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A STUDY OF *TETRAMERYX* AND ASSOCIATED FOSSILS FROM PAPAGO SPRING CAVE, SONOITA, ARIZONA

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INTRODUCTION

During the summer of 1934, Messrs. Quentin Roosevelt and J. W. Burden explored a limestone cave near Papago Spring, some two and one-half miles southwest of Sonoita, Santa Cruz County, Arizona, and, as a result of their field work, discovered various skull and skeletal remains of the Pleistocene antilocaprid, *Tetrameryx*. These fossils were sent to the American Museum, where they were prepared and stored. In November of the same year, Roosevelt and Burden[1] described some of the material that they had collected, allotting it to a new species of the genus *Tetrameryx*, namely: *Tetrameryx onusrosagris*.

In the spring of 1936, these two gentlemen made an additional exploration of the Papago Spring cave, with the result that additional specimens of *Tetrameryx* were discovered, so that we now have fairly complete skull and skeletal material of *Tetrameryx onusrosagris*, as well as a few other fossils that were associated with this extinct antelope.

Because of the complete series of fossil skulls and skeletal remains from Sonoita, we are able for the first time to make an adequate comparative study of this now extinct genus. This form is of particular interest in that it resembles very closely the modern pronghorn (as will be shown below) in most of its structural characters, yet is quite different as to the development of its horns. Not only is *Tetrameryx* of interest because of its anatomical features, but also because of its association, for Roosevelt and Burden found pottery fragments and other artifacts in Papago Spring cave that would seem to point to the fact that *Tetrameryx onusrosagris* was contemporaneous with early man in southwestern United States. Moreover, among the associated mammalian remains is a bone of the Pleistocene North American horse, *Equus*, which also once lived in the Southwest with early man. Evidently these fossil animals, now extinct in North America, persisted on this continent to within a few thousands of years ago, as did many other typically "Pleistocene" mammals, and the discovery at Papago Spring cave constitutes one more record of the post-Pleistocene persistence of Pleistocene types.

The purpose of this contribution is to make a detailed study of *Tetrameryx onusrosagris*, comparing it point for point with the recent *Antilocapra americana*, and so far as the known material permits, with other fossil antilocaprids. The fossils associated with *Tetrameryx* in the Papago Spring cave will also be described.

Acknowledgments are due to Messrs. Roosevelt and Burden for the interest they have shown in the Papago Spring cave deposit, and for their laborious and careful work of collecting the fossils hereinafter described. The American Museum of Natural History is also indebted to these gentlemen for their kindness in presenting the fossils to this institution.

[1] Roosevelt, Quentin, and Burden, J. W., 1934, "A New Species of Antilocaprine, *Tetrameryx onusrosagris*, from a Pleistocene Cave Deposit in Southern Arizona." Amer. Mus. Novitates, No. 754.

OCCURRENCE OF THE FOSSILS

Papago Spring cave is located in a limestone hill in the Canelo Hills, some two and a half miles southwest of Sonoita, Arizona. This locality is in the basin range section of western United States, characterized by block mountains and igneous cores separated by wide bolson deposits. Faulting, folding and tilting of the sedimentary beds is common in this region, and the deposits in which Papago Spring cave is formed are tilted to an angle of some thirty or forty degrees. The is probably of a relatively recent geologic date, having been formed by solution during Pleistocene, or perhaps late Tertiary times. Certainly the deposits within the cave are all of Pleistocene or post-Pleistocene age.

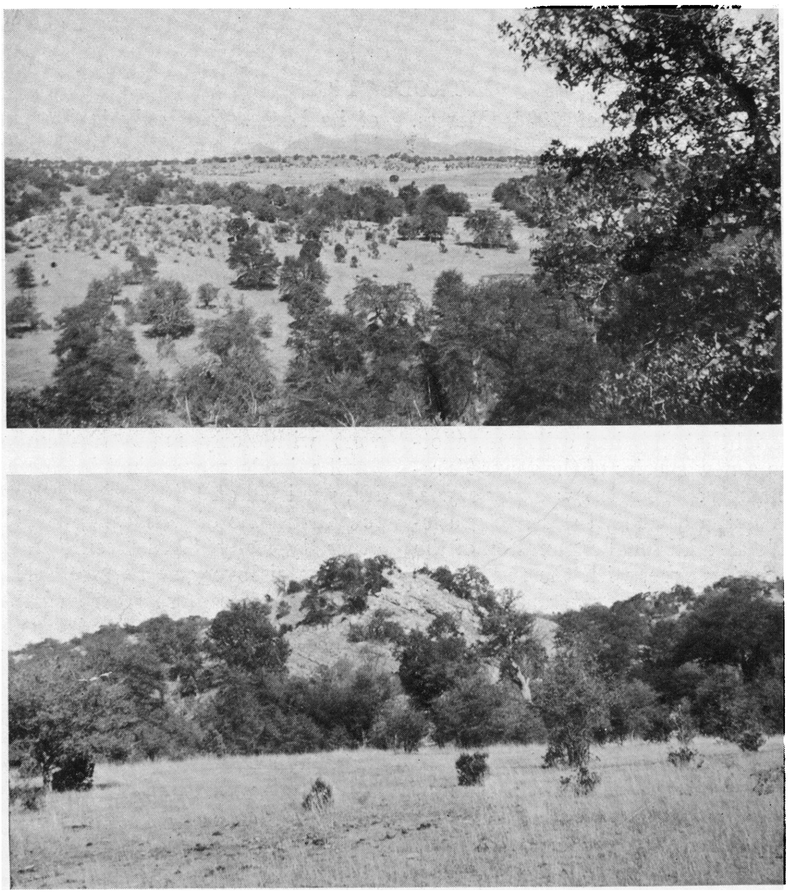


Fig. 1. (Above) View to the northwest from the summit of the cave-hill. (Below) View of the cave-hill from a point one-fourth of a mile southwest of the cave entrance. The cave entrance is on the side of the hill facing the observer, but is screened from view by the trees.

limestones of the Canelo Hills are of Devonian, Carboniferous and Permian age, related to the Martin and Tornado limestones of adjacent regions. In this connection it might be said that some productids found in the wall of the cave would indicate a probable Permian age for the beds containing them. The cave, itself,

Mr. Burden's description of the cave is presented at this point, to serve as an explanation for the figure of the cave, shown in the accompanying illustration.

Entrance "A" is the largest of the two known entrances and is simply a direct drop of approximately twenty-five feet. Its walls bear signs of water erosion and it seems likely that a stream once ran through it into the cave. At its northwest end big rocks and boulders have fallen in. Its mouth is about sixty feet up the hillside and is sheltered by overhanging rocks and a tree.

Entrance "B" is the one we used all the time, and it is exceedingly narrow. Its mouth is about forty feet above the ground (i.e., up the hill) and is almost hidden by a dense clump of bushes. This entrance consists of a narrow bending passage between large, loose boulders, and it descends at an angle of 45 to 60 degrees for about twelve feet and then turns northeast into a small cavern. This in turn opens first into a still larger cavern, and, finally, into the main room of the cave. The floor, all the way down the cave, from the first small cavern to the sixty foot mark, descends at an angle of 25 to 30 degrees and is composed of loose rocks and soft earth. From the sixty foot to the eighty foot mark it dips still more to about 45 degrees. It then levels out (down the tunnel) to about a 10 degree angle as far as the one hundred and ten foot mark, drops a bit more and then goes up at a 15 degree angle as far as the one hundred and sixty-five foot mark. It then continues on a level as far as the two hundred and ninety-five foot mark, where it drops directly down in a corkscrew shaped tunnel.

The height of the tunnel varies from three feet to about twenty feet, while the main cavern is about thirty feet high in its widest part.

The first fossil deposit contained the first skull we ever discovered, together with three other skulls and numerous bones. This deposit was apparently connected with deposit 2, because the strata seemed to continue up to the tunnel mouth. The second deposit has apparently been exposed to the air too long, for the bones it contains are exceedingly brittle. The third deposit has furnished us with most of our bones. It is a "jutting-out" promontory of hard limestone-cemented rubble almost entirely undermined, and was probably a section of the old cave floor. (Burden, J. W., Letter to Walter Granger, dated April 29, 1936.)

Fig. 2. (Left) View from the top of the tunnel, showing fragmentary fossils exposed on a ledge. (Right) Interior of Papago Spring cave, near the main fossil deposit.

