CAPROMERYX (ARTIODACTYLA: ANTILOCAPRIDAE) FROM THE RANCHOLABREAN TRAMPEROS CREEK FAUNA, UNION COUNTY, NEW MEXICO, WITH A REVIEW OF THE OCCURRENCE AND PALEOBIOLOGY OF CAPROMERYX IN THE RANCHOLABREAN OF NEW MEXICO

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Abstract—Tramperos Creek is an open site in Union County, northeastern New Mexico, which has produced a Rancholabrean vertebrate fauna characterized by the presence of Bison and Mammuthus. A partial skull with both right and left horn cores of Capromeryx furcifer is described from this site in which the anterior prong of the horn core is reduced to little more than a nubbin of bone about 3 mm in height. This represents the most extreme reduction in the anterior prong of the horn core of Capromeryx yet known. We suggest that the anterior prong may not have been expressed at all in the keratinous horn sheath, or that, alternatively, a fairly substantial keratinous expression of the anterior sheath may have been present despite the absence of a concomitantly developed horn core. We further speculate that the reduction in the anterior prong may have been associated with a progressive invasion of less-open vegetation and the adoption of a more solitary lifestyle, paralleling similar differences in the elaboration of cranial appendages in living bovids and cervids.

INTRODUCTION

We document here the occurrence in the Tramperos Creek Local Fauna (Rancholabrean) of an example of Capromeryx furcifer with extreme reduction of the anterior tip of each horn core, so that the tine may not have been expressed in the external keratin sheath covering the horn core. The skull described here is an adult, most likely male, individual with posterior horn cores at least 115 mm in height. The anterior horn cores are reduced to small points only 3 mm in height. We note that Capromeryx in the Rancholabrean of New Mexico is known from 14 different localities, mostly cave sites, but never in abundance. This may reflect a taphonomic bias, or it may be related to the behavior of the diminutive pronghorn.

The fossils from the Tramperos Creek Local Fauna are housed in the vertebrate paleontology collection of the New Mexico Museum of Natural History and Science (NMMNH). Other specimens of Rancholabrean Capromeryx from New Mexico are cited from the following museums: Natural History Museum of Los Angeles County (LACM), Los Angeles, California; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts; Maxwell Museum of Anthropology (MMA), University of New Mexico, Albuquerque; Shuler Museum of Paleontology (SMP), Southern Methodist University, Dallas, Texas; Texas Memorial Museum (TMM), University of Texas, Austin, Texas; University of Arizona Laboratory of Paleontology (UALP), Tucson, Arizona; United States National Museum (USNM), Washington, D.C. (USNM); Laboratory for Environmental Biology, Centennial Museum (UTEP), University of Texas at El Paso, Texas; University of California Museum of Paleontology (UCMP), Berkeley, California; Florida Museum of Natural History (UF), University of Florida, Gainesville. Other abbreviations used are Local Fauna (LF), kiloanna or thousands of years before present (ka), kilometer (km), megananna or millions of years before present (Ma), meters (m), North American landmammal “age” (NALMA), and United States Geological Survey (USGS).

LOCALITY AND GEOLOGY

The Tramperos Creek Local Fauna (NMMNH site number L-5083) is located just west of the old Woodson Ranch (identified as “Miera” on the Minnie Butte USGS 7.5 minute quadrangle), about 50 km southwest of Clayton in southern Union County, northeastern New Mexico (Fig. 1). Coordinates for the site are 36°05’N latitude and 103°33’W longitude, and the elevation is 4,890 ft. (1,490 m). Tramperos Creek is an intermittent stream that flows eastward into Texas where it eventually becomes a tributary of the Canadian River. Although the creek is mostly dry, a pond or wet marsh is periodically present in a low area just northwest of the outcrops. The Tramperos Creek site was discovered in April 2002 by Ken Garrison and was worked by NMMNH field crews in May 2002 and August 2004. Morgan and Lucas (2005) briefly reviewed the vertebrate fauna.

The fossils occur in nearly vertical outcrops along the south and east sides of Tramperos Creek. The exposed section is about 200 m long and reaches a maximum of 10 m in thickness. The outcrop is broadly horseshoe-shaped, trending almost east-west for about 100 m and then taking a sharp bend north for another 100 m. Fig. 2 is a stratigraphic section measured about midway along the Tramperos Creek exposures, near site TC 6 where a Mammuthus tooth was collected. The section consists of unnamed Quaternary alluvium composed of fine-grained sediments, silt and silty sand in the lower 3-4 m, clays in the upper 4-5 m, and a 1 m thick soil horizon at the top. Bones occur primarily in the lower 3 m, which consists of mottled bluish-gray to yellowish-orange silts and silty sands and dark brown clays. This lower part of the section also contains abundant freshwater mollusks, as well as fish, frogs, salamanders, and muskrats, indicating the former presence of permanent water such as a stream or pond.

