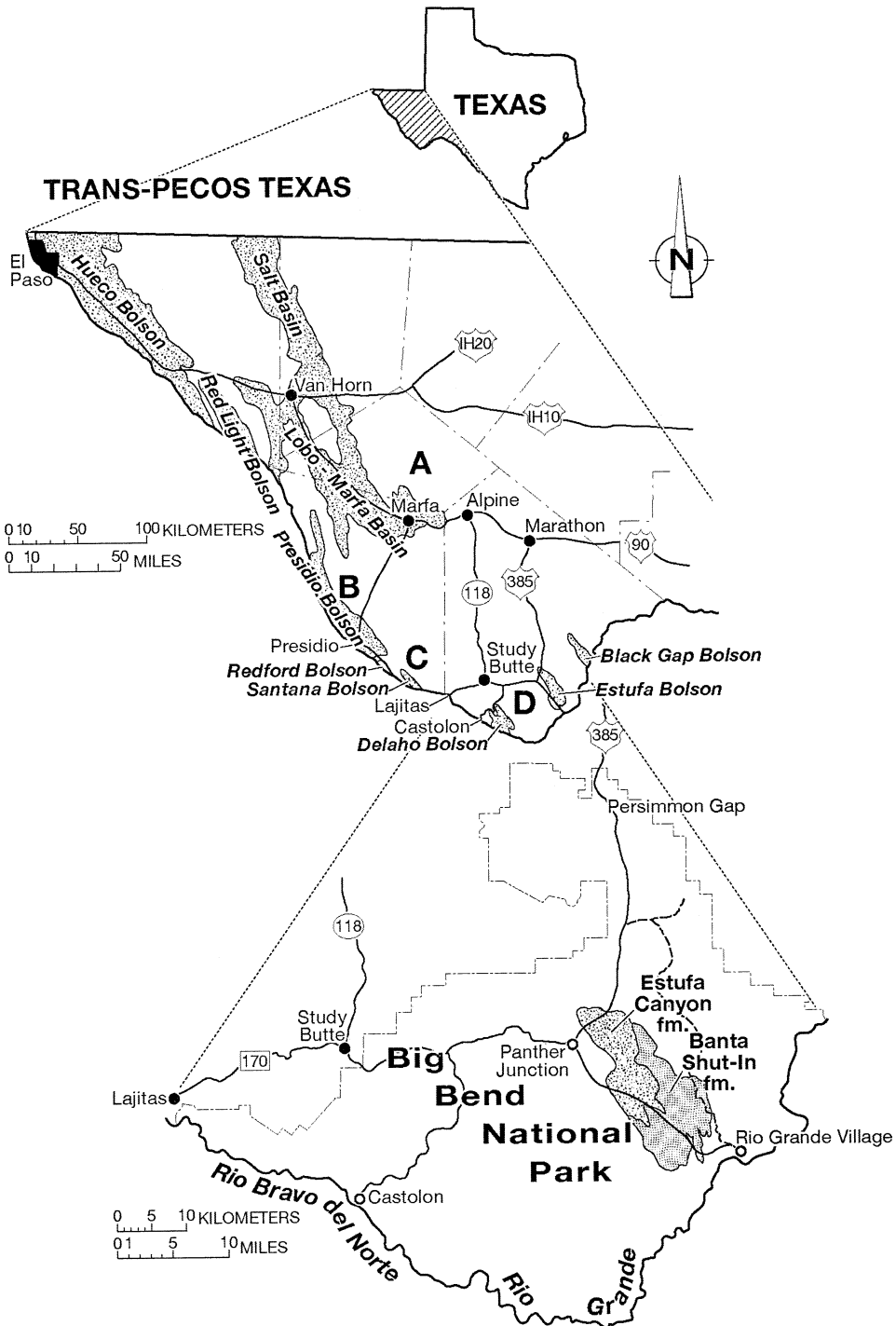

Fig. 9.1.   Index map of Texas, Trans-Pecos Texas, and the Big Bend, progressively enlarged. Major Neogene bolsons are indicated: **A,** Davis Mountains; **B,** Chinati; **C,** Bofecillos; and **D,** Chisos Mountains volcanic centers.

eastern Basin and Range Province, and the Rio Grande Rift and related areas (e.g., Dickerson and Muehlberger, 1994; Henry, 1998; Stewart, 1998; Henry and Aranda-Gomez, 2000). This paper reports the fossil carnivores from these rocks, and presents a local informal stratigraphy sufficient to place them in stratigraphic position and in depositional context.

DISCOVERY AND DISPOSITION OF FOSSILS: The first late Miocene fossils found in Trans-Pecos Texas were discovered in 1980 by Jim Liles, Chief Ranger, Big Bend National Park. Mr. Liles reported the fossils to Dr. Wann Langston, Jr., then Director of the Vertebrate Paleontology Laboratory, The University of Texas at Austin. Dr. Langston was helicoptered into the initial fossil site, TMM 42247 (Liles measured section; fig. 9.2F), collected more specimens, and documented its location. We have collected more fossils since 1980. Supraspecific classification used in this paper follows that suggested by McKenna and Bell (1997).

All fossils and rock samples were collected in accordance with regulations outlined by collecting permits, 1980–1997, issued to the Vertebrate Paleontology Laboratory, Balcones Research Center, The University of Texas at Austin, by the United States Department of the Interior. Other permits were issued directly to us by Science and Resources Management, Big Bend National Park, 1998–2000. All specimens are preserved in the TMM collections; measurements in millimeters. This paper is a contribution of the Vertebrate Paleontology Laboratory, The University of Texas at Austin. Systematic descriptions are the responsibility of MSS, and JBS is responsible for discussion of stratigraphy and geologic setting.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York
DMNH	Denver Museum of Natural History, Denver
F:AM	Frick Collection, AMNH, New York
KUMNH	University of Kansas Museum of Natural History, Lawrence
KUMVP	University of Kansas Museum of Vertebrate Paleontology, Lawrence
LACM	Los Angeles County Museum, Los Angeles
MU	Midwestern University Department of Mammalogy, Wichita Falls
MUC:FV	Midwestern University Collection, Fossil Vertebrates, Wichita Falls
TMM	Texas Memorial Museum, The University of Texas at Austin
UF	University of Florida, Gainesville
UO	University of Oregon, Eugene
UCMP	University of California Museum of Paleontology, Berkeley
UMMP	University of Michigan Museum of Paleontology, Ann Arbor
UOMP	University of Oklahoma Museum of Paleontology, Norman
USNM	United States National Museum, Smithsonian Institution, Washington, D.C.
WTM	West Texas Museum, West Texas State University, Canyon

MEASUREMENTS

AP	Anteroposterior diameter
T	Transverse diameter
alv	Alveolar measurement
*	Measurement approximate
**	Measurement estimated
()	Minimum measurement, as preserved

GEOLOGIC SETTING AND STRATIGRAPHY

PREVIOUS WORK: Neogene sediments of Trans-Pecos Texas (fig. 9.1) have long been associated with basins formed by extensional faulting (Hill, 1900; Tolman, 1909; Groat, 1972). Udden (1907) was the first to call attention to sediments of this kind in the Dugout Wells–Lower Tornillo Creek area (figs. 9.3, 9.4), Big Bend National Park, Texas. He noted the conspicuous twofold lithology of the deposits, and called them the Dugout clays and gravels. Placement of the roads (now abandoned) that Udden traveled make probable the identification of the "clays" as the rocks we call the Banta Shut-in formation. The "gravels" probably refers to coarse deposits of a considerably younger system of composite alluvial fans (informally, Estufa Canyon formation). Maxwell et al. (1967: pl. II, 152–153) mapped the Dugout clays and gravels as Quaternary-Tertiary older gravels, but correlated the "gravels" portion with undoubted Pleistocene deposits near Grapevine Springs. Thurwachter (1984a, 1984b, 1984c) studied the sedimentology of these "older gravels." He viewed the "clays" and "grav-
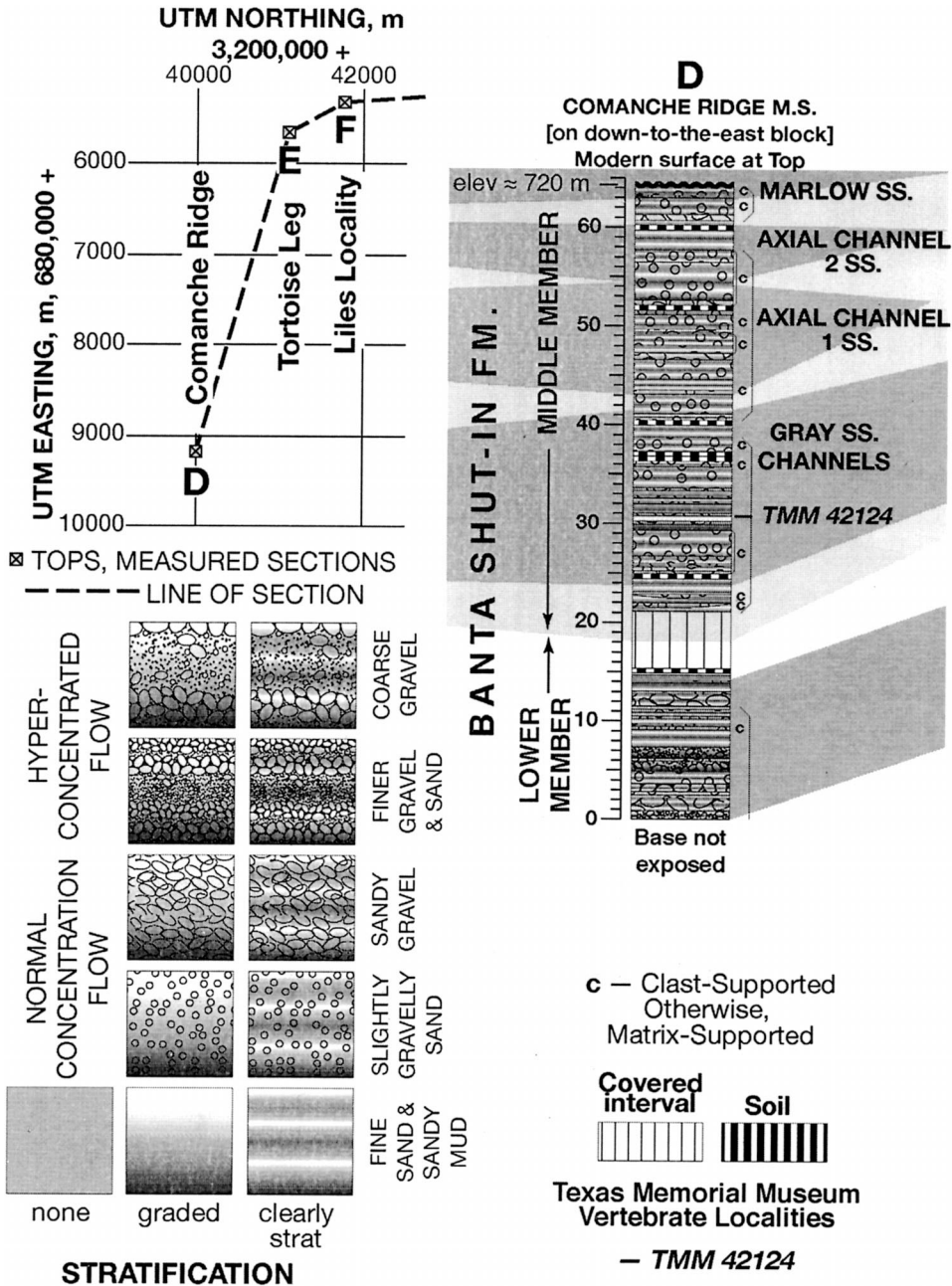
Fig. 9.2.   Measured sections that show the localities from which fossil Carnivora were recovered, and informal members and key beds of the Banta Shut-in formation, Big Bend National Park, Texas. The top part of section D correlates with the bottom part for section E. Location and orientation of the traverses used in measuring sections is shown on figure 9.3A. Universal Transverse Mercator (UTM) coordinates of the section-tops are shown on the insert, upper left. Explanation of the lithologic symbols appears in the insert, lower left. Use of the term ''hyperconcentrated flow'' follows Coussot and Meunier (1996), Chien and Wan (1999), and Wan and Wang (1994). Vertical exaggeration is 28.7×.

Fig. 9.2.   Continued.