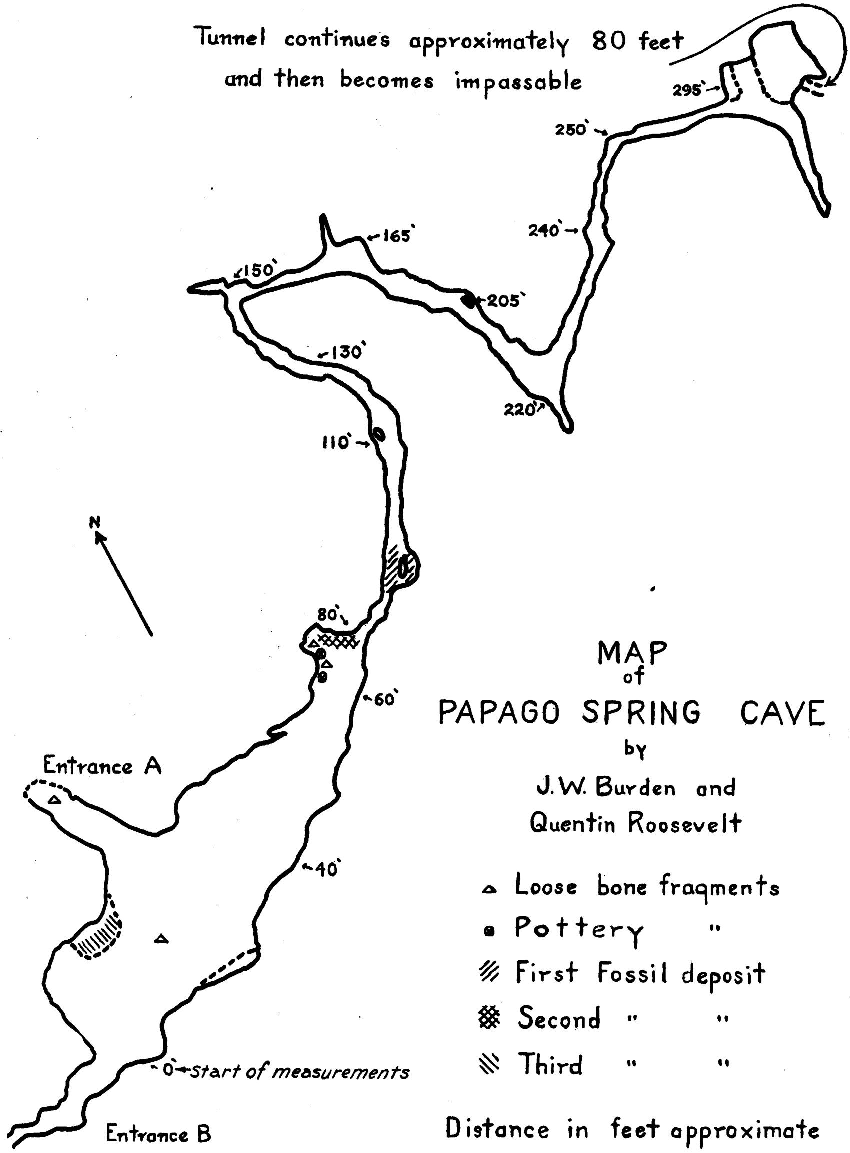


Fig. 3. Map of Papago Spring cave, near Sonoita, Arizona. (Drawn by J. W. Burden and Quentin Roosevelt.)

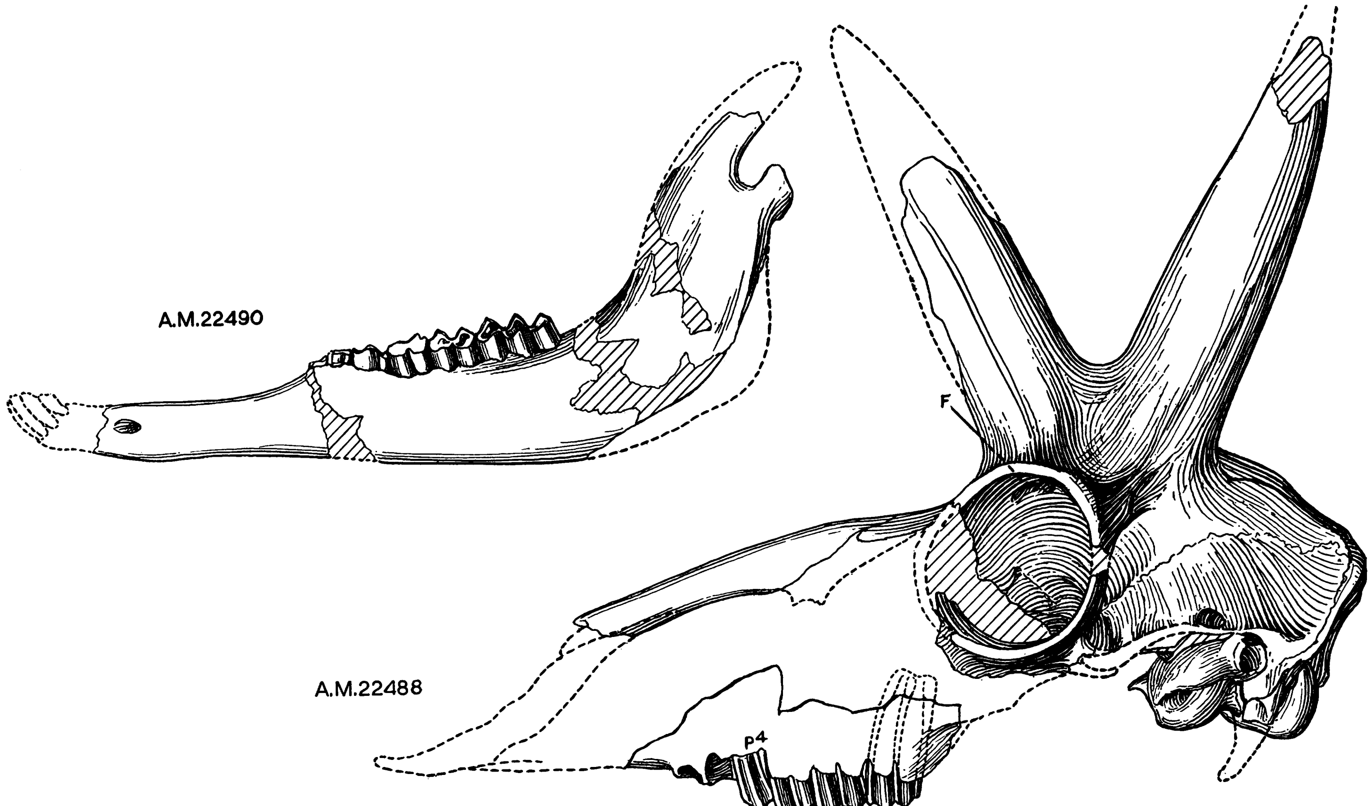


Fig. 4. Type figures of *Tetrameryx onusrosagris* Roosevelt and Burden. Amer. Mus. Nos. 22488, type skull, and 22490, referred mandibular ramus. Lateral views, one-half natural size. (From Roosevelt and Burden, 1934.)

DESCRIPTIONS AND DISCUSSIONS

Tetrameryx onusrosagris Roosevelt and Burden

Tetrameryx onusrosagris, ROOSEVELT AND BURDEN, 1934, Amer. Mus. Novitates, No. 754.

Stockoceros onusrosagris, FRICK, 1937, Bull. Amer. Mus. Nat. Hist., LXIX, p. 527.

TYPE.—Amer. Mus. No. 22488, a broken skull with the horn cores, cranium, basicranium, cheek-teeth and nasals preserved. Maxillae broken, premaxillae missing.

REFERRED SPECIMENS.—(Referred to this species in the original type description.)

Amer. Mus. No. 22489, a broken skull with right horn cores, occiput, basicranium, right upper M^3, left upper M^2 and M^3, maxillae and nasals broken, premaxillae missing.

Amer. Mus. No. 22484, fragment of occiput, five detached horn cores, and four fragments of rami.

Amer. Mus. No. 22490, left ramus with M_{1-3} complete, P_{2-4} broken, and condyle missing.

Amer. Mus. No. 22483, "skeletal elements of several individuals, including: Three fragments of scapulae. Four partial humeri, two distal and two proximal ends. One ulno-radius (broken), distal half of second, and top of ulna. Metacarpus. Right and left femora, proximal ends missing, eight fragments. Tibia. Metatarsus and distal end of second. Astragalus. Two 1st, three broken 1st, two 2d, and one 3d phalanges. Pelvis. Sacrum. Sternum fragment. Three cervicals (including atlas). Five lumbars and two fragments. One dorsal and two fragments. One rib and four fragments. Miscellaneous fragments including two distal ends of metapodials." (Roosevelt and Burden, *op. cit.*, p. 4.)