Large mammals are fairly common in the Tramperos Creek fauna, with the most widespread taxa being an extinct species of Bison, the large camel Camelops, and the horse Equus. There are also several concentrations of small vertebrates in the lowermost part of the stratigraphic section. One of these sites is composed mostly of small terrestrial vertebrates, including toads, ground squirrels, pocket gophers, and rabbits, whereas the second site has a large component of freshwater vertebrates, including small fish, frogs, and salamanders, as well as rodents and other small terrestrial species, particularly snakes. The Tramperos Creek vertebrate fauna consists of 30 species, including at least 13 species of lower vertebrates (fish, amphibians, reptiles, and birds) and 17 species of mammals (Table 1).

Parts of three individuals of Bison were excavated from a small area at the base of the stratigraphic section at the northern end of the outcrop. Two of these specimens consist of partial articulated postcranial skeletons, but no skulls or horn cores have been found that would allow us to make a positive species-level identification, although the
extinct *Bison antiquus* is most likely. *Bison antiquus* is the only species reported from late Rancholabrean faunas in New Mexico, while *Bison latifrons* in known from earlier Rancholabrean sites. *Bison latifrons* is much larger than the bison represented by the two partial skeletons from Tramperos Creek. The large sample of aquatic vertebrates and associated freshwater mollusks from the lower part of the section, as well as the fine-grained sediments in which the fossils occur, suggest a quiet-water depositional environment.

The Tramperos Creek LF is Rancholabrean in age based on the presence of *Bison* and *Mammuthus columbi*, but no further refinement of the age is possible. We submitted a sample of bone from the *Capromeryx* skull to Beta Analytic, Inc. for an AMS radiocarbon date; however, the specimen did not contain enough collagen for a reliable date. There are several reasons that a bone sample may lack sufficient collagen for dating, including an age greater than 50 ka or leaching of the organic matter from the bone. Numerous attempts by the junior author and others to date bones from Rancholabrean open sites in New Mexico have been unsuccessful, including sites that were thought to date between 10 and 20 ka based on other data, suggesting that leaching of collagen from the bone may be a recurring problem.

**CAPROMERYX FROM THE RANCHOLABREAN OF NEW MEXICO**

*Capromeryx* is known from 13 late Pleistocene (Rancholabrean) faunas in New Mexico, including Tramperos Creek, and one mid Pleistocene (late Irvingtonian?) cave site (Fig. 1). *Capromeryx* also occurs in six late Pliocene and early Pleistocene (Blancan) faunas in New Mexico (Morgan and Lucas, 2003; Morgan et al., this volume). Most of the Rancholabrean records consist of limited samples of isolated teeth and/or postcrania, elements that are identified as *Capromeryx* primarily on the basis of their small size. *Capromeryx* is the only very small ruminant artiodactyl known from late Pleistocene faunas in New Mexico. Most of these specimens are here referred to *Capromeryx* sp., although they probably belong to the small species *C. furcifer*, the only recognized Rancholabrean member of the genus (see taxonomic discussion below).

Among the 13 New Mexico Rancholabrean faunas with *Capromeryx*, three are open or stratified sites and ten are caves. The three open sites are all located in northeastern New Mexico, including Tramperos Creek and Perico Creek in Union County and Blackwater Draw in Roosevelt County (Fig. 1). Tramperos Creek is the only Pleistocene open site in New Mexico containing fossils of *Capromeryx* that are diagnostic at the species level, consisting of the posterior portion of the skull with both horn cores intact, described herein.

The Perico Creek site is located along the north side of Perico Creek on the Kiowa National Grassland, about 15 km southeast of Clayton in Union County in northeastern New Mexico just west of the Texas line (Fig. 1, site 2), and about 60 km northeast of the Tramperos Creek site. The fossiliferous unit is a channel sand deposit 3-5 m thick, overlying the Miocene Ogallala Formation and about 1-2 m below the local land surface. The vertebrate fossils occur mostly as isolated elements in a tan, fine clayey to silty sand with abundant small freshwater bivalves and freshwater and terrestrial gastropods, indicating a freshwater depositional environmental such as a small stream or pond. The Perico Creek vertebrate fauna consists of about 15 species, including a single postcranial element of *Capromeryx*, as well as *Equus*, the peccary *Platygonus compressus*, *Camelops hesternus*, and *Mammuthus* sp. (Schumacher, 2001; Morgan and Lucas, 2005). An Irvingtonian or Rancholabrean age is indicated by the presence of *Mammuthus*. Although the site lacks *Bison*, the presence of the small peccary *Platygonus compressus* suggests a Rancholabrean age.

The Blackwater Draw Fauna (also known as Blackwater Draw Locality 1, the Clovis site, and the Brown Sand Wedge and Gray Sand Local Faunas) is located in Blackwater Draw, about 16 km southwest of Clovis and about 10 km north of Portales in northeastern Roosevelt County in east-central New Mexico (Fig. 1, site 3). Although better known as a Paleoindian archaeological site (Hester, 1972; Haynes, 1995; Holliday, 1997, 2005), Blackwater Draw has the most diverse late Pleistocene vertebrate fauna known from an open site in New Mexico (Lundelius, 1972; Slaughter, 1975; Morgan et al., 2001). Two latest
TABLE 1. Vertebrate faunal list for the Rancholabrean (late Pleistocene) Tramperos Creek Local Fauna, Union County, New Mexico. Extinct species indicated by †.