B
Geologic Map

C
Joint Set

A
Location of some Measured Sections

els'' as the result of two depositional, basin-filling events, and, in part, mapped them separately. Because his mapping units were established on the basis of depositional styles that recurred at various times, he included late Miocene, ?Blancan, and late Pleistocene deposits in the same unit (''faci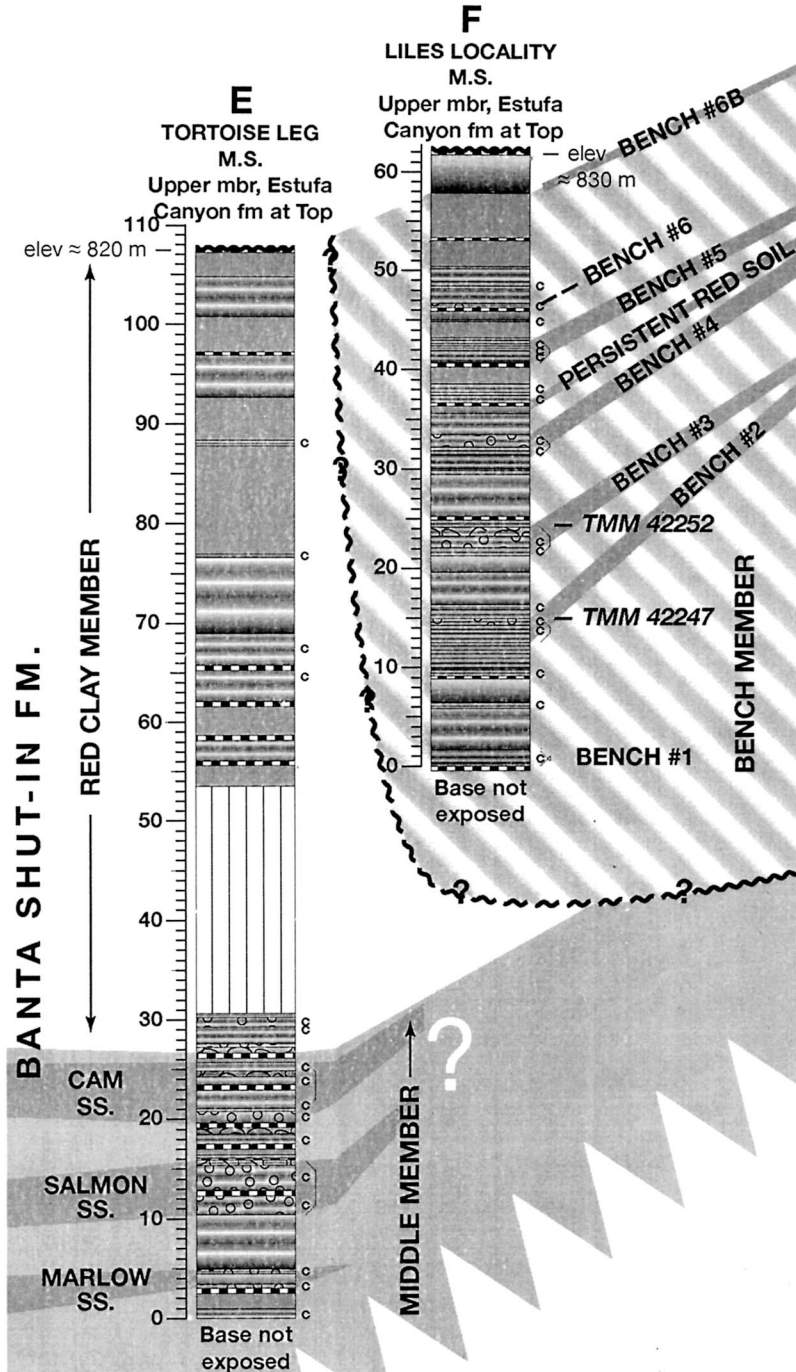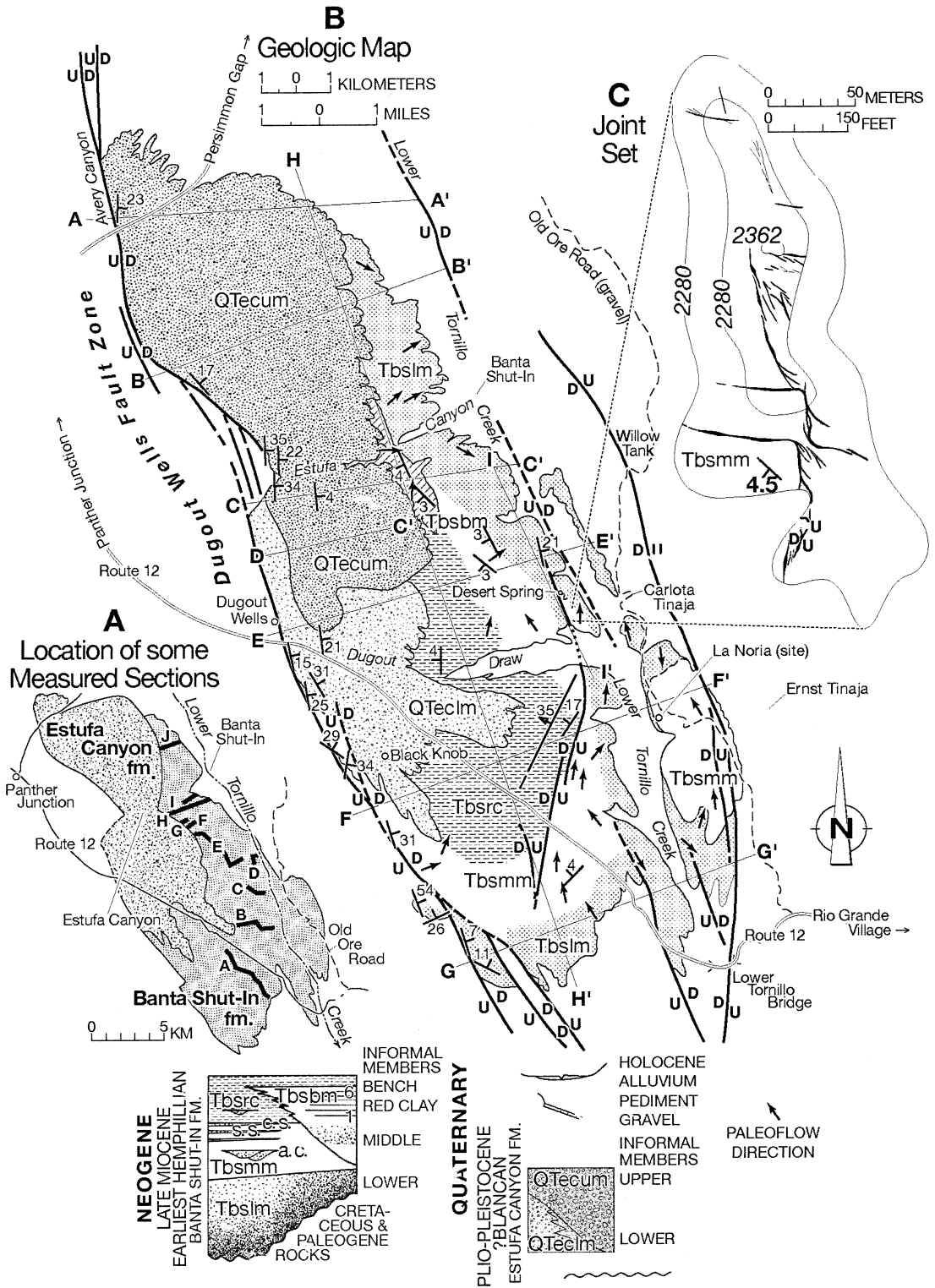es,'' or ''member'') in some places. Thurwachter (1984c) called the ''clays,'' ''La Noria member,'' and the gravels ''Estufa member,'' but did not assign a formation name. His ''members'' do not entirely coincide with any units we recognize.

TECTONIC AND STRUCTURAL RELATIONSHIPS OF LATE MIOCENE ROCKS: King (1935: 251–261) considered the initiation of normal faulting and associated basin filling to be ''later Tertiary (Miocene or Pliocene),'' noted that movement on the faults continued into recent times, and commented on the absence of a major through-flowing stream during basin formation and filling and the later integration of the Rio Grande system. These points stand refined today, but only slightly modified (e.g., Muehlberger et al., 1978; Stevens and Stevens, 1985, 1989, 1990; Xie, 1998; Henry et al., 1998). Tectonic and structural geology of the area has been the subject of a number of studies, the most pertinent of which are those of Muehlberger (1989), Dickerson and Muehlberger (1994), and Dickerson (1995), who defined and discussed the Tornillo graben, in which later Miocene rocks are preserved. Tornillo graben (figs. 9.3, 9.4; west northwesterly elongated; ≈32 × 11 km) lies between the Chisos Mountains and the Sierra Del Carmen in the eastern part of Big Bend National Park, southern Brewster County, Trans-Pecos Texas. It is bounded on the west-southwest by Dugout Wells fault zone (figs. 9.3B, 9.4; Stevens and Stevens, 1986, 1989, 1990), on the north by an area of persistent uplift (during at least the Cenozoic; Dickerson, 1980, 1995; Stevens and Stevens, 1990), and on the east-northeast by Sierra Del Carmen (Moustafa, 1988). The southern margin is not well understood, but is a structural high, possibly related to the tentatively proposed Santa Elena zone (Dickerson, 1980). Tornillo graben is within, but near the northeastern margin of, tectonic provinces mentioned above. In addition, the Sierra Del Carmen is commonly discussed as the Laramide front in Trans-Pecos Texas (e.g., King, 1935; Muehlberger, 1989).

EXTENT, STRUCTURAL, AND STRATIGRAPHIC RELATIONSHIPS OF LATER MIOCENE ROCKS: The later Miocene rocks in the Tornillo graben usually rest on rocks near the top of the Late Cretaceous Aguja Formation, but as young as Eocene along the Dugout Wells fault zone. To the east of Lower Tornillo Creek from near C′ to near G′ (figs. 9.3B, 9.4), later Miocene rocks rest with substantial angularity on the San Vicente Member, Boquillas Formation or on lower parts of the Pen Formation. Reddish to reddish buff Banta Shut-in rocks are most deeply dissected and widely exposed to the west of Lower Tornillo Creek, between the creek and Park Route 12 (Panther Junction–Rio Grande Village road; fig. 9.3B). Remnants of pediment gravels and pre-pedimentation alluvial fan deposits cover the Banta Shut-in formation adjacent to Route 12 (fig. 9.3B). Good exposures of the Banta Shut-in formation southwest of Route 12, somewhat obscured by pediment cover, inadvertently had been mapped as Aguja Formation (Maxwell et al., 1967: pl. II). The irregularly northwest-ta-

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Fig. 9.3. Geology of the Estufa bolson. **A,** Generalized outcrop of the Estufa Canyon and Banta Shut-in formations, and the location of selected measured sections, insert A. Measured section A, Light layer; B, Hell hole; C, Calcites; D, Comanche ridge; E, Tortoise leg; F, Liles; G, Dry camp; H, Cannon ball; I, SAS; and J, Boxing Day. Sections D, E, and F apply to figure 9.2. **B,** Generalized geologic map of the Estufa Canyon and Banta Shut-in formations with emphasis on the Banta Shut-in formation. Major faults are shown. Arrows indicate mean paleoflow directions at specific localities. Stippled, Lower member; white, Middle member, dashed, Red clay member, diagonal, Bench member, Banta Shut-in formation. Cross sections A–A′ to H–H′ coincide with the panels for the fence diagram, figure 9.4. **C,** Joint sets at the top of Comanche ridge, Hill 2362, Roys Peak Quadrangle Map, 1971. The calcite-filled fractures suggest latest Neogene or Quaternary left-lateral motion.
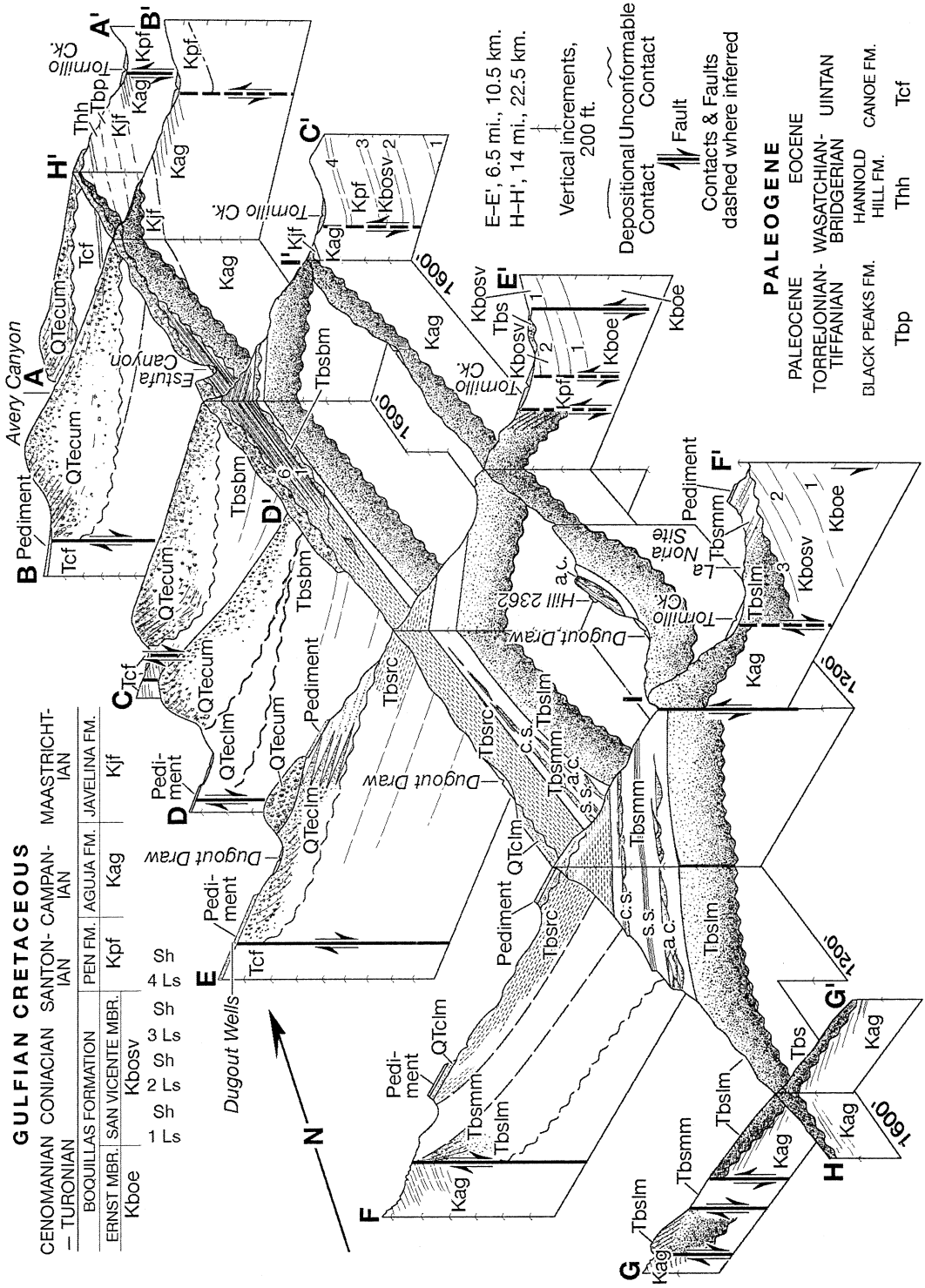
Fig. 9.4.   Fence diagram of the Estufa bolson shown in perspective, with emphasis on the Banta Shut-in formation. The location of the panels, A–A′ to H–H′ as in figure 9.3B.

pering outcrop area of the Banta Shut-in formation, apparently a remnant of a more extensive deposit, is about 200 km² (figs. 9.3, 9.4), but an additional ≈100 km² of the formation is covered by the possibly Blancan Estufa Canyon formation. The exposure area of the units taken together has the form of an elongate oval flattened against the Dugout Wells fault zone (figs. 9.3B, 9.4; Stevens and Stevens, 1989), which suggests the sag common along high-angle normal faults (Jackson and McKenzie, 1983; Alexander and Leeder, 1987; Leeder and Gawthorpe, 1987; Schlische, 1991). Internal structures, high-angle normal faults, and a westerly-facing monocline appear consistent with structures discussed for extensional basins by Schlische (1995) if associated with down-to-the-east displacement on the Dugout Wells fault zone.