ADDITIONAL REFERRED SPECIMENS.

Amer. Mus. No. 22657, a broken skull with cranium, basicranium, left orbit, and both right and left M^{2-3} preserved; maxillae, nasals, palate and horn cores broken, premaxillae missing.

Amer. Mus. No. 22658, a right ramus complete except for three broken incisors.

Amer. Mus. No. 22659, skeletal elements of several individuals as follows: Five fragments of rami. Thirteen partial horn cores and skull fragments. Twenty-one vertebrae and fragments. One left femur, three right distal ends, one right and two left proximal ends, and four fragments. One tibia, five proximal ends, two distal ends, and one fragment. One partial sternum. Six fragmentary scapulae. One right and two left humeri, one right and one left distal end, and one left proximal end. One radius and three distal and three proximal ends. One distal and three proximal ends of metacarpals. Two metatarsals, two distal and three proximal ends. Five metapodial fragments. Miscellaneous upper teeth. Miscellaneous lower teeth. Carpals and tarsals. Phalanges. Unidentified fragments.

HORIZON AND LOCALITY.—Cave deposits, uppermost Pleistocene or subrecent. Papago Spring cave, south of Sonoita, Arizona.

DIAGNOSIS.—Approximately equal to *Antilocapra* in size, but with shorter, stockier limbs and a heavier body. Orbits less protruding than in the modern pronghorn, and but slightly turned anteriorly. Canine-premolar diastema and muzzle relatively shorter than in *Antilocapra*. Two pairs of subequal horn cores with elliptical cross-sections, arising on either side from a common base above the orbit. These horn cores branch in an antero-posterior plane and at an angle of about 45 degrees. (*T. shuleri*, the generic type, has a long posterior branch; *T.* (*Stockoceros*) *conklingi* has horn cores more nearly parallel to each other; *T. onusrosagris* ref. from Burnett cave has a 27 degree angle between the branches; *Hayoceros* has an elongated cross-section of the anterior core as in *Antilocapra*, and a sub-rounded cross-section of the posterior core as in *Tetrameryx*.) Teeth tending to be shorter and wider than in *Antilocapra* and smaller than those of *Tetrameryx shuleri*. Upper third molar often with a postero-internal column, absent in *Antilocapra* and *Tetrameryx shuleri*.

COMPARISON OF *Tetrameryx* AND *Antilocapra*

Generally speaking, *Tetrameryx* shows a close structural resemblance to *Antilocapra*, the differences between the two forms being mainly those of proportions. For it is quite evident that *Tetrameryx* was a heavier, stockier animal than the modern pronghorn—and thus probably not quite so fleet a runner as the one surviving antilocaprid.

The most striking single difference between the two genera is, of course, the presence of the double horn cores in *Tetrameryx*, which on either side of the skull spring from a wide base above the orbits to diverge at an angle of approximately 45 degrees in an antero-posterior plane. The anterior core of the pair has the same position over the orbit as the single core of *Antilocapra*, but in cross-section is elliptical or nearly round, as compared with the transversely flattened core in *Antilocapra*. The posterior core is similar to the anterior one in size and form.

The orbits of *Tetrameryx* do not protrude as much as do those of *Antilocapra*, nor do they face forwardly to the same degree that is characteristic of the prong-

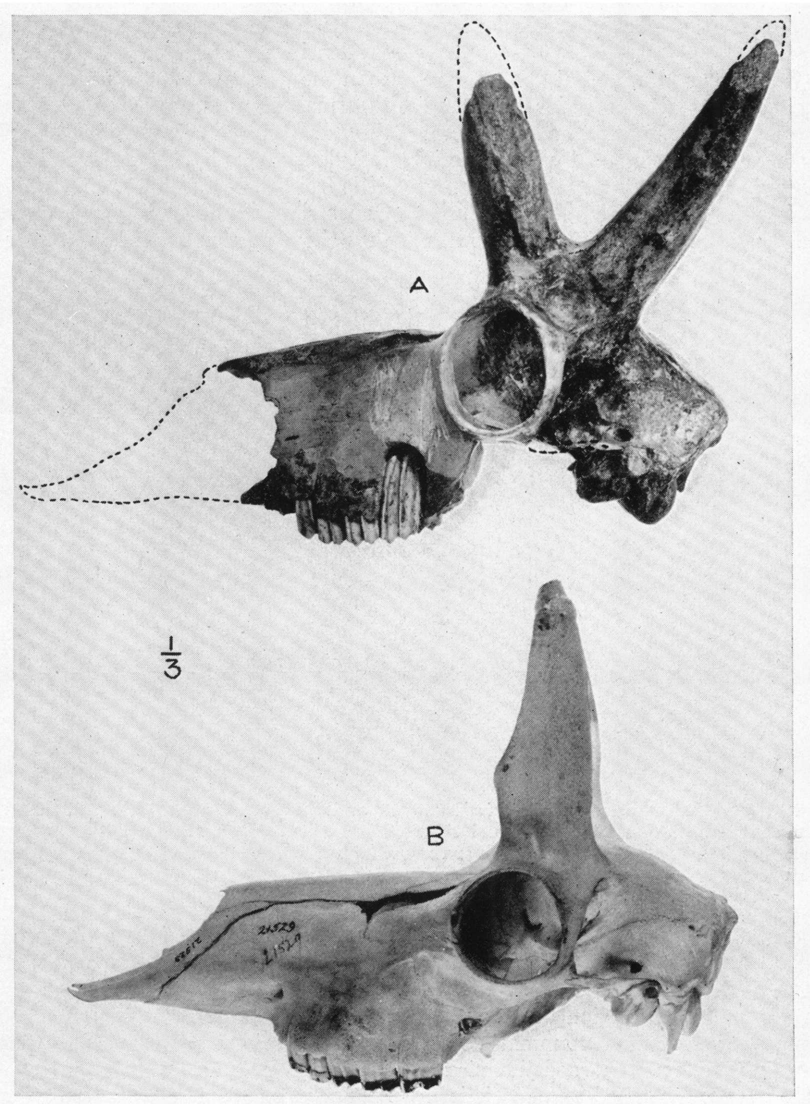


Fig. 5. (A) *Tetrameryx onusrosagris* Roosevelt and Burden. Amer. Mus. No. 22488, type skull, lateral view. (B) *Antilocapra americana* (Ord). Amer. Mus. (Mammalogy) No. 21529, lateral view. Both figures one-third natural size.

horn. Here we see an accentuation, in the modern genus, of a character that evidently is closely correlated with alertness and a dependence upon rapid flight across wide plains.

In *Tetrameryx* the nasal bones are slightly wider at the posterior end than they are in *Antilocapra*, a structural difference with no especial phylogenetic significance. Furthermore, the auditory bullae in *Tetrameryx* are slightly more swollen than they are in the modern pronghorn, which may be indicative of a somewhat more primitive condition in the extinct genus, for it would seem that a certain amount of reduction of the bulla takes place when hoofed mammals leave a more primitive forest or wooded environment for a more advanced and specialized plains habitat. Otherwise the skulls in these two genera are alike, except for a slightly shorter muzzle in *Tetrameryx*.

In the mandible of *Tetrameryx* the diastema is definitely shorter than it is in *Antilocapra*, which, of course, is to be correlated with the shorter, less progressive maxillary and premaxillary region of the fossil form.

The teeth of *Tetrameryx onusrosagris* are in general narrower than those of *Antilocapra*. There is, however, in the fossil form a considerable range in size, the largest dentitions being perhaps slightly larger than the dentition of the pronghorn, while the smallest ones are much smaller than the teeth of the recent animal. In form the dentition of *Tetrameryx* differs but little from that of the modern *Antilocapra*. One striking difference, when present, is that the posterior half of the upper third molar of *Tetrameryx* is more pointed than it is in *Antilocapra*. In a fairly large series this feature grades from a sharp angle in the generic type, *T. shuleri*, through various degrees of sharpness in *T. onusrosagris*, to a rather blunt angle in *Antilocapra*. In the older individuals of *T. onusrosagris* an extra column is apparent on the postero-internal edge of this third upper molar. The lower dentition of *Tetrameryx* has the heel of the third molar considerably smaller and shorter, as compared with the total length of this tooth, than it is in *Antilocapra*.

