

NOTES ON PLEISTOCENE AND RECENT TAPIRS

GEORGE GAYLORD SIMPSON

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INTRODUCTION

IN 1942 Mr. Loyd E. Grimes of Eldon, Missouri, and Mr. A. C. Burrill of Jefferson City forwarded to the American Museum of Natural History for identification a collection of fossil vertebrates found in lead mining operations in that region. On being prepared and sorted, this collection was found to include, among many other things, a tapir skeleton more nearly complete than any previously known from the Pleistocene. The study of this interesting specimen required assembling observations and specimens of numerous other tapirs, fossil and recent, and so much new or revised information was acquired that it has seemed worth while to supplement the description of the Missouri specimen by notes

and data on several other species.

I am much indebted, in the first place, to Mr. Grimes and Mr. Burrill. Mr. Albert Thomson skillfully prepared the specimen sent by them. The Academy of Natural Sciences of Philadelphia, through Dr. E. H. Colbert (of the American Museum, consultant in the Academy), lent the important series of fossil tapirs from Port Kennedy. The Peabody Museum of Yale University, through Dr. S. C. Ball, lent a specimen of *T. roulini*. My wife, Dr. Anne Roe, made many of the statistical calculations. Mr. John C. Germann prepared the illustrations. Dr. Colbert supervised completion of the manuscript.

GENERA AND SPECIES OF RECENT TAPIRS

THE RECENT TAPIRS fall into four groups with varying degrees of resemblance. The common South American tapir, *Tapirus terrestris*, is best known and is the type of the genus. The South American mountain or páramo tapir, *T. roulini*, is commonly considered a close ally of *T. terrestris* and referred to the same genus or subgenus.¹ It is in some characters intermediate between *T. terrestris* and *T. indicus*, for instance in the flattened dorsal cranial contour, broad dorsal frontal region, and elongate P¹. The oriental *T. indicus* is in most respects further from *T. terrestris* and is often placed in a separate group, *Acrocodia* Goldman, 1913, which is sometimes given full generic rank.² This species is in some (of course not in all) respects intermediate between *T. roulini* or *terrestris* and *T. bairdii*, for instance in the greater ossification of the mesethmoid, incipient clasping of the mesethmoid by the maxillae, and the separation of the temporal crests. Most aberrant of recent tapirs are *T. bairdii* and its close ally, subspecies, or synonym *T. dowi*, of Central America, now usually placed in a separate genus, *Tapirella* Palmer, 1903 (*Elasmognathus* Gill, 1865, *nec* Fieber, 1844). The dentition is more as in *T. terrestris* and almost indistinguishable from the latter, but the cranium represents an extreme of the tendency seen in *T. indicus*, and the mesethmoid is still further ossified in the adult and is firmly clasped by ascending maxillary processes (already present in the young before the ethmoid is ossified).

Another extreme is seen in *T. augustus* from the Pleistocene of China, placed in a separate subgenus *Tapirus* (*Megatapirus*) by Matthew and Granger, given generic rank by Colbert in a study in progress. This appears to be derived from a form closely similar to *T. indicus*, but it is decidedly more specialized, probably more than *T. bairdii*, and in quite a

different direction except for the molarization which is more advanced than in *T. indicus* and comparable to, or even slightly more progressive than, *T. terrestris* or *bairdii*.

Leaving aside *Megatapirus*, sharply distinct from anything definitely recognized in the Western Hemisphere, it is seen that even the recent groups form a complex, intergrading in all but a few characters and with step-like intermediates between the extremes in these diagnostic characters. The two best-defined Pleistocene North American forms fit into this series, as will be seen, and provide additional intermediate types.

Anyone who examines them from any but the most narrowly analytical point of view must be struck by the fundamental similarity of all the living and of the American Pleistocene tapirs. The groups specified above can be distinguished at a glance on the basis of complete skulls, but they ring variations on a common theme and their possible higher grouping depends on what particular character is subjectively emphasized. The dentition would probably separate *T. roulini*, unite *T. terrestris* and *bairdii*, and leave *T. indicus* intermediate or in either group. The cranium might unite *T. bairdii* and *T. indicus*, separate *T. terrestris*, and place *T. roulini* between these groups or in either of them. The mesethmoid region, which is in fact stressed by most students although I see no particular reason for doing so to the exclusion of other characters, unites *T. terrestris* and *roulini*, separates *T. bairdii*, and leaves *T. indicus* more or less intermediate. Still other characters would give almost any other desired grouping. The phylogenetic relationships are not directly known. On geographic grounds it would seem probable that the American species had a common ancestry separate from that of *indicus*, and it is curious that this is one grouping for which it would be particularly difficult to find a solidly morphological basis.