Osteichthyes
Ictaluridae
Several species of small bony fish

Amphibia
Anura
Bufonidae
Bufo sp.
Ranidae
Rana sp.

Caudata
Ambystomatidae
Ambystoma tigrinum

Reptilia
Serpentes
Colubridae

Aves
Anatidae

Mammalia
Lipotyphla
Soricidae

Lagomorpha
Leporidae
Sylvilagus audubonii

Lepus sp.

Rodentia
Sciuridae
Cynomys ludovicianus

Spermophilus sp. - two species, one small, one large

Geomyidae
Geomys bursarius

Thomomys sp.

Heteromuridae
Perognathus sp.

Cricetidae
Peromyscus sp.

Arvicolidae
Microtus sp.

Ondatra zibethicus

Perissodactyla
Equidae
†Equus niobramensis

Artiodactyla
Camelidae
†Camelops hesternus

Antilocapridae
†Capromeryx furcifer

Bovidae
†Bison cf. B. antiquus

Proboscidia
Elephantidae
†Mammuthus columbi

Pleistocene (late Rancholabrean) vertebrate faunas have been named from Blackwater Draw based on the stratigraphic units from which they were derived, the Gray Sand LF (Lundelius, 1972) and the Brown Sand Wedge LF (Slaughter, 1975). The Gray Sand immediately pre-dates Paleoindian occupation of this region, whereas Clovis artifacts are found in the Brown Sand Wedge, together with remains of extinct Pleistocene megafauna (Haynes, 1995). The Gray Sand and Brown Sand Wedge occur in stratigraphic superposition over a thickness of about 2 m of section and represent a time interval of less than 3000 years (radiocarbon ages between 11 ka and 13 ka; Haynes, 1995), and lack notable differences in their large mammal faunas. Therefore, Morgan and Lucas (2005) combined the vertebrate assemblages from the Gray Sand and Brown Sand Wedge Local Faunas into the more inclusive Blackwater Draw Fauna, which includes all late Pleistocene (late Rancholabrean) vertebrates from Blackwater Draw Locality 1. In addition to the latest Pleistocene radiocarbon dates, a Rancholabrean age for the Blackwater Draw is indicated by the presence of the dire wolf Canis dirus, Bison antiquus, and Mammuthus columbi (Lundelius, 1972). The Brown Sand Wedge LF has a rich microvertebrate fauna obtained primarily by screenwashing (Slaughter, 1975). The screenwashing of sediment from the Brown Sand Wedge also produced a distal radius-ulna and a hoof of Capromeryx sp.

The northernmost New Mexico cave containing Capromeryx is Sandia Cave, located in the Sandia Mountains about 20 km northeast of Albuquerque in Sandoval County (Fig. 1, site 4). At an elevation of 2208 m, Sandia Cave is also the highest site in New Mexico with Capromeryx. Like Blackwater Draw, Sandia Cave is a well known latest Pleistocene archaeological site, and was one of the first sites in North America where Paleoindian artifacts were found in association with extinct Pleistocene megafauna (Hibben, 1941). There are at least eight species of large extinct mammals in the Sandia Cave collection at the Maxwell Museum of Anthropology at the University of New Mexico, including the Shasta ground sloth Nothrotheriops shastensis, Equus sp., Camelops hesternus, the big-headed llama Hemiauchenia macrocephala, the American mastodon Mammut americanum, and Mammuthus columbi, as well as an upper molar of Capromeryx sp. (Thompson and Morgan, 2001; Thompson et al., 2008). Three radiocarbon dates on collagen from large mammal bones from Sandia Cave range from 11-14 ka (Haynes and Agogino, 1986). Doolittle Cave is a rock shelter situated at an elevation of 1640 m in a canyon west of the Mimbres River in southeastern Grant County in southwestern New Mexico (Fig. 1, site 5). It appears that there must have been a Rancholabrean level beneath the rich archeological deposit reported by Cosgrove (1947). A horn core of Capromeryx is known from Doolittle Cave (Cosgrove, 1947). The specimen (MCZ 15238 M) is the base of a left horn core.

U-Bar Cave is located in the Alamo Hueco Mountains in Hidalgo County, at an elevation of 1540 m, in the Bootheel region of southwestern New Mexico, approximately 10 km from the border with the Mexican state of Chihuahua (Fig. 1, site 6). U-Bar Cave consists of a large chamber with an extensive accumulation of sediment that was mined for fertilizer. This cave has a diverse late Rancholabrean vertebrate fauna, including Capromeryx and the larger antilocaprid Stockoceros, as well as Nothrotheriops shastensis, Canis dirus, the giant short-faced bear Arctodus simus, several species of Equus, the extinct mountain deer Navahoceros fricki, Bison, and the shrub ox Euceratherium collinum (Harris, 1985a, 1993). U-Bar Cave is the southernmost and westernmost record of Capromeryx from New Mexico (31°28’ North, 108°26’ West). Harris (1993) reported Capromeryx sp. in both mid Wisconsinan and late Wisconsinan stratigraphic units in U-Bar Cave, with radiocarbon ages ranging from about 13-36 ka.