The greatest differences in the vertebral column are to be seen in the atlas

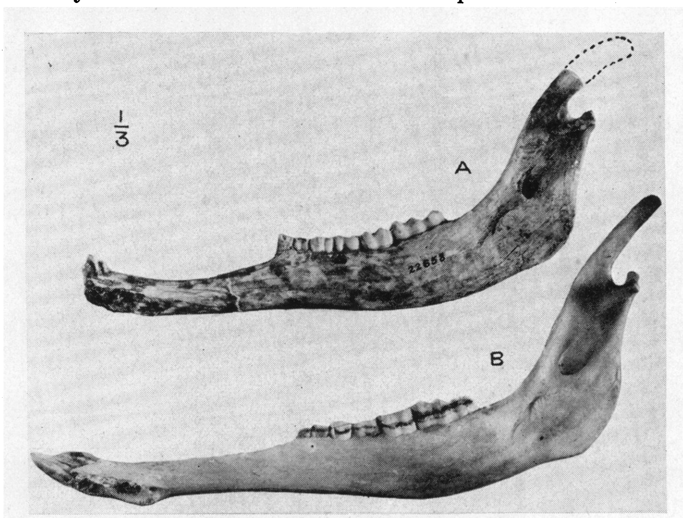


Fig. 6. (A) *Tetrameryx onusrosagris* Roosevelt and Burden. Amer. Mus. No. 22658, right mandibular ramus, lateral view of lingual side. (B) *Antilocapra americana* (Ord). Amer. Mus. (Mammalogy) No. 120947, right mandibular ramus, lateral view of lingual side. Both figures one-third natural size.

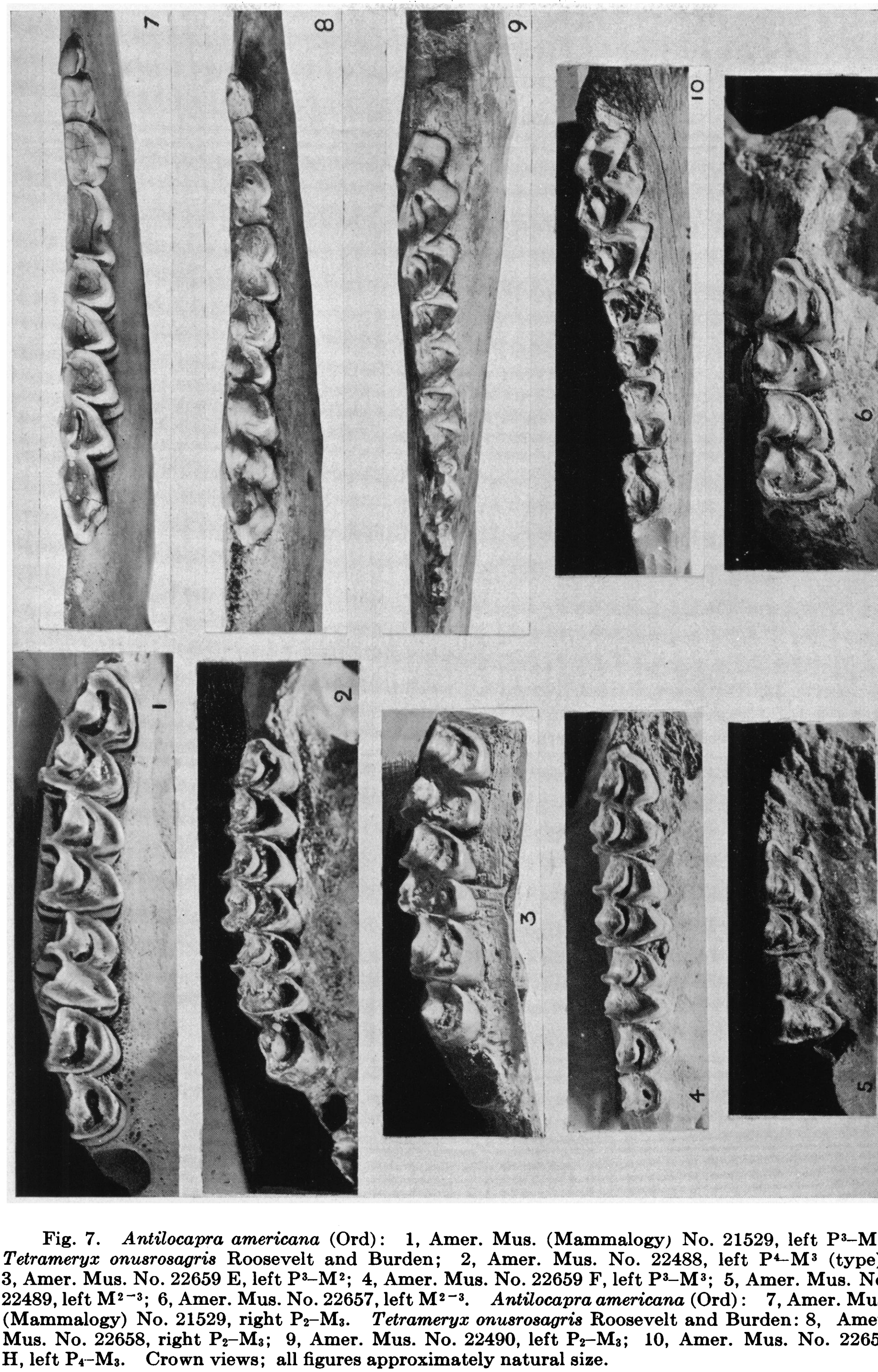


Fig. 7. *Antilocapra americana* (Ord): 1, Amer. Mus. (Mammalogy) No. 21529, left P^3–M^3. *Tetrameryx onusrosagris* Roosevelt and Burden; 2, Amer. Mus. No. 22488, left P^4–M^3 (type); 3, Amer. Mus. No. 22659 E, left P^3–M^2; 4, Amer. Mus. No. 22659 F, left P^3–M^3; 5, Amer. Mus. No. 22489, left M^{2-3}; 6, Amer. Mus. No. 22657, left M^{2-3}. *Antilocapra americana* (Ord): 7, Amer. Mus. (Mammalogy) No. 21529, right P_2–M_3. *Tetrameryx onusrosagris* Roosevelt and Burden: 8, Amer. Mus. No. 22658, right P_2–M_3; 9, Amer. Mus. No. 22490, left P_2–M_3; 10, Amer. Mus. No. 22659 H, left P_4–M_3. Crown views; all figures approximately natural size.