BANTA SHUT-IN FORMATION AND ASSOCIATION OF FOSSILS WITH DEPOSITS: The later Miocene rocks were deposited under various regimes that produced distinctive lithologies. Differences in depositional architecture, coarse clast lithology, grain size, and mud content suggest informal division into a Lower (symbol: Tbslm; thickness: ≈60–105 m), Middle (Tbsmm: ≈75–85 m), Red clay (Tbsrc: >80 m), and a Bench member (Tbsbm: >90 m; figs. 9.2, 9.3B, 9.4). Contacts between the Lower and Middle, and between the Middle and Red clay members are gradational over a thickness of a few meters, and drawn arbitrarily at soil zones. The Bench member rests erosionally, but not apparently angularly, on Lower and Middle member rocks to the north of Liles locality, and is inferred to have an erosional contact with the Red clay member south and west of Liles locality (figs. 9.2–9.4). There is no evidence to suggest hydrologic closure of the basin during deposition. Banta Shut-in formation does not record much penecontemporaneous tectonic activity, beyond that necessary to form and maintain a depositional basin, and that necessary to establish an initially rugged source area for the coarse Lower member.

Fossils have been found wherever the deposits are well exposed, except in the coarsest conglomerates low in the Lower member. Most fossils come from muddier parts of the Middle and Bench members, but isolated teeth and tortoise ''rings'' have been found low in the Red clay member. Rapidly eroding footprints, including a coyote-size canid, have been found in recently fallen blocks from a probable floodout waterhole (Melville and Erskine, 1986; Tooth, 1999) deposit in the Cam sand (Middle member; figs. 9.2, 9.4), near the Hellhole measured section (fig. 9.3A, section B). Only three localities have proved worthy of repeated prospecting. Of these, two moderately productive Middle member localities include one near the base of the Tortoise Leg measured section (at ≈8 m; figs. 9.2E, 9.3A, section E; TMM 42864), and another at the north base of Hill 2362 (''Comanche ridge''; TMM 42124; fig. 9.2D). The most productive site is the area of the Liles locality section, benches 2–3 (figs. 9.2F, 9.3A, section F; TMM 42247, 42252), Bench member (Roy's Peak Quadrangle, 1971).

SYSTEMATIC PALEONTOLOGY

ORDER CARNIVORA BOWDICH, 1821

SUBORDER FELIFORMIA KRETZOI, 1945

FAMILY FELIDAE FISCHER DE WALDHEIM, 1817

SUBFAMILY FELINAE FISCHER DE WALDHEIM, 1817

Pseudaelurus Gervais 1850
?*Pseudaelurus* sp.
Figure 9.5A–T; table 9.1

REFERRED MATERIAL: TMM 42247-237, proximal end, left ulna; TMM 42247-144, distal end, right humerus; TMM 42247-136, distal end left humerus; TMM 42247-127, proximal end, left radius; TMM 42247-114, distal end of metacarpal or metatarsal; and TMM 42247-182a and -182b, proximal and distal ends of a metacarpal III.

STRATIGRAPHIC OCCURRENCE: TMM locality 42247, from float derived from the top of Bench 2, Liles measured section (fig. 9.2F), Bench member, Banta Shut-in formation, Big Bend National Park, Texas; Screw Bean Local Fauna, early early Hemphillian, late Miocene.

DESCRIPTION: The presence of ?*Pseudaelurus* in the Screw Bean Local Fauna rests on the identification of postcranial fragments. The proximal end of an ulna, TMM 42247-237 (fig. 9.5N, O), lacks the epiphysis and is
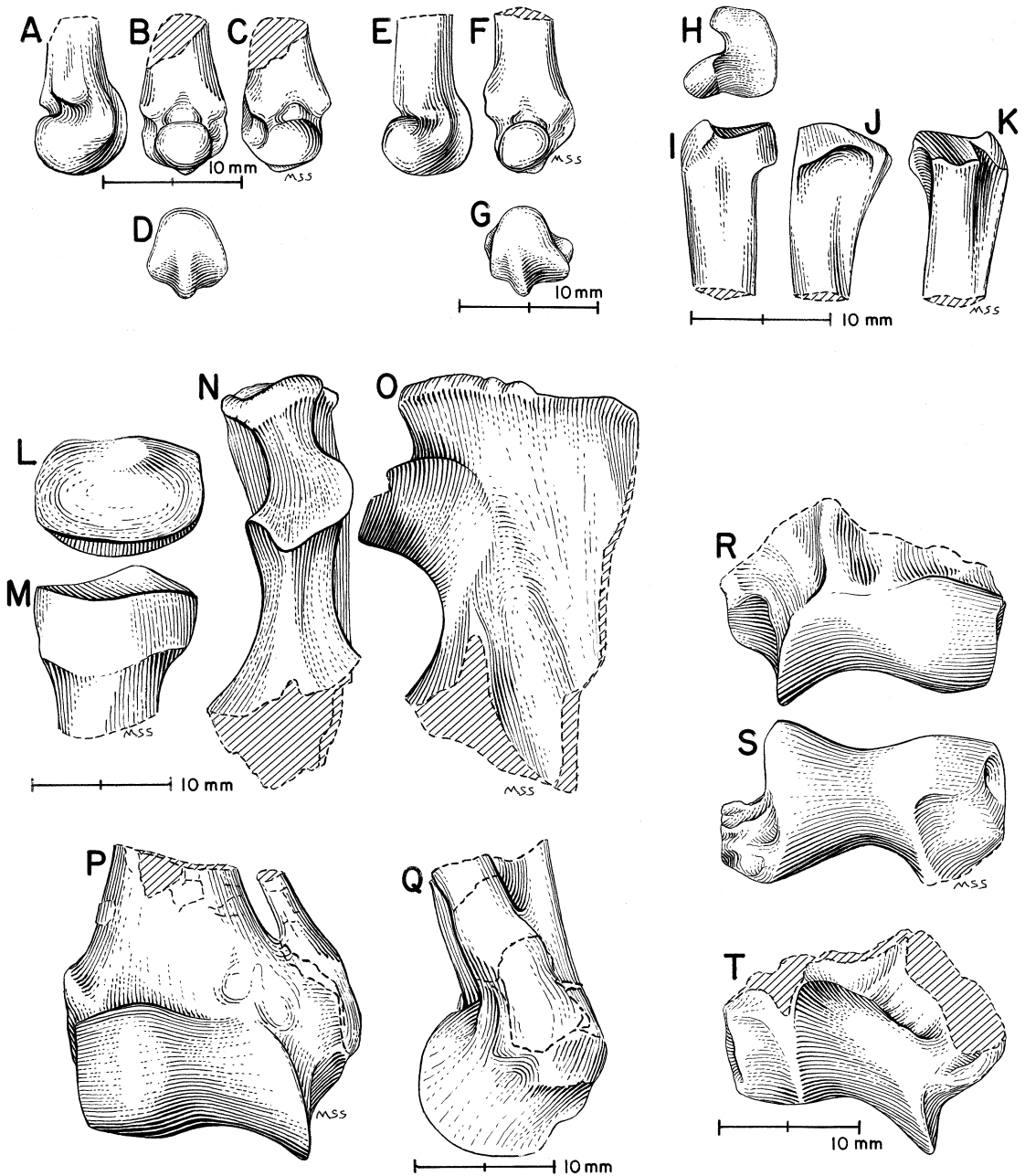
Fig. 9.5. Cf. *Pseudaelurus* sp., Screw Bean Local Fauna. A–D, TMM 42247-182b, distal end of medial metacarpal or metatarsal: **A,** lateral; **B,** dorsal (anterior); **C,** oblique; and **D,** condylar view. E–G, TMM 42247-114, lateral metacarpal or metatarsal: **E,** lateral; **F,** dorsal; and **G,** condylar view. H–K, TMM 42247-182a, proximal end of left metacarpal III: **H,** proximal articulation; **I,** dorsal; **J,** external; and **K,** ventral (posterior) view. L, M, TMM 42247-127, proximal end of radius: **L,** capitulum; **M,** anterior view. N, O, TMM 42247-237, proximal end of ulna: **N,** anterior; **O,** external view. P, Q, TMM 42247-144, distal end of right humerus, slightly restored (entepicondylar bridge appressed against shaft as preserved): **P,** anterior; and **Q,** medial view. R–T, TMM 42247-136, distal end of left humerus: **R,** anterior; **S,** ventral; and **T,** posterior view of trochlea.

TABLE 9.1
Measurements of cf. *Pseudaelurus* sp. Specimens at Texas Memorial Museum (in millimeters)

Humerus	42124-136	42247-144	42247-86	Mean
AP diameter medial epicondyle	23.2	26.6	34.8	28.2
AP diameter lateral epicondyle	21.5	22.4	28.6	24.2
AP diameter epicondyle, at constriction	14.4	14.9	17.7	15.7
T diameter, distal articulation	31.8	33.0	35.8	33.5
T diameter, maximum, distal end	41.7	41.8	—	41.8
Ulna	42247-237			
AP diameter of proximal epiphyseal surface	34.4			
T diameter of proximal epiphyseal surface	17.9			
T diameter of ulnar notch, proximal end	15.7			
T diameter of ulnar notch, at constriction	11.8			

broken across the coronoid process. The bone has a strong, squared olecranon process and a well-splayed semilunar notch. It is similar to *Puma concolor*, the mountain lion, but has a shorter olecranon process. The head of the proximal radius (AP and T diameters, 165 and 25.1 mm) has a shallow capitulum with an elevated, pointed posterior margin, and is similar to *P. concolor* (fig. 9.5L, M). The two distal humeral fragments are referred to *Pseudaelurus* because of size and felid morphology (fig. 9.5P–T). Only TMM 42247-144 preserves part of the entepicondylar foramen (fig. 9.5P, Q). The condyle lacks a supratrochlear foramen. The humeral condyles are similar in size and morphology to those of humeri of *P. concolor*.

The distal ends of two metacarpal or metatarsal elements, TMM 42247-182b, 42247-114 (fig. 9.5A–G) also represent this puma-sized felid. Their distal articulations are well rounded, have an extensive radius of curvature, strong ligament attachments, and great similarity with homologues in the extant *Puma concolor*. The proximal end, TMM 42247-182a, of the left third metacarpal, identical in structure to *P. concolor*, has been recovered (fig. 9.5H–K).

DISCUSSION: The Banta, scavenger-ravage, *Puma*-sized, felid limb bone and toe fragments have been difficult to identify because no comprehensive modern revision of Neogene North American cats has been published. The bones indicate a cat slightly less than one half the size of cf. *Nimravides catocopis*, discussed below. Hibbard (1934) de-

scribed a *Puma*-sized, saber-toothed kind of felid from Edson Quarry, late Hemphillian, Sherman County, Kansas, as *Adelphailurus kansensis*. Harrison (1983) was the first to describe some of the postcranial bones of this animal. The distal end of the Screw Bean humerus is transversely less expanded, and has a longer entepicondylar foramen than in *Adelphailurus kansensis*. Also, the proximal end of the Screw Bean ulna is deeper and more distinctly squared than in *Adelphailurus*, and more like *Puma*. Although generally size similar to *Puma concolor*, *A. kansensis* is not ancestral to *P. concolor*, and the late Hemphillian age of the Edson Quarry fossils would seem to deny a faunal relationship between the Edson and the Screw Bean assemblages. The Banta *Puma*-sized fragments tentatively are referred to *Pseudaelurus* Gervais, the ancestor of the modern cats.

The genotypic species of *Pseudaelurus* is *P. quadridentatus* (Blainville) from the middle Miocene of Sansan (Gers), France. Leidy (1858: 22; see 1869: 52, and pl. I, fig. 8) was the first to recognize *Pseudaelurus* in North America through the description of *Felis (Pseudaelurus) intrepidus*, based on a lower jaw from the ''sands of the Niobrara River,'' Valentine Formation, later Barstovian. *P. intrepidus* and *P. intrepidus sinclairi* Matthew (1918), early Barstovian Lower Snake Creek Fauna, Olcott Formation, Sioux County, Nebraska (Skinner et al., 1977: 347), are much older and smaller than the Screw Bean felid. *Pseudoaelurus marshi* Thorpe (1922: 446) is based on YPM 12865, a lower jaw from near

the mouth of Minnechaduza Creek, Cherry County, Nebraska, Niobrara River Fauna (Webb, 1969: 35), late Barstovian. *P. marshi* is smaller and considerably older than our species. MacDonald (1954: 67) described *P. aeluroides*, from the northeast rim of Sinclair Draw, Snake Creek Fauna, late Clarendonian (Skinner et al., 1977: 347), which also is much smaller than the Screw Bean cat.

Nimravides Kitts, 1958
cf. *Nimravides catocopis* (Cope)
Figure 9.6A–M; table 9.2

Machairodus catocopis Cope 1887: 1019.
Nimravides catocopis (Cope), Martin and Schultz, 1975: 60.

REFERRED MATERIAL: TMM 42247-33, posterior one half of m1; TMM 42247-138, partial right upper canine lacking enamel; TMM 42124-21, distal one half of left humerus; and TMM 42247-171, pollex, right medial phalanx.

STRATIGRAPHIC OCCURRENCE: TMM 42124, Comanche ridge measured section (fig. 9.2D); and TMM locality 42247, from float derived from the top of Bench 2, Liles measured section (fig. 9.2F), Middle member and lower part, Bench Member, Banta Shut-in formation, Big Bend National Park, Texas; Screw Bean Local Fauna, early early Hemphillian, late Miocene.

DESCRIPTION: The posterior one half of a slightly worn, African lion-sized m1, broken through the carnassial notch (fig. 9.6A, B, arrow), is the most diagnostic specimen. The apex of the protoconid is broken away. A sharp ridge extends anterior from the protoconid to the vertical carnassial notch. A distinct metaconid is located posterior to the protoconid. A sharp, low ridge, extends posterior from the apex of the metaconid to the base of the enamel. The partial canine (fig. 9.6C, D), a little less than one half as broad transversely as long anteroposteriorly, is believed to be an upper right on the basis of its limited curvature and flattened medial surface. The weathered fragment, about the size of, but differently shaped than in the African lion lacks the tip, root, and enamel.