Conkling Cavern is located on the eastern slope of Bishop’s Cap (also known as Pyramid Peak), a limestone peak at the southern end of the Organ Mountains, about 15 km southeast of Las Cruces in Doña Ana County in southern New Mexico (Fig. 1, site 7). It lies at an elevation of 1290 meters. Conkling Cavern and the nearby Shelter Cave (see below) were discovered by Roscoe Conkling and excavated in 1929 and 1930 by field parties from the Natural History Museum of Los Angeles County (LACM). Besides Capromeryx, other large mammals from Conkling Cavern include Nothrotheriops shastensis, Canis dirus, Equus, Camelops, Hemiauchenia, and Bison (Conkling, 1932; Harris, 1993, 2011). Although the fauna from Conkling Cavern is almost certainly late Rancholabrean in age, there are no available radiocarbon dates to confirm the age.

Shelter Cave is on the western slope of Bishop’s Cap in Doña Ana
County in southern New Mexico, about two miles west of Conkling Cavern (Fig. 1, site 8) but somewhat higher in elevation at 1475 meters. As its name indicates, Shelter Cave is a rock shelter. The vertebrate fauna includes the antilocaprids Capromeryx and Stockcercos conklingi (Stock, 1930, 1932), as well as Nothrotheriops shastensis, two species of Equus, and Camelops. Shelter Cave has one of the largest samples of Capromeryx furcifer known from New Mexico, including a horn core, maxilla, mandible, and numerous postcranial elements. Radiocarbon ages on three coprolites of Nothrotheriops from Shelter Cave range from 11-12.5 ka (Thompson et al., 1980).

Pendejo Cave is located in Rough Canyon, about 20 km east of Orogande on the Fort Bliss Military Reservation in Otero County, southeastern New Mexico, at an elevation of 1490 meters (Fig. 1, site 9). It is a rather small cave, but preserves a diverse fauna of late Rancholabrean vertebrates dating from the mid to late Wisconsinan (about 11 to >55 ka; Harris, 2003, 2011). Capromeryx occurs in both mid and late Wisconsinan strata in Pendejo Cave, and is represented by a nearly complete horn core of C. furcifer (= C. minor) (Harris, 2003, 2011). Other extinct mammals from the Pendejo Cave fauna include Nothrotheriops shastensis, two species of Equus, Camelops, Hemiauchenia macrocephala, Stockcercos conklingi, and Bison antiquus.

Five caves in the vicinity of the Guadalupe Mountains in Eddy County in southeastern New Mexico have produced specimens of Capromeryx, including Algerita Blossom Cave, Big Manhole Cave, Dry Cave, and Muskox Cave, all of late Pleistocene age (Harris, 1993), and Slaughter Canyon Cave of mid Pleistocene age, probably late Irvingtonian (Lundberg and McFarlane, 2006; Morgan and Lucas, 2006; Polyak et al., 2006). Harris (1993) listed Capromeryx sp. from Dark Canyon Cave near Carlsbad in Eddy County, but this material has since been reidentified as Stockcercos (Harris, 2011).

Algerita Blossom Cave is located west of Carlsbad between McKintridge Cave and Dry Cave (Fig. 1, site 10) at 1280 m. The cave opening is a fissure that was excavated by cavers (Harris, 2011). Algerita Blossom Cave has a mammalian fauna of 35 species, including four members of the Pleistocene megafauna: Nothrotheriops shastensis, the Mexican horse Equus conversidens, Hemiauchenia macrocephala, and Capromeryx sp. (Harris, 1993, 2011). The fauna suggests a late Rancholabrean age.

Big Manhole Cave is located just north of Carlsbad Cavern National Park near Lechuguilla Cave (Fig. 1, site 11). The small entrance at an elevation of 1280 m leads to a large chamber almost 30 m in diameter and about 35 m deep that appears to have functioned as a natural trap (Logan, 1981). The diverse mammalian fauna of nearly 50 species includes nine members of the Pleistocene megafauna: Canis dirus, Panthera atrox, the cheetah-like cat Miracinonyx trumani, Equus, Capromeryx furcifer, Stockcercos conklingi, Euceratherium collinum and Harrington’s extinct mountain goat Oreomnos harringtoni. Capromeryx is represented by a skull (USNM 521305) and a small sample of postcranial elements. Radiocarbon dates on bone collagen from Muskox Cave range from 18-26 ka (Logan, 1981).