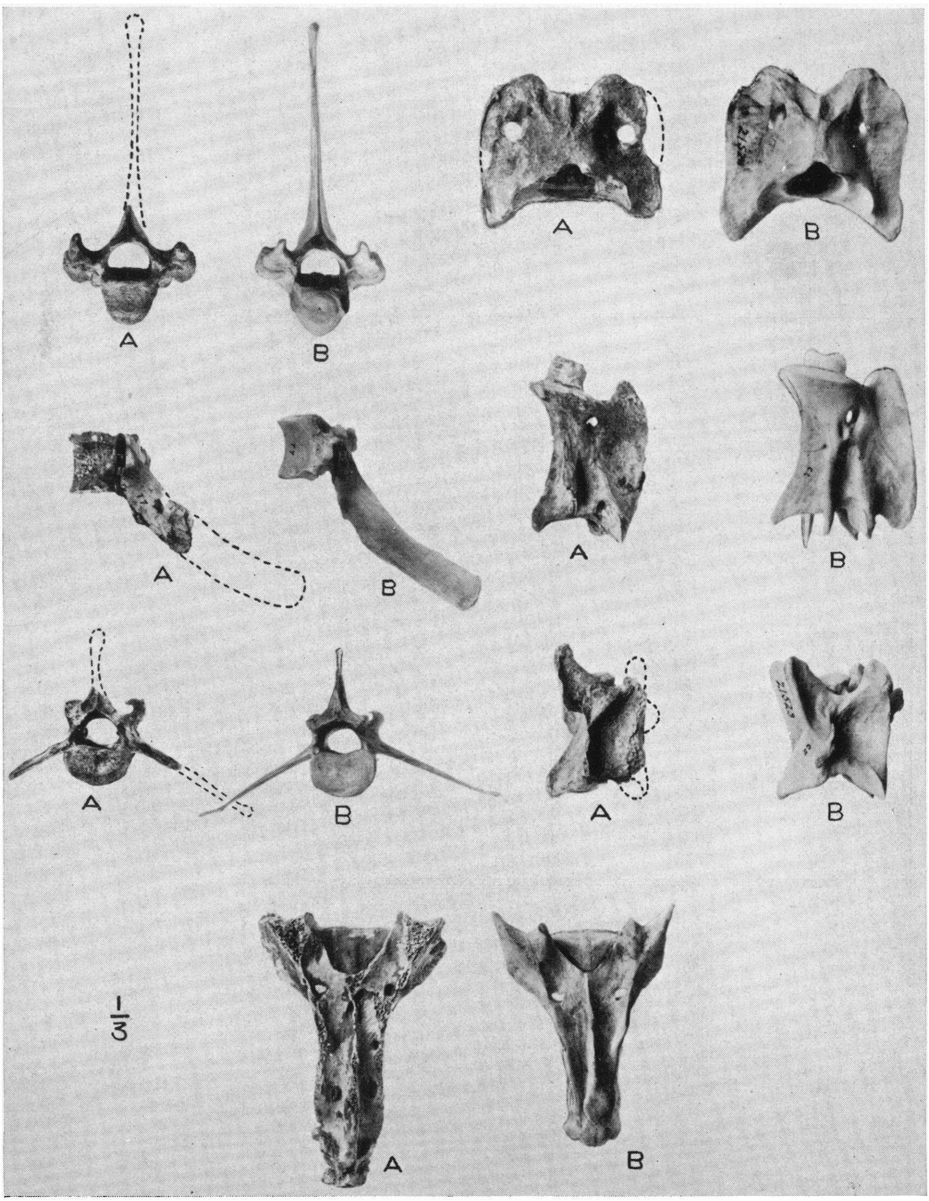


Fig. 8. (A) *Tetrameryx onusrosagris* Roosevelt and Burden. Amer. Mus. No. 22483, vertebrae. Atlas, dorsal view; axis, lateral view; fifth cervical, lateral view; third dorsal, anterior view; seventh dorsal, lateral view; third lumbar, posterior view; sacrum, dorsal view. (B) *Antilocapra americana* (Ord). Amer. Mus. (Mammalogy) No. 21529, vertebrae. The vertebrae of *Antilocapra* (B), and the views shown of them, correspond in each case to those of *Tetrameryx* (A). All figures one-third natural size.

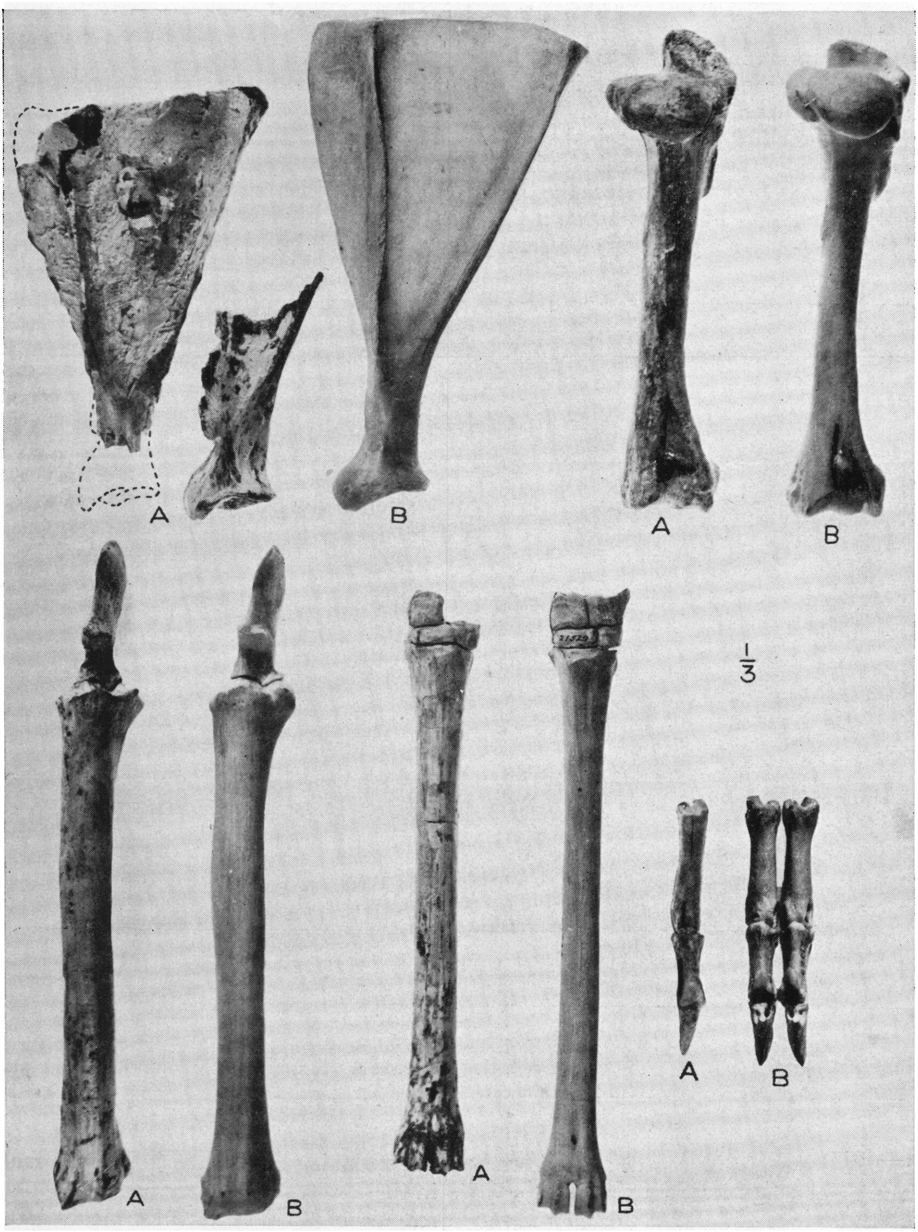


Fig. 9. (A) *Tetrameryx onusrosagris* Roosevelt and Burden. Amer. Mus. Nos. 22483 and 22659, fore-limb. Left scapula, lateral view; right humerus, posterior view; left radius-ulna, anterior view; left fore-foot, including scaphoid, magnum, unciform, metacarpals III and IV (cannon-bone) and phalanges, anterior view. (B) *Antilocapra americana* (Ord). Amer. Mus. (Mammalogy) No. 21529, fore-limb. The fore-limb elements of *Antilocapra* (B), and the views shown of them, correspond in each case to those of *Tetrameryx* (A), except that the complete fore-foot is illustrated. All figures one-third natural size.

vertebra, which in *Tetrameryx* is considerably wider in the centrum than it is in the pronghorn. Also, the foramen for the inferior branch of the first spinal nerve is much larger in the atlas of this fossil than it is in *Antilocapra*. As for the other vertebrae, the resemblances between those of the two genera are generally close, except that in the fossil the centra are uniformly broader and heavier than they are in the recent form.

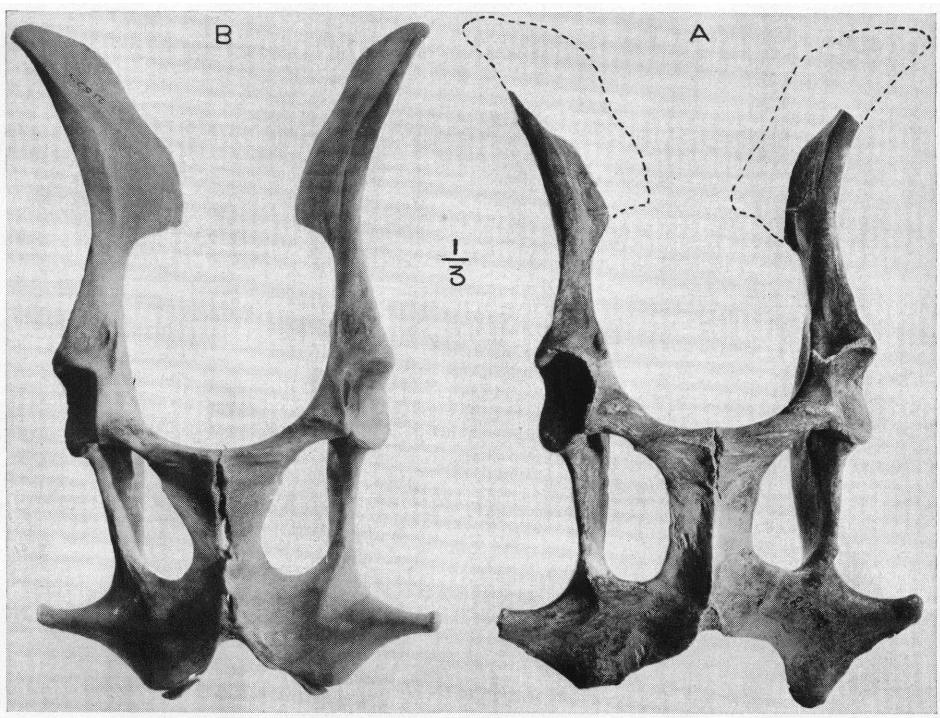


Fig. 10. (A) *Tetrameryx onusrosagris* Roosevelt and Burden. Amer. Mus. No. 22483, pelvis, dorsal view. (B) *Antilocapra americana* (Ord). Amer. Mus. (Mammalogy) No. 21529, pelvis, dorsal view. Both figures one-third natural size.