The distal one half of humerus TMM 42124-21 (fig. 9.6I–M) is broken just below the deltoid tuberosity. The condyle is well preserved, but the medial part of the trochlea has been deformed downward whereas the external part of the trochlea is deformed upward (arrows) as preserved (fig. 9.6K–M, restored). A large entepicondylar foramen and entepicondylar bridge, a deep olecranon fossa, and an especially enlarged medial epicondyle are developed. The deep coronoid fossa lacks a supratrochlear foramen. The humerus closely resembles that of the modern mountain lion, *Puma concolor*, but is much larger. A nearly complete right pollex (fig. 9.6E–H) is the same magnitude larger than homologues in *P. concolor*, as the other bone fragments here referred to *Nimravides catocopis*. The phalanx, however, differs from *P. concolor* in greater medial flexion, in being longer and slightly narrower laterally, and in some of the details of the distal articulation. If the toe is identified correctly, this animal had a relatively larger and more diverging pollex than the modern cats used for comparison.

DISCUSSION: The m1, canine, phalanx, and humeral fragment show that an African lion-sized felid with oval canine is present in the Screw Bean Local Fauna. Lion-sized, scimitar-toothed cats of comparable age are *Nimravides* Kitts (1958) of the late Clarendonian to the end of the early Hemphillian (Tedford et al., 1987; Martin, 1998), and *Machairodus* Kaup (1833), late early to latest Hemphillian (Tedford et al., 1987). *Machairodus* differs from *Nimravides* by having a serrated upper canine and an indistinct or absent m1 metaconid. Additionally, *Machairodus* arrived from Eurasia along with other index taxa (unknown in the Screw Bean Local Fauna), in the late part of the early early Hemphillian, during a low sea level stand. The Screw Bean Local Fauna is believed to predate that immigration event. The distinct m1 metaconid suggests that our species is *Nimravides*, and not *Machairodus*.

Martin (1998: 238) recognizes three species of *Nimravides*, *N. catocopis* (= *Pseudothinobates* Kitts), *N. pedionomus* (Macdonald, 1948b, originally *Pseudaelurus*), and *N. galiani* (Baskin, 1981). *N. pedionomus* (misprinted as *pediomus* in Martin, 1998) is based on a puma-sized jaw from the Cap Rock base of the Ash Hollow Formation, Minnechaduza Fauna, early Clarendonian,
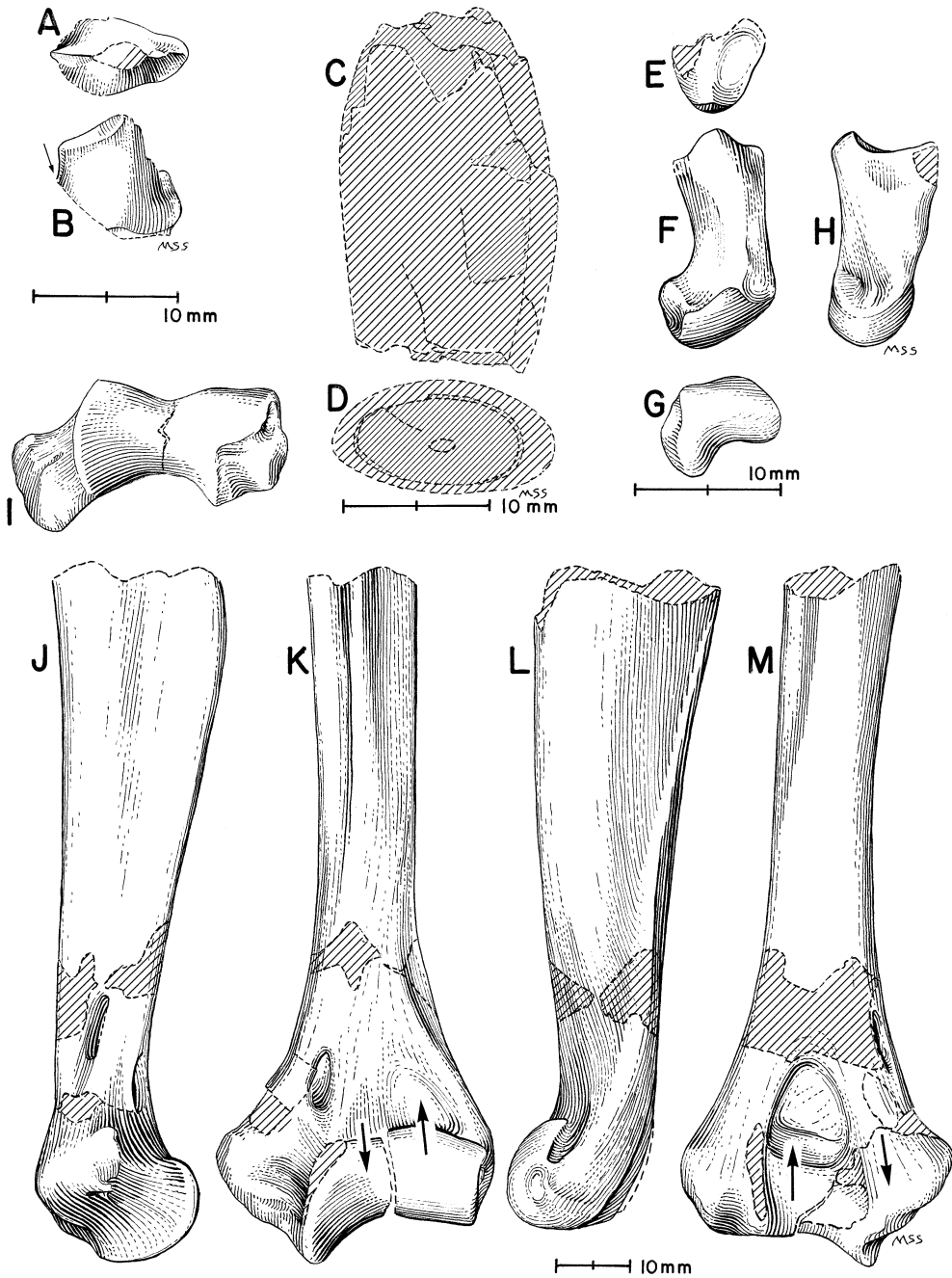
Fig. 9.6.   Cf. *Nimravides catocopis*, Screw Bean Local Fauna. A, B, TMM 42247-33, posterior one half of left m1, protoconid, and metaconid: **A,** occlusal; **B,** labial view; arrow indicates carnassial notch. C, D, TMM 42247-138, partial right upper canine, lacking enamel: **C,** labial; **D,** cross section view where broken. E–H, TMM 42247-171, right proximal phalanx, pollex: **E,** proximal articulation; **F,** dorsal (anterior); **G,** distal articulation; and **H,** medial view. I–M, TMM 42124-21, distal one half of left humerus, slightly restored, arrows indicate directions of deformation: **I,** distal end of trochlea; **J,** medial; **K,** anterior; **L,** external; and **M,** posterior view.

TABLE 9.2
Measurements of cf. *Nimravides catocopis* Specimens at Texas Memorial Museum (in millimeters)

Upper canine	42247-138
AP diameter, maximum	29.9
T diameter, maximum	15.8
Carnassial	42247-33
AP diameter, as preserved	17.22
T diameter, as preserved	10.10
Humerus	42124-21
AP diameter, medial epicondyle	45.8
T diameter, medial to lateral epicondyle	75.0[a]
Length of bone, as preserved	194.5
Pollex, proximal phalanx	42247-171
Length, as preserved	28.7
T diameter, proximal end	13.1
AP diameter, distal end	12.6
T diameter, distal end	15.6

[a]Approximate.

Cherry County, Nebraska. Baskin (1981: 137) retained *P. pedionomus* in *Pseudaelurus* and suggested that it is probably ancestral to *Nimravides*. The Screw Bean species under discussion differs from *P. pedionomus* by a more prominent metaconid, wider talonid, and larger size. Additionally, the Screw Bean Local Fauna is certainly younger than early Clarendonian.

Nimravides galiani (Baskin, 1981) is based on a partial jaw with a canine and m1, UF 24461, from the latest Clarendonian, Love Bone Bed Local Fauna, Alachua County, Florida. *N. galiani* has also been identified from the Shoreline assemblage (Leite, 1990), Lake McConaughly, Ash Hollow Formation, Keith County, Nebraska, late Clarendonian. Our carnassial fragment, TMM 42247-33, closely resembles the posterior one half of UF 24461 with its distinct metaconid, but the Texas species is slightly larger. Of the three recognized species of *Nimravides*, the Screw Bean fragmentary material matches *N. catocopis* best in size and morphology.

The earliest occurrence of *Nimravides catocopis* is from the Black Hawk Ranch (see Macdonald, 1948a) and the North Tejon Hills faunas, late Clarendonian (Tedford et al., 1987). *N. catocopis* has been reported from

various early Hemphillian faunas, such as the Gabaldon Badlands, New Mexico, Arnett, Capps Pit, Port-of-Entry Pit, Higgins (Sebits's Ranch), Texas and Oklahoma, and the upper part of the Ash Hollow Formation, Lemoyne, Feltz Ranch and Oshkosh faunas, Nebraska (Kitts, 1958; Martin and Schultz, 1975; Schultz, 1977; Tedford et al., 1987; Voorhies, 1990; Lozinsky and Tedford, 1991). The youngest occurrence as known is in the Box T, Wolf Creek fauna, Lipscomb County, Texas (Schultz, 1977: 69), early Hemphillian.

The presumed late Hemphillian occurrences of "*Nimravides catocopis*" reported for the Coffee Ranch Fauna, Hemphill County, Texas (see Burt, 1931: 262; Dalquest, 1969), the Optima fauna, Texas County, Oklahoma (Savage, 1941: 697), the Yepómera fauna, State of Chihuahua, and the State of Guanajuato, Mexico, are based on specimens of *Machairodus coloradensis* Cook (Schultz, 1977; Dalquest, 1983; Lindsay et al., 1984; Carranza-Castañeda and Miller, 1996).

SUBORDER CANIFORMIA KRETZOI, 1943

INFRAORDER CYNOIDEA FLOWER, 1869

FAMILY CANIDAE FISCHER DE WALDHEIM, 1817

SUBFAMILY BOROPHAGINAE SIMPSON, 1945

Epicyon Leidy, 1858
Epicyon haydeni Leidy, 1858
Figure 9.7E–G, P, Q; table 9.3

Canis (*Epicyon*) *haydeni* Leidy 1858: 21.
Epicyon haydeni (Leidy): Baskin, 1980: 1350.
Epicyon haydeni (Leidy): Baskin, 1998b: 207.
Epicyon haydeni (Leidy): Wang et al., 1999: 252.
Bone-eating dog, unident.: Stevens and Stevens, 1989: 79.

REFERRED MATERIAL: TMM 42252-28, associated, detached, right and left maxillary fragments with M1–2 and partial P4 root; and TMM 42247-86, distal end of left humerus, tentatively referred.

STRATIGRAPHIC OCCURRENCE: Derived from float from the top of Bench 2, and from between Bench 2 and 3, Liles measured section (fig. 9.2F), Bench member, Banta Shut-in formation, Big Bend National Park, Texas; Screw Bean Local Fauna, early early Hemphillian, late Miocene.
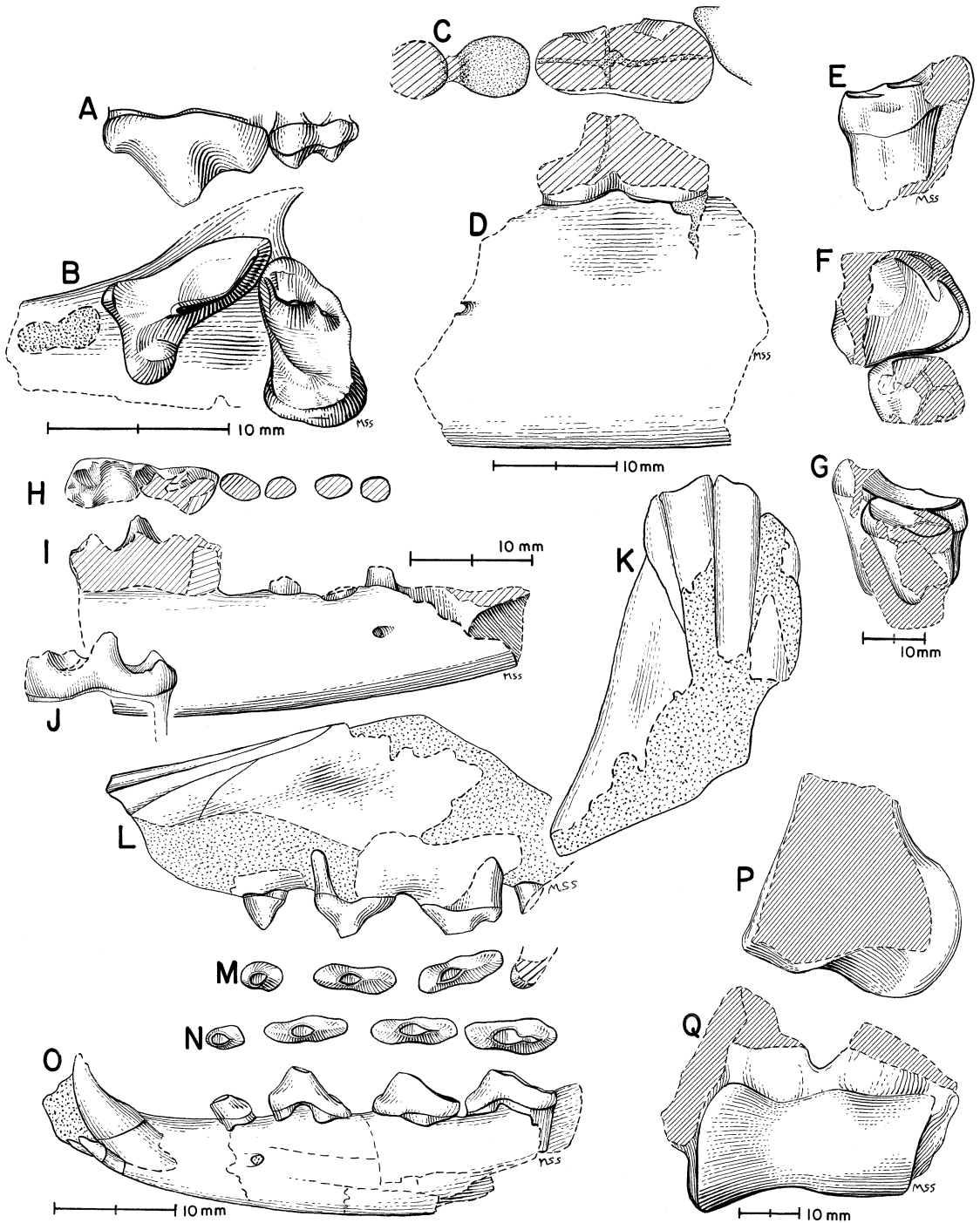
Fig. 9.7. Mustelidae and Canidae from the Screw Bean Local Fauna. **A, B,** *Martes* sp., TMM 42247-75, alveolus for left P3, left P4–M1; M1 slightly restored from the right side. **C, D,** *Eucyon* sp. TMM 42247-46, left jaw fragment with alveolus for p3, fragmentary p4, and anterior margin of m1 alveolus. **E–G, P, Q,** *Epicyon haydeni*: **E–G,** TMM 42247-28, right M1–2; **P, Q,** TMM 42247-86, distal end, left humerus: **P,** medial; and **Q,** anterior view. **H–O,** *Vulpes* sp.: **H–J,** TMM 42247-183, partial right lower jaw with alveoli for canine and premolars, and a partial right m1; **K–O,** TMM 42247-250, dorsal and lateral views of rostrum and views of P1–3, and canine, p1–4. Scale bars as indicated.