Slaughter Canyon Cave (also known as New Cave) is located in Carlsbad Caverns National Park in Eddy County at an elevation of 1517 m (Fig. 1, site 14), about 14 km southwest of Carlsbad Cavern. Slaughter Canyon Cave contains extensive guano deposits that were mined for fertilizer until the 1950s. The vertebrate fauna of about 15 species is overwhelmingly dominated by the extinct free-tailed bat Tadarida constatitaei (Lawrence, 1960; Morgan, 2002). There are only two large mammals in the fauna, the extinct mountain deer Navahoceros fricki, represented by two nearly complete skeletons, and several isolated postcranial elements of Capromeryx (Morgan and Lucas, 2006). Uranium-series dates of 209 ka (Lundberg and McFarlane, 2006) and 212 ka (Polyak et al., 2006) were obtained from a calcite flowstone layer overlying the guano deposit containing the Slaughter Canyon Cave vertebrate fauna. Polyak et al. (2006) proposed an age greater than 400 ka (Irvingtonian) for the guano deposit and vertebrate fauna.

**DESCRIPTION OF TRAMPEROS CREEK CAPROMERYX**

Material: NMMNH 50387 (Fig. 3 A-E): partial skull consisting of right and left horn cores, most of the frontals and parietals, part of the basicranium, part the occipital shield and miscellaneous cranial fragments. Skull lacks the rostrum and dentition; the mandible is likewise absent. Collected May 30, 2002 by Gary S. Morgan and Kenneth Garri-

Description: Both right and left horn cores are nearly complete. The left horn core posterior prong is nearly complete, lacking an estimated 10-15 mm of the tip. The left anterior prong is complete. The right horn core is less well preserved, but still substantially complete. The missing portion of the tip is estimated to be at 30-35 mm in length. The right anterior prong is complete.

The larger posterior prongs as preserved are 105 mm (left) and 85 mm (right) in length, measured from the saddle between the prongs. They are estimated to have been approximately 115 mm in length when complete. Both posterior prongs are straight, without any suggestion of curvature or torsion. There is a marked sulcus on the posterior side of the horn core, which extends from the base of the horn core to the tip. The distal-most half of the sulcus spirals very slightly toward the medial side of the horn core, but the horn core itself does not appear twisted. About half way along its course, a smaller sulcus appears to branch off from the lateral side of the main sulcus, extending about 30 mm towards the tip, diverging laterally slightly, but remaining about 3 mm from the main sulcus at its farthest separation. Other grooves, much less well-defined, shorter and shallower, occur on the horn core, particularly on the anterior edge, 180 degrees from the main sulcus. All appear to begin just below the base of each horn core.
FIGURE 3. NMMNH 50387, *Capromeryx furcifer* from Tramperos Creek Local Fauna, Union County, New Mexico. Partial skull in **A**, **E**, posterior views, **B** anterior view, **C**, right lateral view and **D**, left lateral view.
any fossil antilocaprine. Where such a feature appears to be present, it is due to the erosion, mechanical or otherwise, of the surface of the horn core exposing the underlying spongy bone which tends to have structures paralleling the axis of the horn core. We have seen this on locations along horn cores ranging from the base to the tips.

The anterior prong of each horn core is a tiny nubbin of bone about 2.5 (left) or 3.0 mm (right) in height. It sits on a slight, flange-like anterior expansion of the horn core base.

Given the preserved portions of the skull, it is difficult to determine accurately the angle which the horn core follows in comparison to the long axis of the skull, usually determined by the basioccipital, or by the occusal plane of the dentition. Our best estimation for the present specimen is that the horn core, as determined primarily by the posterior prong, angles slightly anteriorly. We estimate this angle at between 10 and 15 degrees from a vertical line orthogonal to the occusal plane of the dentition. We note here that the basioccipital plane and the occusal plane of Capromeryx are not parallel to each other; in an as yet undescribed skull (USNM 521305) from Muskox Cave, Eddy County, New Mexico, the occusal plane dips anteriorly from the basicranial plane approximately 10 degrees.

Viewed posteriorly, the long posterior prongs of the horn cores do not diverge from each other, but appear to be parallel, and also parallel to the sagittal plane.

The posterior border of the base of the posterior prong describes a line which passes just behind the posterior edge of the orbit. The anterior prong sits over the orbit at a point midway along the anterior half of the orbit. The posterior prong in this individual is gracile, long and gently tapering to the tip. Some specimens of Capromeryx such as LACM 49, from Rancho La Brea (Chandler, 1916; see Fig. 5F), appear shorter, more robust and have an inflated appearance with the widest part of the posterior prong well distal to the base. Others, such as LACM 8523, also from Rancho La Brea (Furlong, 1946; see Fig. 5E) appear much more similar to the Tramperos specimen. Our specimen also has a very straight posterior prong, quite unlike the gently curved posterior prong on the type of Capromeryx minor (UCMP 26648) from Mexico as illustrated by Furlong (1925). However, there is a slight bend in the posterior prong about one quarter of the way distal to the base, but it is sharply angled and not gently curved as in other specimens.