The limbs of *Tetrameryx* portray to best advantage the general stockiness of this animal as compared with the recent genus. The total length of the limb, both fore and hind, is somewhat less in the former genus than it is in the latter. Yet in *Tetrameryx* the proximal elements are both actually and proportionately longer than they are in *Antilocapra*, the general shortness of the limb being due to the abbreviated lower limb bones and metapodials of *Tetrameryx*. This shift in the relative lengths of the limb elements between the extinct and the surviving forms upholds the supposition that *Tetrameryx* was perhaps a slightly less speedy animal than his modern cousin.

Continuing this comparison of the limbs in the two genera, it may be said that the scapula of *Tetrameryx* is seemingly somewhat shorter than the same element in the pronghorn. Likewise, the pelvis of *Tetrameryx* is shorter and more strongly braced than is the pelvis of *Antilocapra*.

The relationships of the several limb elements in the two genera under discussion are shown in the accompanying figures, tables, and chart.

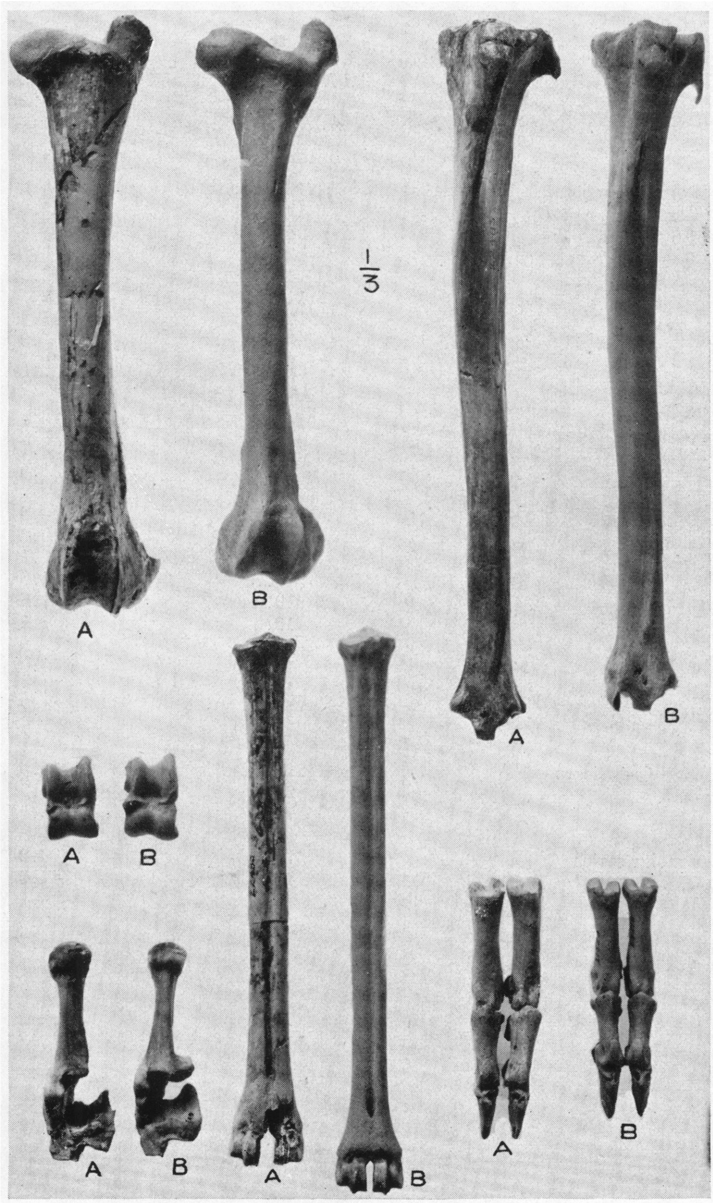


Fig. 11. (A) *Tetrameryx onusrosagris* Roosevelt and Burden. Amer. Mus. Nos. 22483 and 22659, hind-limb. Left femur, anterior view; left tibia-fibula, anterior view; left astragalus, right calcaneum and cuboid-navicular, left metatarsals III and IV (cannon-bone) and phalanges, anterior views. (B) *Antilocapra americana* (Ord). Amer. Mus. (Mammalogy) No. 21529, hind-limb. The hind-limb elements of *Antilocapra* (B), and the views shown of them, correspond in each case to those of *Tetrameryx* (A). All figures one-third natural size.

Comparative Measurements

	Antilocapra americana A.M. 21529, skull and skeleton A.M. 120947, jaw	*Tetrameryx onusrosagris* A.M. 22488, skull A.M. 22658, jaw A.M. 22483, 22659, skeletal elements
SKULL		
Ant. border orbit to pmx.	178.4 mm.	169.0* mm.
Ant. border orbit to condyle	123.0	125.5*
Height of maxilla at M^3	46.9	38.8*
Width at top of orbits	123.7	116.7*
Width of palate	45.5	55.3
Width at base of horn cores	111.9	102.7
Width of occiput	72.7	80.4
Height of occiput to bottom of condyles	53.8	55.0
Vert. diam. of orbit	20.7	26.7
Hor. diam. of orbit	23.5	18.8
Horn cores:		
Antero-posterior diam.	36.0	60.1
Diam., ant.-post. of ant. branch	...	29.7
Diam., ant.-post. of post. branch	...	31.5
Teeth:		
Premolar-molar series	71.7	64.8
Molar series	44.5	40.4
P^4 length	8.0	8.1
width	7.7	6.6
M^1 length	10.9	11.7
width	10.6	9.1
M^2 length	14.9	13.0
width	10.9	9.9
M^3 length	17.3	14.8
width	10.5	8.7
JAW		
Length condyle-incisors	227.0	211.0
Depth at M_1	21.4	22.9
Diastema	71.8	66.8
Teeth:		
Premolar-molar series	70.3	66.2
Molar series	48.6	44.6
P_2 length	5.0	6.4
width	3.5	3.8
P_3 length	6.3	5.7
width	4.0	4.7
P_4 length	9.0	9.6
width	5.1	5.6
M_1 length	10.9	10.1
width	6.1	5.9
M_2 length	12.9	12.8
width	7.2	6.3
M_3 length	24.7	21.1
width	7.7	6.6

* Approximate measurements.

COMPARATIVE MEASUREMENTS (*Continued*)

	Antilocapra americana A.M. 21529, skull and skeleton A.M. 120947, jaw	*Tetrameryx onusrosagris* A.M. 22488, skull A.M. 22658, jaw A.M. 22483, 22659, skeletal elements
VERTEBRAE		
Atlas, length, centrum	33.9 mm.	34.3 mm.
width	71.1	70.1
Axis, length	57.1	55.2
width	22.4	20.2
Cervical 6, length	27.9	28.9
width	26.1	26.4
Dorsal 7, length	24.0	23.5
width	20.1	19.5
Dorsal 13, length	30.6	28.5
width	20.5	20.3
Lumbar 4, length	33.3	31.0
width	21.5	24.4
Sacrum, 4 vert., length	85.5	85.5
width	70.4	77.0*
Total length to back of sacrum	936.0	885.0*
LIMB ELEMENTS		
Fore limb:		
Scapula, greatest length	195.0	183.5*
Humerus, articular length	162.5	168.0
greatest length	178.0	186.5
Radius-ulna, articular length	201.5	195.0
greatest length	257.0	254.5
Carpals, articular length	21.1	20.6
Metacarpals, articular length	209.5	195.7
Phalanges, greatest length	92.5	93.2
Hind limb:		
Pelvis, width at acetabulum	76.1	74.4
greatest length	218.0	215.5*
constriction behind obturator foramen	78.2	82.4
Femur, greatest length	216.0	229.0
articular length	206.0	217.5
Tibia-fibula, greatest length	267.0	282.0
articular length	254.0	267.0
Tarsals, articular length	42.5	40.9
Metatarsals, articular length	214.0	203.5
Phalanges, greatest length	93.9	99.2

* Approximate measurements.