TABLE 9.3
Measurements of *Epicyon haydeni* Specimens at Texas Memorial Museum (in millimeters)

Upper teeth	42252-28 (left)	42252-28 (right)
M1-M2, AP diameter, labial	(27.7)	(26.6)
M1 AP diameter	(18.4)	(18.3)
M1 T diameter	(22.0)	(23.2)
M1, AP diameter of talon	17.2	16.8
M2, AP diameter, labial	(9.8)	10.4
M2, T diameter	(16.1)	17.0

Humerus	42247-86
AP diameter, distal end	36.5
AP diameter, trochlea	24.8
AP diameter, capitulum	19.4
T diameter, distal articulation	36.3

( ) Indicate minimum measurements, as preserved.

DESCRIPTION: The associated but detached maxillae fragments preserve a root for the right P4, and right and left M1–2 (fig. 9.7E–G). Both M1s have the paracone broken away. M1–2 are strong, crushing, well-worn teeth as preserved. They are considerably larger than homologues in modern gray wolves, *Canis lupus* Linnaeus. M1 is canid in outline but has a broad, little posteromedially flexed talon. A slight anteromedial cingulum is present on M1. The M2 is about three-fourths the size of M1.

The distal end of the humerus, TMM 42247-86, is larger than counterparts in *Canis lupus* used for comparisons. The distal end has the distinctly ''squared'' medial profile, although the medial epicondyle is broken away, and a small supracondylar foramen, typical of canids (fig. 9.8P, Q). The humeral fragment has a relatively broad troachlea, unlike the more transversely constricted articulation of the modern cursorial canids. The olecranon fossa of TMM 42247-86 is constricted less than in *Canis*. The presence or absence of an entepicondylar foramen cannot be determined due to incompleteness. The humeral fragment is morphologically similar to that figured by Munthe (1989) for *E.* ''*validus*,'' but is not as large. TMM 42247-86 is referred tentatively to *Epicyon haydeni*.

DISCUSSION: Baskin (1980, 1998a, 1998b) and Wang et al. (1999) have aptly reviewed the chaotic taxonomic history of *Epicyon*, and have paired cranial and other skeletal elements to the type lower jaw. Wang et al. (1999: 266) reviewed *E. haydeni*, early Clarendonian through the early Hemphillian. *E. haydeni* survived, apparently in isolation, on into the late Hemphillian in Florida. The Screw Bean specimen adds very little to our knowledge of this species, except to expand the geographic distribution of this broadranging taxon (Baskin, 1998b) southward toward Mexico. The identification of our specimens as *E. hayden*, rests on morphology and size. Examples of very worn teeth of *E. haydeni* (see Wang et al., 1999), F:AM 61428 and F:AM 61523B, Port-of-Entry Pit, Arnett fauna, Ellis County, Oklahoma, late early Hemphillian, closely match in size and shape TMM 42247-86, but our specimen is slightly smaller than F:AM 61512, an unworn tooth. Richard H. Tedford (written commun., Dec. 7, 1993) provided measurements of five specimens of the sympatric species, *Epicyon saevus*, from Port of Entry Pit. The observed range for AP M1 ranged from 18.3 to 20.5 mm, and the TM1 observed range varied between 21.6 and 24.0 mm. These dimensions are somewhat smaller than for the well-worn teeth of TMM 42252-28. Additionally, he graciously provided measurements of several specimens from *Aphelops* Draw, Johnson Member, Snake Creek Formation, late early Hemphillian. An APM1 diameter at 22.5 and a TM1 at about 25.3 mm were obtained for AMNH 20482, and an APM1 at 22.0 mm and a TM1 at 24.0 mm were obtained for AMNH 20482a. The Screw Bean teeth fall within the observed range but below the mean for a large statistical sample of *E. haydeni* (Wang et al., 1999: 389). If unworn, the Screw Bean teeth would have yielded slightly larger measurements.

Borophagine canids are believed to have been solitary hunters as determined from brain configuration (Radinsky, 1973), or scavengers. The excessive wear on the posterior teeth of *Epicyon* supports the view that they literally devoured all nutritional parts of their prey. The large size of *E. haydeni* relative to the size of the Screw Bean ungulates, especially the abundant and diminutive antilocaprid, would have permitted the consumption of most of the skeleton. This would
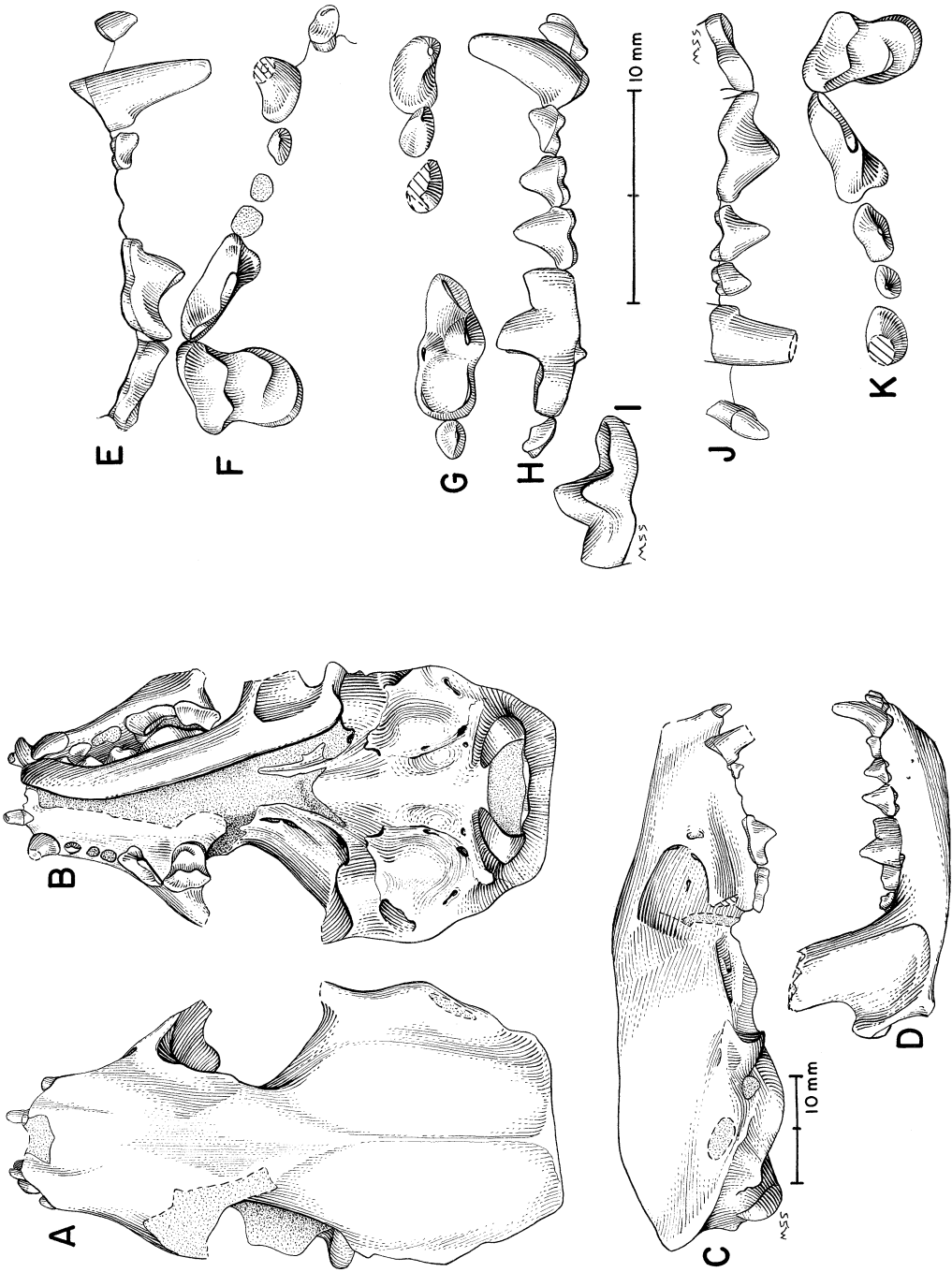
Fig. 9.8. *Buisnictis chisoensis*, new species, Screw Bean Local Fauna, Big Bend National Park, Texas. A–I, TMM 24427-29, skull and jaws, type: **A**, dorsal; **B**, ventral; **C**, lateral view of skull; **D**, lateral view of right lower jaw; **E**, labial; and **F**, occlusal view of right I3–M1; **G**, occlusal; and **H**, labial view of i2–m2; and **I**, lingual view of m1. J, K, TMM 42247-27: **J**, labial; and **K**, occlusal view, I3–M3. A–D and E–K have different scale bars.

well explain the taphonomy of the Screw Bean Local Fauna.

Munthe (1998) states that *Epicyon* (*E. saevus*) was a cursorial predator adapted to open habitats that were expanding progressively northward from the Southwest into the Great Plains, during the late Miocene. Munthe (1989: 93) notes that *E.* "*validus*" (now *E. haydeni*) was a heavy animal (see Wang et al., 1999: 2) presumably incapable of long distance running, and implies that *E.* "*validus*" hunted as an ambush stalker. The metacarpal and metatarsal elements presented in Wang et al. (1999: 262–263) do not suggest a cursorial animal. The humeral fragment, TMM 42247-86, tentatively referred to *E. haydeni* (and the humerus illustrated by Munthe, 1989, F:AM 67603, as *E.* "*validus*," [= *E. haydeni*], Jack Swayze Quarry, Clark County, Kansas, early Hemphillian [see Wang et al., 1999: 256]) lacks the narrowed and "rigid" distal articulation, a cursorial specialization, thus is somewhat bear like. Munthe failed to compare *E.* "*validus*" with bears, which is curious, because Munthe notes that *E.* "*validus*" died out when the bear *Agriotherium* appeared in North America.

SUBFAMILY CANINAE FISCHER DE WALDHEIM, 1817

TRIBE VULPINI HEMPRICH AND EHRENBERG, 1832

Vulpes Frisch, 1775
Vulpes sp.
Figure 9.7H–O; table 9.4

Leptocyon, cf. *L. vafer* (Leidy): Stevens and Stevens, 1989: 79.

REFERRED MATERIAL: TMM 42247-250, partial rostrum with nasals and P1–3, and protocone of P4, associated with lower jaws with canine–p4, and TMM 42247-183, lower jaw fragment with premolar alveoli and a partial m1.

STRATIGRAPHIC OCCURRENCE: Bench 2, Liles measured section (fig. 9.2F), Banta Shutin formation, Big Bend National Park, Texas; Screw Bean Local Fauna, early early Hemphillian, late Miocene.

DESCRIPTION: The partial rostrum preserves some of the nasals and pieces of the maxillary bones with the premolars (fig.

TABLE 9.4
Measurements of *Vulpes* sp. Specimens at Texas Memorial Museum (in millimeters)

Upper teeth	42247-183	42247-250
P1, AP diameter	—	3.70
P2, AP/T diameter	—	6.50/2.40
P3, AP/T diameter	—	7.30/2.30
Lower teeth, jaw	42247-183	42247-250
c-p4, inclusive	—	39.40
p2-m1, inclusive	32.30, alv.	—
p2-p4, inclusive	—	28.20
p4-m1, inclusive	19.16, alv.	—
p1, AP/T diameter	—	3.00/1.70
p2, AP/T diameter	—	6.60/2.30
p3, AP/T diameter	7.20/	7.20/2.20
p4, AP/T diameter	6.40, alv./	7.70/3.00
m1, AP diameter	12.40[a]	—
m1, trigonid AP	8.40[a]	—
m1, talonid AP/T	4.00[a]/4.40[b]	—
m1, height, metaconid	4.00	—
m1, height, entoconid	2.90	—
Jaw depth, at p2, labial	8.50	9.00
Jaw depth, at m1, labial	10.00	—

[a] Approximate.
[b] Estimated.

9.7L, M). The well-spaced premolars lack distinct accessory cusps. TMM 42247-183 preserves the alveoli for the canine, the roots for p2–4, and a damaged m1. The premolar spacing between TMM 42247-250 and TMM 42247-183 is very similar. The Screw Bean lower jaws are shallower and have more attenuated and more widely spaced premolars (fig. 9.7H–J, N, O) than in *Leptocyon vafer* examined, including the type. The Screw Bean specimens closely match homologues in *Vulpes macrotis*, the desert kit fox (see Hall and Kelson, 1959; Thornton and Creel, 1975) that lives in Trans-Pecos Texas today.

The m1 trigonid crown is broken away for TMM 42247-183, but its talonid is adequately preserved (fig. 9.7H–J). The metaconid is an enlarged, divergent cusp. The low lingual valley between the entoconid and metaconid supports a very small cuspule. The anteroposteriorly elongated talonid basin is rimmed lingually by a low entoconid and labially by a tall hypoconid. A slight cingular heel occurs between the entoconid and hypoconid.