The parietals and frontal bones have a strongly defined ridge that forms a parasagittal crest, extending from the lateral base of the horn core in an S-shaped curve backward and inward to meet a similar ridge at the edge of the occipital. The surface of the frontal and parietal bones posterior to a line connecting the posterior-most extension of the base of the horn core has a distinctly roughened or pebbly appearance. This same surface topography appears in specimens of Capromeryx arizonensis from Florida in the UF collections (RSW, personal observation).

There is a small pit approximately one centimeter in diameter lateral and slightly anterior to the base of the posterior prong of the horn core. This shallow pit does not connect with either of the two major sulci on the horn core. A similar pit is present on other specimens of Capromeryx, including the Blancan species C. arizonensis, complete enough to be evaluated. It does not occur on specimens of Tetrameryx shuleri, on the paratype of Ceratomyx prenticei, or on skulls of Stockoceros. In Antilocapra americana, the supraorbital foramen occupies the same approximate position as does the pit on Capromeryx; in other genera (Tetrameryx, Stockoceros, Ceratomyx) the supraorbital foramen is in a more anterior position, forward of the horn cores. A shallow pit medial and slightly anterior to the posterior prong of the horn core appears to be an apomorphy of Capromeryx, but awaits a more extensive character analysis of the antilocaprinae.

Taxonomic assignment: We here consider all Capromeryx with anterior horn core prongs less than 50% of the length of the posterior prong to belong to a single species, Capromeryx furcifer (Matthew, 1924). We follow this taxonomy for the present paper as a convenience pending a formal revision of the genus. Several other species have been named for specimens of Capromeryx of Rancholabrean, and perhaps Irvingtonian, age, all of which have reduced anterior prongs. The trend towards reduction of the anterior prong of Capromeryx begins with the Blancan species C. tauntokensis and C. arizonensis, as noted by Morgan and Morgan (1995). The trend continues in the surely Rancholabrean species (C. furcifer, C. minor, C. mexicana). Capromeryx horn cores from the Slaton Quarry in Texas, which were described as Capromeryx minusinus by Meade (1942), also show much reduced anterior prongs on the horn cores. However, their dating is not certain. Womochel, in an unpublished dissertation, placed the age of the Slaton Quarry Fauna as late Yarmouthian interglacial stage (Womochel, 1977, p. 134-137). This would place the fauna sometime just prior to about 0.6 Ma, and firmly in the Irvingtonian NALMA (Bell, et al., 2004). The type of C. furcifer has been considered to be Irvingtonian as well, but deposits and fossils of Rancholabrean age are also known from the Hay Springs area, and early collections do not have precise stratigraphic placement. If the type of C. furcifer and the subsequently referred horn cores from Hay Springs are in fact Irvingtonian, they likely date to the latter part of that NALMA in the “Sheridanian” subage (Bell et al., 2004, p. 274). A Capromeryx horn core is known from the Noye’s Prospect site in the San Pedro Valley, Arizona, sequence described by Johnson et al. (1975). This horn core, UALP 14790 (Fig. 5B), which is intermediate both in overall size and in the reduction of the anterior horn core between C. arizonensis and known Rancholabrean C. furcifer, is found in sediments above the upper boundary of the Olduvai event and below the lower boundary of the Brunhes, and so dates to between 1.21 and 1.77 Ma (Bell, et al. 2004). This would have been considered to be within the Irvingtonian prior to the publication of Bell et al. (2004); the Blancan/Irvingtonian boundary is now placed at the first well-dated occurrence of Mammuthus in New Mexico at 1.3 Ma (Morgan and Lucas, 2003). While this makes the Noye’s Prospect locality Late Blancan, it then becomes the latest securely dated Blancan occurrence of Capromeryx, and its intermediate size and morphology are still relevant.

PALEOBIOLOGY

In the case of Capromeryx, there has been little discussion in the literature about possible sexual dimorphism in horn cores. However, in a subsequently overlooked comment, Chandler (1916, p. 112) describes a specimen, UCMP (?) 21445, as the skull roof from the nasals to the occipital ridge, which shows a “...very minute tubercle which, by analogy with Antilocapra, represents a rudimentary horn-core of a female animal...” We have not been able to locate this specimen in the UCMP collections; that catalog number is now associated with an incomplete dentary of Bison from Rancho La Brea. This is the only claimed instance of a female Capromeryx which we have found in the literature or seen in any collection. If Chandler (1916) is correct that the specimen represents a female individual, and if the specimen he referred to can be located, then the variation seen in the large horn cores is more likely geographical or ontogenetic variation rather than sexual dimorphism. For the present, then, we consider all horn cores of Capromeryx to represent male individuals.