Comparative Measurements (in mm.) of Horn Cores

		Angle of Divergence (degrees)	Long. Dia. at Base	L. of Ant. Core	L. of Post. Core	Long. Dia. Ant. Core	Tran. Dia. Ant. Core	Long. Dia. Post. Core	Tran. Dia. Post. Core
T. shuleri									
A.M. 13220 (cast), genotype	L.	32	61.1	93.3	..	26.8	17.9	29.5	20.9
	R.	36	63.0	96.8	..	29.8	18.3	30.1	19.0
T. onusrosagris									
22488, type	L.	47	60.2	...	..	29.7	22.5	29.6	21.0
	R.	50	59.7	...	..	28.8	23.0	31.4	21.2
22489	R.	49	57.0	...	..	30.8	22.4	30.8	22.9
22657	L.	..	49.6	...	..	25.3	19.9	..	..
22484 A	L.	43	51.4	...	..	27.2	20.9	27.6	19.0
22484 C	L.	40	57.8	...	..	29.4	21.4	29.9	22.6
22659 A	R.	41	54.9	112.9	..	26.4	21.9	27.9	19.0
22659 B	L.	45	56.8	...	..	30.4	23.5	30.5	22.2
22659 C	R.	55	56.0	...	..	27.7	20.2	28.4	22.0
22659 D	R.	65	56.3	...	..	26.8	20.9	28.3	19.5
A.N.S. 14033 (ref.)	R.	27	52.3	...	..	25.9	21.4	23.8	19.1
T. conklingi[1]									
L.A.M. 174	L.	24	40.5	53.0	50.7	16.0	14.6	15.7	13.1

[1] Stock: "Quaternary Antelope Remains from New Mexico," Los Angeles Museum Publication No. 2, May 29, 1930.

Comparative Measurements (in mm.) of Upper Teeth

		P^2		P^3		P^4		M^1		M^2		M^3	
		long.	tran.	long.	tran.	long.	tran.	long.	tran.	long.	tran.	long.	tran.
T. shuleri													
A.M. 13220 (cast), genotype	L.	7.0	6.0	8.4	7.7	7.1	8.2	14.7	10.7	18.6	12.1	21.4	11.2
13220	L.	7.4	3.8	9.6	5.3	8.8	6.6	14.1	9.0	17.7	10.4	20.9	11.0
T. onusrosagris													
22488, type	L.					8.1	6.6	11.6	9.0	13.8	9.7	14.7	8.7
22489	R.					8.0	6.7	11.6	9.0	13.5	9.8	14.8	8.3
	L.									12.0	9.4	16.3	8.8
22657	L.									14.7	10.5	17.9	9.8
22659 E	L.			8.3	6.8	8.5	7.1	12.9	8.8	14.9	9.6		
22659 F	L.			6.5	5.9	6.8	6.7	9.1	7.6	12.2	8.6	13.9	8.1
22659 G	R.					8.5	7.3	11.8	8.7	14.5	10.1		

Lower Teeth

		P_2		P_3		P_4		M_1		M_2		M_3	
		long.	tran.	long.	tran.	long.	tran.	long.	tran.	long.	tran.	long.	tran.
T. onusrosagris													
A.M. 22490	L.							10.4	6.2	11.7	6.7	20.4	7.2
22658	R.	6.6	3.8	6.8	4.7	9.3	5.6	10.8	5.9	12.6	6.7	21.5	6.6
22659 H	L.					9.5	6.0	10.3	5.9	12.6	7.0	19.9	7.7
22659 I	R.	5.2	3.3	6.0	3.6	8.0	5.0	10.7	5.7				

Tetrameryx, *Stockoceros* and *Hayoceros*

The genus *Tetrameryx* was named by Lull in 1921, the genotypic species, *Tetrameryx shuleri*, being characterized by two pairs of horn cores, coalesced at their bases on either side, and strongly divergent antero-posteriorly from each other. Of these, the posterior horn cores are somewhat more than twice as long as the anterior ones. The cheek teeth are similar to, but slightly larger than the cheek teeth of *Antilocapra*.

Tetrameryx conklingi, described by Stock, differs from the generic type by reason of its much smaller size, and also in that the horn cores are both short and approximately equal to each other in dimensions. *Tetrameryx onusrosagris* Roosevelt and Burden is similar to *T. conklingi*, except for the fact that it is much larger and the horn cores are more widely divergent. These two species, which obviously are closely related to each other, were placed in a new subgenus, *Stockoceros*, by Frick in 1937.

Another new subgenus and species recently named by Frick, namely: *Hayoceros falkenbachi*, is similar to *Tetrameryx*, except that the anterior horn core is the larger of the two, and is shaped like the horn core of *Antilocapra*.

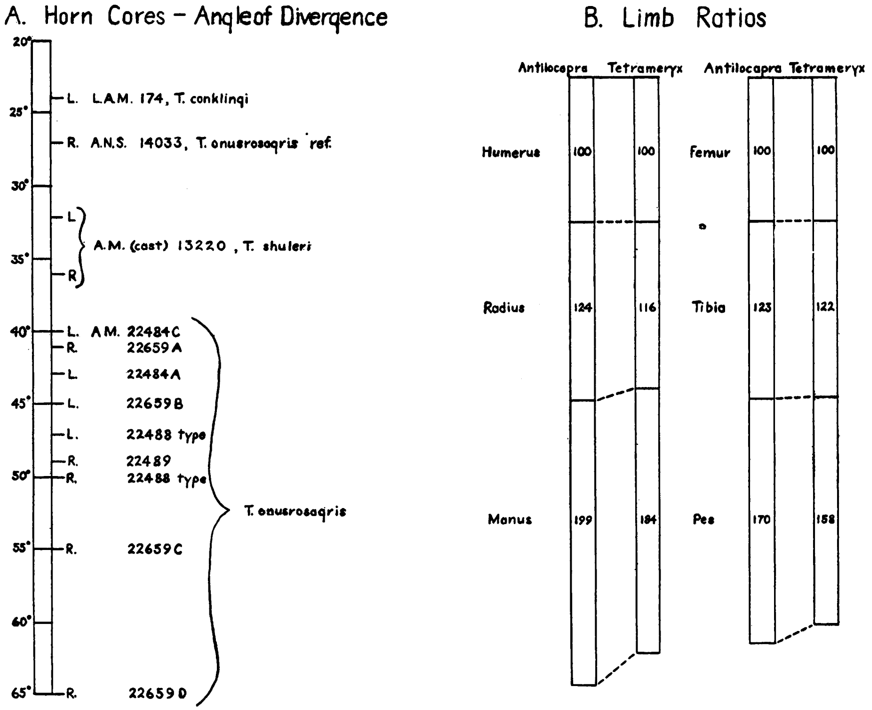


Fig. 12. (A) Diagram to show the angle of divergence between the anterior and posterior horn cores in *Tetrameryx shuleri*, *Tetrameryx conklingi* and several individuals of *Tetrameryx onusrosagris*. (B) Limb ratios in *Tetrameryx onusrosagris* and *Antilocapra americana*, based on a uniform length for the upper limb elements (humerus and femur).

Of course, there is the question as to whether or not *Tetrameryx*, *Stockoceros* and *Hayoceros* are validly separable. It is an interesting fact that these forms are closely related to each other, not only because of the similarity of their horn cores, but also because of their age. All of them are Pleistocene forms. At the present time the separation of the four species into three genera is based solely upon characters of the horn cores, which may be at least to some extent of no more than specific significance. In some of the bovids, *Gazella*, for instance, there is a considerable degree of difference in horn core development within a genus. On the basis of this analogy, therefore, the fact must be recognized that *Stockoceros*, at least, is very possibly congeneric with *Tetrameryx*. This possibility evidently was realized by Frick, for he regarded *Stockoceros* as a subgenus of *Tetrameryx*.

Stock, in his description of *Tetrameryx conklingi*, definitely stated that the differences to be seen between the horn cores of this species and those of the generic type are probably not of generic significance.

"In the light of the variation in structure of horn core of the modern pronghorn, some of the more striking characters which distinguish *T.* (?) *conklingi* from *T. shuleri*, and which may be regarded as of generic value, are attributed to a difference in age and sex."[1]

In this connection it might be said that the material from Papago Spring cave, based on horn cores of at least seven individuals, would seem to indicate that the horn cores are probably similar in the sexes, at least in *Tetrameryx onusrosagris*. Moreover, there is no indication in this material that one horn core became excessively long as a result of age, as is the case in *T. shuleri*. Therefore, the differences between the horn cores of the generic type and of *T. conklingi* and *T. onusrosagris* are to be regarded as of specific import.

Hayoceros, on the other hand, is more definitely separable from the generic type of *Tetrameryx* than is *Stockoceros*. In *Stockoceros* the only difference from *Tetrameryx* is the difference in the length of the posterior horn cores, for in both of these forms the cross-sections of the horn cores are similar. In *Hayoceros*, however, the anterior horn core is very similar in its shape and general development to the horn core of *Antilocapra*. Consequently, if a separation is to be made, *Hayoceros* is by far the more logical form to regard as being distinct from *Tetrameryx*, than is *Stockoceros*. As in the case of *Stockoceros*, Frick made *Hayoceros* a subgenus of *Tetrameryx*.