DISCUSSION: The Screw Bean fox was previously identified as cf. *Leptocyon vafer*. *L. vafer* continued into the earlier Hemphillian (Whistler and Burbank, 1992), or to the onset of the late Hemphillian (Munthe, 1998: 139). The type, USNM 126 (see Leidy, 1869: 29, pl. 1, fig. 11), is a pair of lower jaws with teeth, from the late Barstovian "Niobrara sands," Niobrara River or Burge Fauna (Webb, 1969: 35), near what is now Valentine, Nebraska. Matthew (1918) distinguished *Leptocyon* from *Vulpes* on the basis of the heel of m1 with a low entoconid crest that is indistinctly divided into two cusps, m2 with a low, shelflike paraconid, and very small m3. Gregory (1942: 348) did not believe that the features set forth by Matthew to separate *Leptocyon* from *Vulpes* had generic significance, but Webb (1969: 40) disagreed. Gregory observed (verified by MSS) that low entoconids are often present in modern red and kit foxes as an atavistic trait. Tedford (written commun., Mar. 20, 1989) noted that within *Leptocyon-Vulpes*, the m1 entoconid progressively becomes a more distinct cusp in younger species.

The lower jaw of the Screw Bean fox is relatively longer and more slender than in the type of *Leptocyon vafer*, and a referred Lapara Creek specimen (Wilson, 1960), TMM 30896-241, used for comparisons. Additionally, the Screw Bean premolars are more separated, and the jaw is shallower. The reduced accessory cusps and the more slender jaw are features derived in the direction of *Vulpes*; thus the Screw Bean fox, despite similar small size, is not referable to *L. vafer*. Our vulpine is interpreted to be a small species of *Vulpes*. Tedford et al. (1987: 190) note that undoubted *Vulpes* makes its first appearance in the Hemphillian as one of the taxa that defines the Hemphillian North American Land Mammal Age. Munthe (1998: 138), however, extends *Vulpes* back to the early Clarendonian; *Leptocyon* and *Vulpes* have often been used interchangeably for Clarendonian and Hemphillian vulpines.

Radinsky (1973: 182) notes on the basis of brain endocasts that *Leptocyon* is the ancestor for all living canids, not *Tomarctus* as previously believed (also see Webb, 1969; Martin, 1989; Tedford and Wang, 1995). One species is best recognized, *V. stenognathus* Savage (1941: 694), based on lower jaws from the Optima Fauna, late Hemphillian. Munthe (1998: 133) recognized "*V. shermanensis*" Hibbard, from Edson Quarry, Sherman County, Kansas. "*V. shermanensis*" also has been reported for the Coffee Ranch Fauna (Dalquest, 1969, 1983) but Schultz (1977) identified the Coffee Ranch fox as *V. stenognathus*, implying synonymy.

Teeth of *Vulpes stenognathus* are very similar in size and structure to the red fox *V. vulpes*, as noted by Savage. Most notable to Savage was the seemingly great depth and compression of the jaw of *V. stenognathus*, which influenced the choice of the name, but the narrowness and jaw depth is probably an artifact of crushing. Savage also compared the Optima fox with? *Vulpes* sp. (Stirton, 1936: 170; MacFadden et al., 1979), from the Coffee Ranch–Hemphill Fauna, Texas, and noted that the Coffee Ranch *Vulpes* is larger, but has a shallower and less compressed jaw, in keeping with a less deformed ramus. Both *V. stenognathus* and "*V. shermanensis*" are substantially larger and stratigraphically younger than the Screw Bean fox, and it is unlikely that these are the same species. The small size, and the relatively low entoconid in our specimen suggests that the Screw Bean fox is a primitive *Vulpes* within the *Leptocyon-Vulpes* transition. To date, no such earliest Hemphillian species have been described.

TRIBE CANINI FISCHER DE WALDHEIM, 1817

Eucyon Tedford and Qiu, 1996
cf. *Eucyon* sp.
Figure 9.7C, D

Unidentified canid, large: Stevens and Stevens, 1989: 79.

REFERRED MATERIAL: TMM 42247-46, left jaw fragment with alveolus for p3, a partial p4, and anterior alveolus for m1.

STRATIGRAPHIC OCCURRENCE: Found as float derived from the top of Bench 2, Liles measured section, Bench Member, Banta Shut-in formation (fig. 9.2F), Big Bend National Park, Texas; Screw Bean Local Fauna, early early Hemphillian, late Miocene.

DESCRIPTION: The jaw fragment (fig. 9.7C, D) matches the size (labial jaw depth at p4, 20.02) and has the alveolar spacing (p3–4,

24.3**) of large individuals of the modern coyote, *Canis latrans* Say. The p3 alveoli are well separated and indicate an anteroposteriorly attenuated and relatively narrow tooth. The partially preserved p4 (13.8* × 6.5*) is larger than p3, and is constricted slightly medially as in the coyote. m1 is not preserved, but part of its anterior alveolus indicates an enlarged, anteroposteriorly aligned, typically canid m1.

DISCUSSION: TMM 42247-46 represents a *Canis*-like jaw fragment. The specimen is much larger than homologues in the Screw Bean *Vulpes* sp. TMM 42247-46 is not referable to the borophagines *Epicyon haydeni*, also present in the Screw Bean assemblage, or *Carpocyon* Webb because the p3 and p4 alveoli are well spaced and do not indicate foreshortened teeth.

The Canini began their adaptive radiation in the late Clarendonian–early Hemphillian (Tedford and Qiu, 1996: 36; Munthe, 1998: 140) from within *Leptocyon* of North America. True *Canis* (and closely related genera) is not defined on the dentition, conservative, but on inflation of the frontal sinuses and on minor features of the occiput (Tedford and Qiu, 1996). The amount of sinus inflation, however, can vary from very little to considerable, at least among *C. latrans*, the coyote. *Canis* may have evolved in Eurasia from canid immigrants originally from North America, at about 3 Ma; the derived descendants returned to North America as a part of the global dispersal event of modern dogs (Flynn et al., 1991: 260). *C. lepophagus* (Johnston, 1938) and *Canis ferox* (Miller and Carranza-Castañeda, 1998) witness the Blancan arrival of these archaic, coyote-like *Canis* in North America.

Canis lepophagus, late Blancan Cita Canyon beds, Randall County, Texas, is slightly smaller than the modern coyote. Johnston (1938) provides no dental measurements. Enlargements of Johnston's plate 3, figure 1, to natural size, indicate that the Screw Bean jaw fragment is similar in size to WTM 881. The age difference between the canine from the Cita Canyon and Screw Bean faunas, and the timing of the Blancan origin of *Canis*, however, imply that these species are not the same.

''*Canis*'' *ferox* is based on a skull and lower jaw, IGM 1130, of a coyote-like dog from near Rancho Viejo, State of Guanajuato, Mexico, late Hemphillian. The Screw Bean jaw fragment is larger than the jaw figured by Miller and Carranza-Castañeda (1998). The size difference and the presumed differences in age between the Screw Bean and Guanajuato specimens detract from identifying our jaw fragment as ''*C.*'' *ferox*.

Older Hemphillian ''coyote''-like canids traditionally have been called *Canis davisi* Merriam (1911). The type of ''*C.*'' *davisi*, M1–2, UCMP 545, came from the late early Hemphillian Rattlesnake beds, John Day Basin. Merriam (1911) describes the red fox-sized upper teeth as generally similar to, but smaller than in the modern coyote. Shotwell (1970) reports ''*Canis*'' *davisi* from the Little Valley and Juniper Creek local faunas, Hemphillian, Juntura Basin, Oregon. Shotwell's (1970) specimen, UO 26742, is smaller than specimens of *C. latrans* and our Screw Bean jaw fragment. ''*C.*'' *condoni* Shotwell (1956) is based on a lower jaw that retains m2 from the McKay Reservoir fauna, Oregon, late Hemphillian. Shotwell (1970) later thought that ''*C.*'' *condoni* may represent ''*C.*'' *davisi*, and this is accepted by Tedford and Qiu (1996; but also see Munthe, 1998). ''*C. condoni*'' is about the size of *Vulpes vulpes*, the modern red fox (Shotwell, 1956), thus ''*C. condoni*'' is considerably smaller than TMM 42247-46.

Tedford and Qiu (1996) designated ''*Canis*'' *davisi* the type species of *Eucyon*, and clarified the distinction between *E. davisi* and true *Canis* (mainly lack of inflation of the frontal sinuses, and minor details of the occiput). The Screw Bean canid and *E. davisi* are approximate contemporaries. *E. davisi*, however, is smaller than the Screw Bean dog (see Tedford and Qiu, 1996), thus probably not the same species. The Screw Bean dog is near the size of the coyote-like, considerably younger *E. zhoui* (ca. 4 Ma) of China. It is apparent that a moderate and a larger species of nonborophagine dog coexisted in the early early Hemphillian in North America. Due to incompleteness, the Screw Bean canine is tentatively placed in *Eucyon*.

TABLE 9.5
Measurements of *Buisnictis chisoensis* Specimens at Texas Memorial Museum (in millimeters)

Upper teeth	42247-29 holotype	42247-27	42247-200	42247-134	Mean
Canine–M1, inclusive	17.27	16.75	—	—	17.01
P2–M1, inclusive	14.25	13.5	—	—	13.88
P2–4, inclusive	10.54	10.45	—	—	10.5
P4–M1, inclusive	9.35	8.75	—	—	9.05
P4, AP/T diameter	5.60/2.35	5.32/2.67	—	—	5.46/2.51
M1, AP/T diameter	4.68/6.07	4.09/6.18	—	—	4.39/6.13
M1, T diameter of "waste"	3.20	2.67	—	—	2.95
M1, T diameter of talon	3.34	3.30	—	—	3.32
Lower teeth					
c–m2, inclusive	19.80	—	—	—	—
c–m1, inclusive	17.95	—	—	—	—
p2–m2, inclusive	16.65	—	—	—	—
p2–m1, inclusive	14.75	—	—	—	—
p2–4, inclusive	7.9[a]	—	—	—	—
p4–m2, inclusive	12.75	—	—	—	—
p4–m1, inclusive	9.6[a]	—	—	—	—
p2, AP/T, diameter	2.32/1.33	—	—	—	—
p3, AP/T, diameter	2.55/	—	—	—	—
p4, AP/T, diameter	2.94/	—	—	—	—
m1, AP diameter	6.84	—	—	—	—
m1, AP diameter, trigonid	3.95	—	—	—	—
m1, T diameter, trigonid	3.33	—	—	—	—
m1, T diameter, talonid	2.94	—	2.82	—	2.88
m2, AP/T, diameter	2.72/2.01	—	2.71/2.05	—	2.72/2.03
Skull					
Basal length of skull, I1 posterior alveolus to condylar notch	42.30	—	—	—	—
Basal length of skull, tip of premaxillae to posterior edge of occipital condyles	49.15	49.43	—	—	49.29
Breadth of skull across the mastoid processes	26.76	25.39	—	26.5[a]	26.22
Interorbital width	15.1[a]	13.6[a]	—	—	14.4[a]
Postorbital width	11.90	11.76	—	11.2[a]	11.62
Length of palate along midline, I1 posterior alveolus to internal nares	—	17.73	—	—	—
Height of cranium, plane of basisphenoid-basioccipital to top of skull, excluding sagittal crest	13.00	13.05	—	—	13.03
Lower jaw					
Maximum length of jaw, anterior edge of incisors to condyle posterior edge	31.47	—	—	—	—
Depth of jaw below M1 metaconid	4.58	—	4.52	—	4.55
Width of jaw below M1 metaconid	3.45	—	3.15	—	3.30

[a] Approximate.

INFRAORDER ARCTOIDEA FLOWER, 1869

PARVORDER MUSTELIDA TEDFORD, 1976

FAMILY MUSTELIDAE FISCHER DE WALDHEIM, 1817

SUBFAMILY MEPHITINAE BONAPARTE, 1845

Buisnictis Hibbard, 1950
Buisnictis chisoensis, new species
Figure 9.8A–K; table 9.5

Buisnictis, n. sp., extinct spotted skunk: Stevens and Stevens, 1989: 79.

HOLOTYPE: TMM 42247-29, complete, slightly laterally skewed skull and lower jaws, with teeth.

HYPODIGM: Type, and TMM 42247-27, a partial skull with left I3–M1; TMM 42247-134, the posterior part of a skull; and TMM 42247-200, a partial lower jaw with partial m1–m2.

DIAGNOSIS: *Buisnictis chisoensis* is distinguished from *B. burrowsi* Skinner and Hibbard, late Blancan, by much more distinct m1 metaconid, a more basined talonid, and much larger size; from *B. meadensis* Hibbard, and *B. breviramus* (Hibbard), early Blancan, by a smaller P4 paracone, slightly wider angle between the lingual sides of P4 and M1, M1 with slightly less expanded talon, a relatively wider m1, an anteroposteriorly shorter m2, and a slightly larger size; differs from *Martinogale alveodens* Hall (1930:147),? late Clarendonian–late Hemphillian, by teeth with "smoother" enamel contours, lack of cingula, jaw with wider ascending ramus, smaller and more anteriorly situated angular process, lack of a "bulbous" symphysis, and larger size; and differs from *Spilogale rexroadi*, early Blancan, by much larger size, a much smaller P4 paracone, and by m1 without a deep notch between the metaconid and entoconid.

ETYMOLOGY: *chisoensis*; *chisos*, for the Chisos Mountains, Big Bend National Park, Texas, and *ensis*, Latin for "from" or "of."

STRATIGRAPHIC OCCURRENCE: From just below and from the top of Bench 2, Liles measured section (fig. 9.2F), Bench member, Banta Shut-in formation, Big Bend National Park, Brewster County, Texas; Screw Bean Local Fauna, early early Hemphillian, late Miocene.

DESCRIPTION AND COMPARISONS: The skull of *Buisnictis chisoensis* is rather low (fig. 9.8A–C), with a slightly depressed rostrum, a short and broad face, nasal tips terminate in line with the canines, and the external nares are small. The internal nares end slightly ahead of the posterior margin of M1. The rostral sutures fuse in early ontogeny. The postorbital processes are very small, postorbital constriction is rather narrow, and the type has a slight sagittal crest. Two other somewhat smaller partial skulls, TMM 42247-27 and TMM 42247-134, lack sagittal crests. The mephitine auditory bulla is small but well rounded. The mastoid sinus invades the mastoid bone laterally (fig. 9.8A, B), as in extant *Spilogale pygmaea* Thomas (see Van Gelder, 1959: fig. 47).

It has not been practical to separate the left jaw from the type, because the teeth are in tight occlusion, but the right jaw has been freed. The dental formula is I3/3, C1/1, P2–4/2–4, M1/1–2. The relatively small upper and lower incisors form a nearly transverse row (fig. 9.8B). I3 is the largest incisor. The ovoid upper canine has a small posterior tubercle, and a very slight internal cingular swelling. Cingula are absent, as is typical among the living skunks *Spilogale*, *Mephitis*, and *Conepatus*. The double-rooted P2–3 increase in size posteriorly, and have small heels.