We have already commented on the fact that Rancholabrean Capromeryx in New Mexico, while occurring over a wide area (and of course the same is true beyond New Mexico) never occurs in significant numbers at any one site. This can be contrasted with a close Pleistocene relative, Stockoceros, and with the living pronghorn (Antilocapra americana). Stockoceros in particular is known from very large samples from two caves, Papago Springs Cave (60+ individuals) in Arizona (Roosevelt and Burden, 1934; Skinner, 1942; Czaplewski et al., 1999) and San Josecito Cave (50+ individuals) in Mexico (Furlong, 1943). In neither case is there evidence on the bones that the materials were accumulated by predators. In Papago Springs, at least, there were a number of articulated skeletons. In addition, a Pleistocene accumulation of Antilocapra americana is known from Natural Trap Cave in Wyoming (Chorn et al., 1988). In the case of Natural Trap Cave, the animals appear
to have entered the cave through a deadfall entrance. This does not seem to have been the case in either Papago Springs or San Josecito Cave, which both had entrances in the Pleistocene easily negotiable by pronghorn. There has been much discussion of the fact that only horned individuals seem to be represented in the case of *Stockoceros*; Skinner speculated that either both sexes had horns of approximately the same size, or that only males congregated in Papago Springs Cave, perhaps due to seasonal aggregation of male-only herds, while the females and young avoided the caves. Skinner felt that the evidence from Papago Springs Cave “strongly indicates that both sexes were well horned” (Skinner, 1942, p. 201). Yet, in the same paragraph he notes that it is not improbable that “the cave collection represents a seasonal phenomenon, in which only males frequent the locality” (Skinner, 1942, p. 201). In any case, a preliminary attempt by the senior author to correlate either the size or morphology of the horn cores with ontogenetic age of the skulls from Papago Springs and San Josecito caves has not been successful.

Given the well documented gradual reduction of the anterior horn core of *Capromeryx* beginning in the early Blancan, and culminating with the extreme degree of reduction documented by the Tramperos Creek specimen described here, several hypotheses about what the animal may have looked like in life suggest themselves. It seems logical to reconstruct the horn core as a close-fitting covering of the bony horn core, but alternative hypotheses are possible. The example provided by the modern pronghorn, *Antilocapra americana*, the sole survivor of a once diverse lineage, is enough to urge caution in such reconstructions. *Antilocapra americana* has a single blade-like horn core, thick posteriorly and tapering anteriorly. The sheath which covers it, however, has a forward-facing hook, which may reflect the presence of a bifurcate horn core with an anterior prong in the ancestor of the modern pronghorn, which is now completely suppressed. We have prepared a series of possible reconstructions of the horn of the Tramperos Creek *Capromeryx* (Fig. 4). We have no way to evaluate which is the most likely reconstruction. On no basis other than a sort of energetic parsimony, we prefer the reconstruction shown in Figure 4A.

Why the anterior horn core should have undergone reduction from the early Blancan form, where both prongs of the horn core appear to have been robust and nearly the same size, to the Rancholabrean forms, culminating in the Tramperos Creek specimen in which the anterior horn core is vestigial and may not have been expressed in the horn sheath at all, is an even more difficult question to answer. One possible interpretation relies on a comparison of horn and antler form among living bovids and cervids.

Jarman (1974) investigated the relationship between the ecology and social organization of the diverse array of African antelopes. He examined feeding strategies, including the nature of the plant communities that the antelopes inhabit, body size, group size, sexual dimorphism and predator avoidance behavior. Jarman (1974) classified the African antelopes into five categories (Classes A, B, C, D and E), each with distinctly different ecological, behavioral and social characteristics. Table 2 presents a summary of the characteristics of Jarman’s five classes. It is important to note that the descriptions in Table 2 are modal in nature; there is overlap between the classes in each category, sometimes significantly so. This attempt to apply Jarman’s classification, developed only to describe African antelopes, to antilocaprids is a preliminary effort. Jarman’s scheme ought to be tested more fully, for example, against living

![FIGURE 4. Suggested reconstructions of the horn sheath of *Capromeryx furcifer* from Tramperos Creek.](image-url)
cervids to see if his Classes have a more general utility. Nevertheless, since we are using it here only to suggest possible interpretations of the paleobiology of *Capromeryx* which can then be tested against other data, we believe the exercise to be worthwhile.

Jarman (1974) started with basic ecological, behavioral and social characteristics as the basis for his classification and then noted that many physically observable characteristics, such as body size, sexual dimorphism, and complexity of horns, could be correlated with his five categories. In the present instance, we have attempted to fit *Capromeryx* into one of his categories, and then use that to construct a hypothesis concerning the feeding ecology, behavior and social organization for this extinct antilocaprid.

The Tramperos Creek *Capromeryx* fits quite readily into Jarman’s Class A. It is a relatively small animal, with a body size estimated at 10-13 kilograms (Saysette, 1999). The adult postcranial skeleton does not exhibit marked sexual dimorphism (based on measurements of the *Capromeryx* material by RSW at the Page Museum), which is also a characteristic of Jarman’s (1974) Class A. The horns (or at least the horn cores) of *Capromeryx* are simple and relatively small, again consonant with Class A. If we then hypothesize, based on these physically observable characteristics, that *Capromeryx* would have been a Class A taxon, what predictions might provide into the ecology, behavior and social structure of Late Rancholabrean *Capromeryx*, or on the evolution of *Capromeryx* through the Plio-Pleistocene?