[1] Stock, Chester, 1930, Los Angeles Museum, Publication No. 2, p. 18.

Evolution of the Antilocapridae

Lull homologized the anterior horn core of *Tetrameryx shuleri* with the horn core of the pronghorn. There is no reason to doubt the validity of this comparison, for in both cases the anterior border of the horn core base is above the middle of the orbit, and in both the horn core is inclined forwardly. This being the case, the posterior horn core of *Tetrameryx* is an independent upgrowth, probably inherited from a Tertiary ancestor such as *Texoceros*.

This conclusion is strengthened by the evidence of *Hayoceros*, from the Pleistocene of Hay Springs, Nebraska. In *Hayoceros*, as was mentioned above, the anterior prong is extraordinarily similar to the horn core of *Antilocapra*, both in the matter of its size and of its shape. As in *Antilocapra*, this horn core is elongated antero-posteriorly, thick at the back and narrowing to a sharp keel at the front. Although broken to a certain extent, the indication is that this horn core was similar to the horn core of *Antilocapra* in length, and also in the manner in which it tapered, from a point part way up on its beam to its upper extremity. The posterior horn core of *Hayoceros* would seem to have been much smaller than the anterior one, and similar to the same structure in *Tetrameryx* in its cross-section and in the manner in which it diverged from the anterior horn core. In fact, *Hayoceros* is virtually an *Antilocapra* with a small posterior horn core, homologous with the posterior horn core of *Tetrameryx*.

The immediate ancestry of *Tetrameryx* and its related forms is almost certainly to be found in *Texoceros*, described by Frick from the Pliocene of Oklahoma. This form is very similar to *Tetrameryx* in size, in the form of the horn cores and in the angle at which they branch away from each other. The main distinction between *Texoceros* and the Pleistocene genus is that in the former the branching of the horn cores begins somewhat higher up; that is, the common base for the two cores is deeper than in *Tetrameryx*.

It is quite evident, however, that this greater height of the common horn core base in the Pliocene form is a more primitive character, for it is exemplified to an even more pronounced degree in the Pliocene genus, *Sphenophalos*. In this latter form there is a rather high, antero-posteriorly elongated horn core, from the upper extremity of which there extend two small prongs.

Sphenophalos, in turn might have been derived from the Lower Pliocene genus *Proantilocapra*, in which there is a short, antero-posteriorly elongated horn core with no distinct tips or prongs, but rather a truncated termination. In this connection it must be said, however, that the position of *Proantilocapra* in the general scheme of antilocaprid evolution is not at all clear. It is probably closely related to *Sphenophalos*, but beyond this no definite statement as to its relationships can be made at the present time.

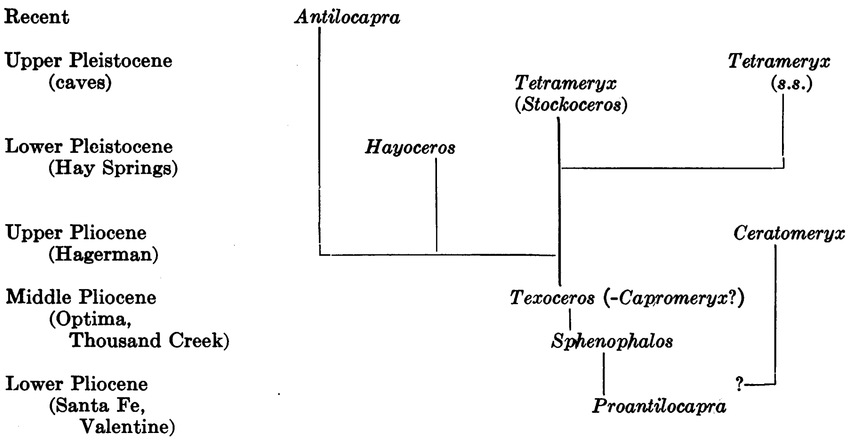
Plioceros of Frick is regarded by Stirton (1938) as a synonym of *Sphenophalos*.

Of the other genera of antilocarprine antilocaprids, *Ceratomeryx*, described by Gazin (1935) from the Upper Pliocene Hagerman formation of Idaho, is distinguished by a large horn core over the orbit, presumably homologous with the anterior horn core of *Tetrameryx* and the single horn core of *Antilocapra*, and a much smaller posterior horn core, evidently homologous with the similarly placed horn core of *Tetrameryx*. The anterior horn core of *Ceratomeryx* is distinguished by its backward tilt, as contrasted with the forward inclination of the anterior horn core of *Tetrameryx* and the single horn core of *Antilocapra*. Gazin supposed that *Ceratomeryx* might occupy a position more or less ancestral to *Tetrameryx shuleri*. But, as mentioned above, the discovery of *Texoceros* would seem to indicate pretty certainly that this genus is the immediate ancestor of *Tetrameryx*. Consequently, it is probable that *Ceratomeryx* is a somewhat separated phylogenetic type, possibly having an ancestry in common with that of *Sphenophalos*.

Capromeryx is a genus which at present is in a very confused state. The generic type *Capromeryx furcifer*, from the Pleistocene of Hay Springs, Nebraska, is based on a lower jaw that shows numerous resemblances to *Antilocapra* and to certain late Tertiary forms, such as *Sphenophalos* and *Merycodus*. Thus, on the basis of the teeth Matthew (1902, 1904), Hesse (1935) and Stirton (1938) have pointed out the possibility of this genus being annectent between ancestral types of the late Tertiary and the recent *Antilocapra*. On the other hand, the referred species of *Capromeryx* in which the horn cores are known, i.e., *Capromeryx minor* and *Capromeryx mexicana*, are so widely divergent from the phylogenetic line leading to the modern pronghorn that they must be regarded as representative of a separate branch of development in antilocaprid evolution. In these species the anterior horn core, although occupying in part the same position as the anterior horn of *Tetrameryx* and *Ceratomeryx*, and the single horn core of *Antilocapra*, is the smaller of the conjoined horns, while the posterior horn core, also occupying in part the position of the anterior horn of *Tetrameryx*, etc., is large, and rakes forward at a decided angle. Both of these horn cores are round in their cross-sections.

Stirton (1938) has recently pointed out the possibility that the horn cores described by Frick under the name of *Texoceros*, may in reality belong to a Tertiary species of *Capromeryx*. (He follows Hesse in regarding *Merycodus altidens* Matthew, as probably of the genus *Capromeryx*.) If such should prove to be the case, then *Capromeryx* would occupy the place accorded *Texoceros* in the above discussion, while of course the two species *Capromeryx minor* and *Capromeryx mexicana* would of necessity be assigned to a new genus.

The other genera of antilocaprine antilocaprids, such as *Ilingoceros*, *Osbornoceros* and the like, are distinctly removed from the forms under consideration, and need not be included in this discussion.



The probable relationships of the four-horned antilocaprids to each other and to *Antilocapra* are shown in the accompanying chart.

Fossil Mammals Associated with *Tetrameryx onusrosagris*

Marmota flaviventris (Audubon and Bachman)

Specimen.—Amer. Mus. No. 22599. Partial skull: palate, anterior portion of cranium, maxillae, partial premaxillae, both incisors, and first and second right upper molars.

The maxillary tooth rows of this specimen are divergent as in the *flaviventris* and the *caligata* groups of the genus *Marmota*, but the measurements closely approximate those of the *flaviventris* group. The modern representatives of the group are not found in Arizona, and the majority of the subspecies are found farther to the north.

Taxidea (?), sp.

Specimen.—The right half of a pelvis, somewhat broken.

This fragment of a pelvic girdle would seem to be referable to the genus *Taxidea*. A specific identification is, however, impossible.

Equus, sp.

Specimen.—The proximal end of a right radius.

This specimen is definitely identifiable as belonging to the genus *Equus*. Its presence in the cave is interesting, in that it constitutes one more record of the association of early man in America with mammals now extinct. It will be remembered, as mentioned in the introduction to this paper, that Messrs. Roosevelt and Burden found associated with the *Tetrameryx* remains, broken fragments of pottery and other indications of human activity. Evidently, man, *Tetrameryx* and *Equus* were contemporaneous with each other when these cave deposits were accumulated.

This piece of horse bone was gnawed by some small mammal when it was fresh. There are numerous tooth marks along its broken edges and on the surface of the bone.

Platygonus (?), sp.

Specimen.—Posterior portion of right upper third molar.

This specimen is too fragmentary for positive identification.

Unidentifiable Fragments

A piece of rib, too large for *Tetrameryx*, probably of horse.

A small piece of bird bone.

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