The P4 is sectorial and musteline-like (fig. 9.8F, K), with a small, anteromedially situated protocone in the two specimens in hand. Protocones, however, can vary from much enlarged (see MU 1110) to moderately small (MU 1405) within modern *Spilogale putorius*. The carnassial blade is long as in *Spilogale*, not foreshortened as in extant *Mephitis* and *Conepatus*, and the valley between the paracone and metacone is unconstricted, the parastyle is small, and the paracone is the tallest cusp. P4 lacks cingula. The angle between the posteromedial border of the P4 and the anterior margin of M1 in *B. chisoensis* is about 50°, about 45° in Blancan *Buisnictis*, and about 10–15° in living *Spilogale*. A maxillary from the Beck Ranch assemblage, Scurry County, Texas, early Blancan, identified as *S. rexroadi* by Dalquest (1972), MUC:FV 8349 (as recatalogued within the museum collections to conform with the published specimen number), has an angle of about 10°, hence is similar to modern *Spilogale*. MUC:FV 8349, however, has a relatively narrower P4 than in extant *S. pygmaea*, thus more closely resembles the Screw Bean taxon.

M1 is broader transversely than long anteroposteriorly, has an expanded talon, a moderately constricted "waist," low cusps and crests, and has a wide labial shelf (fig. 9.8F, K). The M1 is proportionally similar to Blancan *Buisnictis* and modern *Spilogale*,

but has a more expanded talon than the Beck Ranch specimen mentioned above.

The lower incisors are small and crowded, and the canine is a stout, upright tooth with a small posterior tubercle, and a very weak lingual cingular swelling. The crowded, doubled-rooted p2–4 increase in size posteriorly. P2–3, and presumably p4, have expanded heels and are slightly oblique to the dental axis, as known (fig. 9.8G, H). P2–3 lack cingula, and a lingual-medial cuspid is not developed.

The m1 has a well-developed metaconid that is set slightly posterior to and diverges from the higher protoconid, and an accessory rootlet beneath the protoconid, like that commonly seen in modern skunks (fig. 9.8H), and various other modern and fossil mustelids. The trigonid occupies about 65% of the crown, and the tooth is relatively as broad as in *Spilogale*. The m1 of *B. chisoensis*, however, is relatively broader than in Blancan *Buisnictis*. The m1 talonid is semi-basined and rimmed by a trenchant, dominant hypoconid, and displays a distinct but subordinate entoconid. The m2 is relatively large, oval, with a flattened crown and a distinct protoconid cusp.

The lower jaw of *Buisnictis chisoensis*, similar to jaws of living *Spilogale pigmaea*, has a slightly convex ventral border, a short, anteriorly placed angular process, and a broad ascending ramus (fig. 9.8D). Multiple mental foramina occur below p3.

DISCUSSION: Many of North American later Tertiary small mustelids are based on isolated teeth or lower dentitions. Usual distinctions between them depend on differences in gross size, the morphology of the phylogenetically conservative m1, and differences in age. The Screw Bean specimens provide an opportunity to associate upper with lower teeth, and to attribute teeth with complete cranial material.

Weasels have retained the sectorial P4, but developed a more hypercarnivorous m1 through reduction or elimination of the metaconid, accompanied by simultaneous development of a trenchant talonid through loss of the entoconid. Among skunks, the M1 is a broad, low, crushing tooth, whereas in weasels the M1 usually is small. There is no doubt that the Screw Bean mustelid is a skunk. Based on cranial and lower jaw morphology, the taxon could be placed within *Spilogale*, extant spotted skunks, but the sectorial P4 bars this placement.

Isolated upper jaws of fossil skunks sometimes have been regarded as weasels because of their sectorial P4. Hibbard (1941a: 340) described a partial lower jaw from Rexroad locality 3, Meade County, Kansas, with a mephitine m1 as *Brachyprotoma breviramus*. The species was recharacterized (Hibbard, 1941b) as having crowded, oblique premolars, on the basis of alveoli. He thought that *B. breviramus* represented the smallest species of the Pleistocene genus, *Brachyprotoma* Brown. Hibbard (1950: 164) based the genus *Buisnictis* on *B. meadensis*, known from a musteline-like P4, UMMP 25769, from the early Blancan Rexroad Formation at Fox Canyon, XI Ranch, Meade County, Kansas. Because he knew at that time that *B. meadensis* had a weasel-like P4, he did not compare the type with the mephitine lower tooth of *Brachyprotoma breviramus*. Hibbard (1950: 165) then reported as *Brachyprotoma breviramus* a second lower jaw with p4–m1, UMMP 25771, from Fox Canyon. Later recovery of the anterior part of a skull with a lower jaw, UMMP 30242, from the Fox Canyon quarry convinced Hibbard (1954a: 224–226) that *Buisnictis meadensis* and *Brachyprotoma breviramus* were the same species. The Rexroad skunk then became *Buisnictis breviramus* (Hibbard). Fieldwork in the lower part of the Rexroad Formation, Buis Ranch, Beaver County, Oklahoma, resulted in the recovery of *Buisnictis schoffi* Hibbard (1954b: 344), based on a partial maxilla, UMMP 30196. Hibbard compared *B. schoffi* with *B. breviramus* (which at that time included the sample from Fox Canyon) and noted minor differences.

Bjork (1970), prompted by the recovery of *Buisnictis* in the early Blancan Hagerman Local Fauna, concluded that the Fox Canyon specimens are more similar in size to the Buis Ranch collection than to *B. breviramus* from the slightly younger Locality 3 of the Rexroad Formation. Bjork removed the Fox Canyon specimens from *B. breviramus* and placed them in *B. schoffi*. The reader, however, is reminded that the Fox Canyon locality produced the type of *B. meadensis*. If

Bjork (1970) is correct in equating the Fox Canyon and the Buis Ranch populations as an older, single species, then the composite population must be called *B. meadensis*, as recognized by Skinner and Hibbard (1972) and Baskin (1998a). This invalidates the species "*schoffi.*"

Skinner and Hibbard (1972: 110) then added *Buisnictis burrowsi*, from the early Pleistocene, late Blancan Keim Formation, Brown County, Nebraska. The valid species of *Buisnictis* thus became *B. meadensis* Hibbard, earliest Blancan, *B. breviramus* (Hibbard), late early Blancan, and *B. burrowsi* Hibbard and Skinner, late Blancan. The report of *B. chisoensis*, if correctly assigned, not only extends the range of *Buisnictis* downward, but also demonstrates the dental stereotypy of the genus and the antiquity of the *Spilogale*-like bulla. When Baskin (1998a) prepared his report, *B. chisoensis* from the Screw Bean Local Fauna had not been described, and Baskin questioned the Screw Bean "Clarendonian" occurrence of *Buisnictis* cited by Stevens and Stevens (1989: 79).

Hibbard (1954b: 348) stated "It is also probable that *Martinogale*, *Spilogale*, and *Mephitis* had a common ancestor in the Lower Pliocene" (at that time the Clarendonian was regarded "Lower Pliocene"). Baskin (1998a: 170) believes that the living North American skunks *Spilogale*, *Mephitis*, and *Conepatus* may descend from within a ca. 4.5 Ma immigration event of mephitines from Eurasia into North America in the early Blancan, initiated from *Promephitis*. Baskin suggested that *Buisnictis*, *Plionictis*, and *Martinogale* are derived from an earlier Clarendonian immigration event, derived from *Mesomephitis*. The occurrence of the *Spilogale*-like *Buisnictis* in the Screw Bean assemblage suggests that at least *Spilogale* of modern skunks is derived from within the Clarendonian immigration event.

The type of *Martinogale alveodens* Hall (1930) came from Edson Quarry, Sherman County, Kansas, late Hemphillian. Dunkle (1938) reported a more complete lower jaw, and upper teeth have been reported by Harrison (1978: 43). Hall (1930) thought that *Martinogale alveodens* was a musteline possibly ancestral to *Mustela*, the modern weasel. Dunkle concluded that the characteristics that separate *Martinogale* from *Mustela* are precisely the features that relate *Martinogale* with *Spilogale*. Harrison (1978: 42) notes that the accessory rootlets beneath the protoconid of m1 of *M. alveodens* provide unequivocal evidence to support a close relationship of *M. alveodens* with *Spilogale*, *Mephitis*, and *Conepatus*. Accessory rootlets, however, occur commonly in other mustelid subfamilies, thus they lack phylogenetic significance. Baskin (1998a: 160) states that *Martinogale* is related closely to *Buisnictis*.

Whistler and Burbank (1992) report *Martinogale* from the *Epicyon aphobus*/*Hipparion forcei* Zone, Dove Springs Formation, Ricardo Fauna, California, late Clarendonian. Baskin (1998a) identifies the fossils as *M. alveodens*, and mentions a skull with associated jaws. The specimen, LACM 56230, from locality 3776, consists of the ventral part of a basicranium and a fragmentary rostrum, associated with dentaries. The rostrum contains one P4 and both M1s. The dentaries contain p2–m1. LACM 56230 is a quarter to a third smaller than *B. chisoensis*, the M1 has a narrower talon, m1 has a distinct labial cingular rim, a taller metaconid, the lower premolars have sharper crests, broader and more cingulated heels, and p3–4 have a distinct medial-lingual cuspid, features that *B. chisoensis* lacks. The entotympanic does not appear to be as inflated as in *B. chisoensis*. The Ricardo species is a *Martinogale* that is surely in line with *M. alveodens*, but has less developed cingula and less sharp dental crests and ridges. *B. chisoensis*, however, is not placeable in *Martinogale*. The main obstacles barring a relationship is the prominent cingula, sharper dental crests and ridges, lower premolars with lingual-medial cuspids, different shaped mandible, and smaller size of *Martinogale*. The two genera were clearly separate as early as the late Clarendonian–earliest Hemphillian.

If correctly identified, *Buisnictis chisoensis* is the only *Buisnictis* for which the basicranium is known. There is no doubt that the skull is specialized toward *Spilogale*. Van Gelder (1959: 246) notes that among living skunks, only *Spilogale* exhibits lateral inflation of the mastoid sinus, so much so as to exceed in some individuals the bizygomatic

diameter, almost achieved in the type of *B. chisoensis*. The oldest known skunk that has a *Spilogale*-like dentition is *S. rexroadi* Hibbard, first described from the Rexroad Formation, early Blancan, Meade County, Kansas. *S. rexroadi* has also been reported from the Beck Ranch (Dalquest, 1972) and Blanco faunas of Texas (Schultz, 1977: 126), early Blancan. No skull is known for this species. The only reported P4–M1, MUCFV 8349 discussed above, comes from the Beck Ranch site, and shows a typically *Spilogale*-like P4, with its enlarged and posterolingual protocone.

Van Gelder believed probably correctly that Mexico was the center of origin for *Spilogale*, because he viewed *S. pygmaea* as the most primitive living species. The Screw Bean Local Fauna is near or within this realm. Some of the presumed "primitive" traits, the gracile skull and lack of a sagittal crest, probably are due to dwarfism. The smaller size of the mastoid sinus relative to *S. putorius*, however, is similar to *Buisnictis chisoensis*, and is probably a true primitive character state (as are the unbroken white stripes of the pelt). *S. pygmaea* is similar in size to *S. rexroadi*, but is smaller than *Buisnictis chisoensis* (see Van Gelder, 1959: 381). *B. chisoensis* probably was a predator of small vertebrates and insects; *Spilogale* is predominantly insectivorous. If so, the lineage that progressed toward *Spilogale* became more insectivorous and diminished in size.

Bjork (1970: 30) observed a progressive size decrease for *Buisnictis* through the Blancan. This trend is consistent with the larger size of *B. chisoensis* relative to the next younger *B. meadensis*. In turn, this implies that the ancestor for *B. chisoensis* was larger still, and would seem to eliminate the Ricardo species as a possible ancestor, as would the morphological differences noted above.

Martes nambianus Cope (1874) from the Pojoaque Member, Tesuque Formation (see Galusha and Blick, 1971: 108), Clarendonian, is now placed in *Martinogale* (Harrison, 1983; Baskin, 1998a). Harrison (1983: 27), however, ventured the suggestion that the broadened heel for p4 of *M. nambianus*, which separates *M. nambianus* from *M. alveodens*, might place *M. nambianus* with equal ease in *Pliogale*. *M. nambianus* resembles our species by lacking cingula and has premolars with more similarly expanded heels, but is as small as *M. alveodens*, thus much smaller than *Buisnictis chisoensis*.

Pliogale, the most generalized member of the *Pliogale*, *Martinogale*, *Buisnictis* clade (Baskin, 1998a: 170), lacks cingula, and m1 has an external accessory rootlet. *Pliogale furlongi* (Merriam, 1911: 249) is a small species from the late early Hemphillian Thousand Creek Local Fauna, Humboldt County, Nevada. Its m1 is small with a small metaconid that is separated from the protoconid posteriorly by a more distinct and deeper groove. *P. manka* Green (1956), Wolf Creek Local Fauna, early Clarendonian, is suitably large enough to have a possible relationship with *Buisnictis chisoensis*. *P. manka*, however, has a taller m1 with a relatively longer trigonid, shorter talonid, and taller and more trenchant hypoconid, within a more hypercarnivorous dentition that is perhaps in keeping with its greater age relative to *Buisnictis*. The immediate ancestry of *Buisnictis* might extend back to an unknown species of *Pliogale* allied with *P. manka* that inhabited the Mexican realm during the Clarendonian. The ultimate ancestry of these animals must be traced back to Eurasia.

If the above scenario is correct, *Spilogale* is a remote descendant of the Clarendonian immigration event, mentioned above. This in turn suggests that the origin of at least *Spilogale*, among the living skunks, is more remote than usually believed. Radinsky (1973) suggested, through study of brain endocasts, that skunks and skunklike animals are only remotely related to typical mustelids. Ledje and Arnason (1996) and Dragoo and Honeycutt (1997) recommend that the Mephitinae should be elevated to the rank of family, on the basis of molecular studies. The antiquity of the *Spilogale*-like mastoid process of *Buisnictis chisoensis* supports the view that skunks have had a long and separate adaptive history.

SUBFAMILY MUSTELINAE FISCHER DE WALDHEIM, 1817

Martes Pinel, 1792
Martes sp.
Figure 9.7A, B; table 9.6

Martes sp., extinct marten: Stevens and Stevens, 1989: 79.