Class A species tend to “feed very selectively on a wide range of plant species, using particular plant parts only, remaining in one vegetation type and in one small home range throughout the year. These species are predominantly browsers…” (Jarman, 1974, p. 222). This prediction provides an opportunity for testing through analysis of the dentition and isotopic signatures recorded in the bones and teeth. *Capromeryx*, under this model, would have selected one feeding habitat vegetation type, and would have selected specific parts of the plants it encountered, rather than consuming entire plants. Individuals would have moved widely over the landscape, moving centimeters to meters between bites.

Species in Class A “live singly, or in pairs, sometimes accompanied by a recent offspring. Thus, the group size varies from one to three, is most commonly two, and does not vary seasonally” (Jarman, 1974, p. 232). This near solitary existence, and the lack of seasonal aggregations, would explain the widespread occurrence of *Capromeryx*, with very few individuals at any one site. This contrasts strongly with *Stockoceros*, where large assemblages of fossils are known from cave sites, suggesting that *Stockoceros* may have been a Class C or D species, in which large seasonal aggregations are typical.

Jarman’s Class A predicts that *Capromeryx* would have relied on hiding as its primary anti-predator behavior. If it was diurnal, it likely fed in or near cover. “In the presence of predators, they either freeze, lie down and freeze, or run to cover and freeze” (Jarman, 1974, p. 235). Because of their small size, they cannot outrun predators, nor can they discourage predator attacks with aggressive displays. Maintaining a solitary, or very small group existence, minimizes the potential for a predator or group of predators to feed leisurely on a herd which could neither outrun them nor defend itself by grouping. Maintaining the distance between animals is facilitated in Class A species by their strong territoriality, which likely characterized *Capromeryx* as well.

Finally, Jarman’s data can suggest that there was little dimorphism in body size between males and females; furthermore, if there was any difference, females may have been slightly heavier than males. Class A species males vary from 84% to 105% of the weight of conspecific females (Jarman, 1974, p. 260). Jarman’s data show that for the antelopes, only the males are horned in Class A. This is consonant with other data mentioned before which indicates that female *Capromeryx* were essentially hornless, although small bosses on the frontal bone mark the location of the horn cores that develop in the males.

In the case of the bovids described by Jarman (1974), and in the case of cervids, as described by Geist (1998), the most ornate and largest cranial appendages (not forked in bovids and generally forked in cervids)
FIGURE 5. Sequence of Capromeryx horn cores from late Blancan through Rancholabrean time. Blancan: A, AMNH 141172, Dry Mountain, Arizona, 2.32 ma; B, UA 14790, Noyes Prospect, Arizona 1.78 ma. Irvingtonian: C, TTU P-19, Slaton Quarry, Texas; D, TTU-P20, Slaton Quarry, Texas. Rancholabrean: E, LACM 8523, Rancho La Brea, California; F, LACM 49, Rancho La Brea, California; G, NMMNH 50387, Tramperos Creek, New Mexico.
correlate with the large size, open landscapes, large social groups and sexual dominance hierarchies. Complexly forked antlers, or strongly ornamented horns (showing annular ridges, spiral form, or extreme size) are used primarily as display ornamentation, although they are also used as sparring weapons specifically designed to minimize fatal injury to both combatants. Conversely, simple, relatively short single horns or simple antlers correlate with a solitary life history, small size, and closed habitat (primarily forests). In these species, the horns and antlers are used as weapons for protection against predators or the protection of territories from conspecifics.

Comparison with Jarman’s classification as outlined above indicate that Capromeryx in the Rancholabrean were solitary, widely dispersed animals which did not form seasonal aggregations. Males and females were roughly the same size in terms of body weight. The animals did not rely on either speed or aggression to avoid predators, but froze and hid, suggesting that they were rather plainly marked, perhaps with dappling or other camouflage to break up their outline. Finally, they were likely territorial, with the males defending their territory against other animals of either sex.

Jarman’s data suggest one other hypothesis. Morgan and Morgan (1995) and a number of others after them, have noted the trend in size reduction which Capromeryx underwent, beginning in the Pliocene and culminating in the Rancholabrean with the tiny Capromeryx furcifer of Mexico and the American West. Capromeryx tautonensis and C. arizonensis may have exhibited feeding strategies, social organization and anti-predator behaviors different from the terminal member of their lineage, C. furcifer. While the data are not yet available to evaluate which Jarman Class those earlier species might best occupy, it should be the goal of future research to examine this problem. The determination of diet from dental wear and isotopic studies, along with the eventual location of larger samples amenable to analysis of potential dimorphism, should allow answers to these questions to be developed.

Capromeryx may have been adapting to changing climatic conditions by gradually adopting a solitary, less open habitat lifestyle. When adequate samples of teeth from all the species of Capromeryx are available for dietary analysis, it will be possible to test this interpretation by determining if the dietary regime changed from a grazing, grass-dominated diet to a diet more centered on leafy browse.

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