TABLE 9.6
Measurements of *Martes* sp. Specimens at Texas Memorial Museum (in millimeters)

Upper teeth	42247-75 left	42247-75 right
P3 alveoli to M1, inclusive	—	19.25
P4-M1, inclusive	13.58	13.73
P4, AP diameter	9.35	9.55
P4, T diameter at protocone-parastyle	5.52	5.70
P4, T diameter at "waste"	3.86	3.86
P4, AP diameter of protocone	2.59	2.70
M1, AP diameter of paracone-metacone	5.34	5.46
M1, AP diameter of crown at "waste"	4.38	4.34
M1, AP diameter of talon	5.25	5.57
M1, T diameter normal to axis of palate	8.70	9.21

REFERRED MATERIAL: TMM 42247-75, detached right and left palatal fragments of a presumed single individual, with alveoli for left P3, and both P4–M1s.

STRATIGRAPHIC OCCURRENCE: From the top of Bench 2, Liles measured section, Bench member, Banta Shut-in formation (fig. 9.2F), Big Bend National Park, Texas; Screw Bean Local Fauna, early early Hemphillian, late Miocene.

DESCRIPTION: No contact exists between the right and left palatal pieces of what must have been a single individual. The left fragment preserves the two alveoli for P3, a complete P4, and an M1 with a damaged metacone. The right fragment preserves the P4 and the M1 with a damaged talon. The teeth are little worn (fig. 9.7A). P4 is a relatively broad, sectorial tooth. The anteromedially placed protocone is a distinct cusp separated from the tall paracone by a deep saddle. The distinct parastyle is connected to the tall paracone by a slight ridge. The metacone, a low cusp that is only slightly taller than the paracone, is connected to the paracone by a concave ridge which forms the carnassial blade. The carnassial "notch" is broadly open, as is characteristic of mustelids. A lingual cingulum is present. The P4 closely matches that for the modern pine marten, *Martes americana* in size and morphology.

The M1 has a low protocone connected to the small protoconule by a ridge. The protoconule, in turn, merges with the anterior cingulum, which communicates with the paracone by a low ridge. The low paracone is set close to the posteromedial metacone as in *Martes*. The paracone is about twice the size of the metacone and is slightly taller. A narrow stylar shelf is present labial to the paracone. No metaconule is present. The hypocone is slightly convex upward in lingual view and is expanded anteroposteriorly and posteriorly, which gives a distinct figure-eight shape to the tooth. The M1, when seen in posterior view, is strongly flexed. The flexure places the talon and the apices of the protocone, paracone, and parastylar shelf practically on the same plane. The M1 is remarkably similar to that of extant *Martes americana*.

Although lower teeth are unknown for our *Martes* sp., m1 probably had a reduced metaconid. The anterior expansion and great flexure of the talon of the M1 usurps the space necessary to accommodate that cusp.

DISCUSSION: The Screw Bean specimen is a mustelid the size of males of *Martes americana*. Many fossil specimens have been referred to *Martes* in the literature, but most are lower teeth or jaws that are not directly comparable to TMM 42247-75. Furthermore, the substantial interspecific size variation that exists among the modern mustelids must be considered.

Martes originated in the Old World, and has been known in Eurasia from the Miocene onward (Franzen and Storch, 1975: 245; Pilbeam et al., 1977; Qi, 1985; Baskin, 1998a). *Martes* (sensu lato) is known in North America since the early Barstovian. Multiple extinctions and reintroductions from Eurasia certainly are possible. Some of the North American presumed *Martes* species are now placed in *Plionictis* Matthew (1924) or *Sthenictis* Peterson (1910; see Baskin, 1998a: 162–163). *Plionictis*, late Hemingfordian to early Clarendonian, is hard to distinguish from *Martes* (Baskin, 1998a). The well-developed parastylar shelf, limited anterior and posterior expansion of the talon of M1 of *Plionictis*, and greater age serve to distin-

guish the Screw Bean species from *Plionictis*. *Sthenictis*, late Hemingfordian through ?early Hemphillian, differs from *Martes* by a broader stylar shelf and less anteriorly and posteriorly expanded M1 talon (Baskin, 1998a).

The great similarity of TMM 42247-75 with the American pine marten, *Martes americana*, demands comparisons with *Martes*. Baskin (1998a) recognizes three Tertiary North American species, *Martes glareae*, *Martes stirtoni*, and *M. oregonensis*. *Martes glareae* (Sinclair, 1915), ranges from the early Barstovian Lower Snake Creek through the early Clarendonian Minnechaduza faunas (see Skinner et al., 1977: 347; Tedford et al., 1987). The type lower jaw is not directly comparable with our specimen, but is a *M. americana*-sized species. Sinclair (1915: 80) notes, however, that the metaconid of *M. glareae* is larger than in *M. americana*. Because our species probably had a reduced metaconid similar to that of *M. americana*, the Screw Bean species probably is not *M. glareae*.

Martes stirtoni Wilson (1968) is known from the early Clarendonian WaKeeney Local Fauna, Trego County, Kansas. *M. stirtoni* differs from the Screw Bean *Martes* sp. by smaller size, heel of M1 less expanded anteroposteriorly and with a distinct lingual cingular ridge, and by the presence of a well-developed metaconule. The teeth of the type are relatively narrower, have sharper cusps and ridges, and are more sectorial than in the Screw Bean *Martes*, and the talon of M1 in lingual view is more distinctly convex upward.

Martes oregonensis (Shotwell, 1970: 79) is based on a partial right jaw with p2–m2, from the Chalk Butte Formation (undivided), Hemphillian, Little Valley, northern Malheur County, Oregon. The type and the Screw Bean species are not directly comparable. *M. oregonensis* is similar in size to the modern *M. americana*, and a referred P3–4 are similar (Shotwell, 1970). Shotwell, however, notes that *M. oregonensis* differs most notably from *M. americana* by having a much larger m1 metaconid. This indirectly suggests that the M1 of *M. oregonensis* had a less anteroposteriorly expanded heel than either modern *Martes americana* or the Screw Bean species. *M. oregonensis* also has better developed cingula and accessory cusps. Based on limited information it seems unlikely that *M. oregonensis* and the Screw Bean species represent the same taxon. Other *Martes* specimens of more or less similar age as the Screw Bean Local Fauna have not been described in detail (see Shotwell et al., 1963: 51; Shotwell, 1970: 5; Voorhies, 1990: 136, 142). The Screw Bean species might be related to any one of these.

CONCLUSIONS

The establishment of an age for the Screw Bean Local Fauna has been difficult due to the fragmentary nature of most of the specimens that can be identified at best only to genus. Study of additional and some better preserved specimens suggests that the fauna, originally thought to be late Clarendonian (Stevens and Stevens, 1989) is Hemphillian in age. None of the index, or first-appearance taxa, however, used to define the Hemphillian Age of Wood et al. (1941) are present. An age of early early Hemphillian, late Miocene, is given to the Screw Bean Local Fauna for the following reasons.

Wood et al. (1941) used the first appearance of ground sloths to mark the beginning of the Hemphillian Land Mammal Age. Marshall et al. (1979) viewed the sloth *Megalonyx* (Oshkosh Local Fauna, upper part of the Ash Hollow Formation, Garden County, Nebraska) as the oldest North American edentate, and placed this occurrence at >9.3 Ma, extrapolating from a 9.3-Ma age determination for an ash in nearby Greenwood Canyon. Breyer (1981) regarded the Oshkosh and Greenwood Canyon local faunas as correlative, and as just predating a mid-Hemphillian extinction event of ≈7 Ma. Tedford et al. (1987) and Voorhies (1990) believe these faunas to be about 6–7 million years old. Wagner (1981) and Lindsay et al. (1984) record an older North American edentate, *Pliometanastes*, from the Siphon Canal Local Fauna, Disaster Peak Member, Mehrten Formation. The Siphon Canal assemblage has been dated at 8.19 Ma (Wagner, 1981; Lindsay et al., 1984; Tedford et al., 1987). These edentate occurrences place the Clarendonian/ Hemphillian boundary of Wood et al. (1941)

at about 8.2 Ma. Tedford et al. (1987) and Whistler and Burbank (1992) have lowered the Clarendonian/Hemphillian boundary to about 8.9 or 9 Ma (also see Wang et al., 1999). This predates the oldest known North American edentates by some 0.7–0.8 million years, mentioned in the explanation for figure 10.1 of Woodburne (1987).

The Clarendonian Land Mammal Age, and thus the Clarendonian Chronofauna (Webb, 1969), is based on the Clarendon Fauna from Donley County, Texas. The Screw Bean Local Fauna lived at a time when various members of that chronofauna were becoming extinct, and when some modern lineages were just appearing. The gradual demise of the Clarendonian Chronofauna was complete by the time of the mid-Hemphillian extinction event (or "major faunal discontinuity") mentioned above at about 7 Ma. Later in the Hemphillian, at about 6 Ma, holarctic immigrants arrived from Eurasia, during a sea level low-stand. Some of these immigrants constitute the Hemphillian index taxa of Wood et al. (1941) and the Mio-Pliocene Chronofauna (see Janis et al., 1998a: 88). This faunal discontinuity has prompted the division of the Hemphillian into an early and a late interval (see Wagner, 1981; Lindsay et al., 1984). Neotropical immigrants (such as edentates) began to arrive from South America and/or the Antilles, as the Clarendonian Chronofauna declined, in the "early" Hemphillian. Because of the extension downward of the Clarendonian/Hemphillian boundary to about 9 Ma, and due to the absence of edentates older than 8.2 Ma, the "early" Hemphillian has been subdivided into an "early early" and a "late early" interval (Tedford et al., 1987; Schultz, 1990; Baskin, 1998b; Janis et al., 1998a). This cumbersome terminology is used in this paper.

To date, no edentate remains occur in the Screw Bean Local Fauna, an assemblage that occupies a strategic position within the invasion route envisioned for South American taxa moving north. However, edentate remains, although rare, are geographically widely distributed in late early Hemphillian faunas (Leidy and Lucas, 1896; Sinclair, 1906; Stirton, 1939; Schultz and Stout, 1948; Hirschfeld and Webb, 1968; Webb and Tessman, 1968; Shotwell, 1970; Schultz, 1977; Marshall et al., 1979; Tedford et al., 1987; Voorhies, 1990). The absence of edentates in the Screw Bean fauna is troubling if the fauna is younger than earliest Hemphillian.

Another consideration is the lack of oreodonts, negative evidence, in the Screw Bean Local Fauna in spite of diligent search. The oreodont *Ustatochoerus* Schultz and Falkenbach, abundant in Trans-Pecos Texas in the earliest Miocene (Stevens, 1977; Stevens and Stevens, 1989), is typical of the Clarendonian Chronofauna. Tedford et al. (1987: 194) note that *Ustatochoerus* probably became extinct at the end of the Clarendonian. Breyer (1981: 1214) regards the presumed Hemphillian oreodont occurrences in Nebraska as suspect. A derived *Ustatochoerus*, *U. californicus*, however, did extend into Member 6 of the Dove Spring Formation, Kern County, California, to about 8 Ma or slightly later, earliest Hemphillian (Whistler and Burbank, 1992). The lack of *Ustatochoerus* in the Screw Bean Local Fauna, thought to be real, suggests that the fauna lived after *Ustatochoerus* had become extinct.

The Screw Bean Local Fauna contains "early early" Hemphillian taxa that are late survivors of the Clarendonian Chronofauna, but contains none of the "late early" Hemphillian Eurasian immigrants (see Webb, 1969, 1983, 1989; Tedford, 1970; Tedford et al., 1987; Lindsay et al., 1984; Voorhies, 1990). Among the Screw Bean carnivores is the borophagine dog, cf. *Epicyon haydeni*, and the cats cf. *Pseudaelurus* sp. and cf. *Nimravides catocopis*. *Epicyon* did not survive the "early" Hemphillian (see Lindsay et al., 1984; Leite, 1990; Munthe, 1998). According to Breyer (1981), *Epicyon* became extinct during the "mid-Hemphillian extinction event," centered at 6–7 Ma. Lindsay et al. (1984) show that *Epicyon* did not survive beyond the beginning of the late early Hemphillian, at what now would be regarded Chron 4r (Berggren et al., 1995; Cande and Kent, 1995). *Nimravides catocopis* extends from the late Clarendonian to the end of the early Hemphillian (Lindsay et al., 1984; Tedford et al., 1987). *Pseudaelurus* has a stratigraphic range from the late Hemingfordian to the late or latest Hemphillian (Martin, 1998).

The Screw Bean *Vulpes* sp. may represent a stem member of its lineage. *Buisnictis* and *Martes* are typical genera of the Mio-Pliocene Chronofauna, late Hemphillian–early Blancan. The mephitine *Buisnictis*, however, was not descended from an immigrant from Asia that shaped the Mio-Pliocene Chronofauna as suggested by Janis et al. (1998a). *Buisnictis* probably derived from an older immigration event (see Baskin, 1998a) that flavored the Clarendonian Chronofauna. The absence of *Buisnictis* in earlier Hemphillian faunas on the High Plains may result from the fact that *Buisnictis* originated far to the south, toward or within the Mexican realm. *Spilogale*, a presumed *Buisnictis* descendant, probably originated there.

Martes-like mustelids long have been in North America. The occurrence of *Martes* sp. in the Screw Bean Local Fauna supports the view that dentally modern martens have been present in North America longer than is usually supposed, contrary to Anderson (1984). The boreal or montane habit of modern *Martes* is inconsistent with the paleoenvironment envisioned for the Screw Bean Local Fauna. Multiple extinctions of *Martes* in North America, and reintroductions of ecologically different relatives from Eurasia is probable.

The fauna occupies a strategic location within North America for north–south and east–west faunal interchange, yet the fauna has a low taxonomic diversity. The impoverishment is thought to be in part the result of depositional style(s) and climatic factors. The lack of an oreodont, thought to be real, is important. The lack of edentate remains is less helpful because of their rarity in early Hemingfordian faunas in general. Given the presence of late members of the Clarendonian Chronofauna and the absence of: (a) oreodonts (disappearance by ≈8.5 Ma), (b) edentates (appearance by ≈8.2 Ma), and (c) characteristic Mio-Pliocene Chronofauna index taxa, the age of the Screw Bean Local Fauna is thought to be early early Hemphillian sensu Tedford et al. (1987) and others. Other members of the fauna, yet to be reported, support this age assessment.

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