Under such circumstances, whether to call the observed groups genera or species is mainly a matter of taste. If, however, generic distinctions are to be made at all, I see little logical reason for grouping any two of the Pleistocene or Recent species in one genus,

¹ Gray, 1873, did propose a subgenus for this species, *Cinchacus* (apparently a misprint for *Pinchacus*), but this does not seem to have been adopted by later students.

² This genus or subgenus was formerly often called *Rhinochoerus* Wagler, 1830, but the latter name is an absolute synonym of *Tapirus* and not available for a group with *T. indicus* as type.

and the genera should probably all be monotypic,¹ which I consider highly undesirable in dealing with so many manifestly closely related species, although some students hold opposite views. For the paleontologist it is also a legitimate practical consideration, al-

¹ Except possibly *Tapirella* which might have two species, *bairdii* and *dowi*, although their right to separate specific status does not appear to be demonstrated. Other species have been proposed in the *T. terrestris* group, but their separation is dubious and improbable.

though not admissible on abstract biological grounds, that such a system would make impossible the generic identification of the majority of fossil finds. All things considered, it is certainly justified and I think it preferable to place all these species in *Tapirus*. *Tapirus* (*Tapirella*) and perhaps others may be used as subgenera if it becomes necessary or convenient to distinguish such groups from species.

NOTES ON *TAPIRUS TERRESTRIS*

ACCURATE EVALUATION of the scattered remains of Pleistocene tapirs (and of a host of other Pleistocene fossils) has been impossible, in part because of the inadequacy of available data on their recent allies. For purposes of direct comparison it is essential to know the modal osteological and dental characters of the recent forms, and for grouping of the fossils it is necessary to have a good idea of the variation to be expected in a race or species of tapirs. No attempt to do this has hitherto been made, and comparisons in the literature are usually with single specimens, which in some cases were really quite atypical for the species they were taken to represent and even seem at times to have been incorrectly identified.

It was, therefore, a necessary preliminary for the present study to gather data on recent

tapirs before attempting to interpret the fossil materials. Limitations of time and specimens kept the data thus obtained from being sufficient for all purposes, but they are at least better than anything hitherto available and they suffice for preliminary orientation. Some specimens of all the recent species have been studied, but only for *T. terrestris* were adequate variation studies possible (and even for this species these studies are manifestly incomplete). Similar studies on other species must eventually be made, but they were not possible for me at this time. In spite of a few clear-cut specific distinctions, the living tapirs are a uniform group in most respects, and it is possible that the variation of the other species is about the same in kind and extent as in *T. terrestris*.

STATISTICAL DATA

The available sample consisted of 28 specimens in the study collection of the Department of Mammals of this Museum, skulls and jaws and about half a dozen more or less complete skeletons. There are 19 adults (as defined below) and nine juveniles. Some of the specimens are not sexed, but after preliminary comparisons of sexed materials it was found that males and females differ little or not at all in the dimensions studied so that the unsexed specimens could be included without fear of significant error.

The sample is geographically heterogeneous. Seven specimens are recorded only as "South America," and the others range from Matto Grosso to Colombia and from eastern Peru to British Guiana. It was found, however, that this heterogeneity does not invalidate the combined data and is not particularly disadvantageous for present purposes. A large number of living tapirs can seldom be found in one locality, and multiple specimens that are from one locality are likely to be individually related and to invalidate the data by introducing definite bias due to this fact. If there were any really well-marked geographic regularity in varia-

tion, even these limited series should show it, and they do not. Series that are from restricted areas are relatively about as variable as the whole sample. For instance, specimens from Matto Grosso have a mean length of palate of 190 ± 5 mm. and coefficient of variation 6.9 ± 2.2 ; for specimens from the vicinity of the Ucayali River in Peru the corresponding figures are 200 ± 6 and 5.5 ± 2.7 ; and for specimens from all other localities combined the figures are 186 ± 3 and 5.3 ± 1.3 . Thus the local samples are relatively more variable than the geographically heterogeneous sample. As regards the populations, no significant differences either in means or in variability are indicated. This is also true of the other variates measured.

It is almost incredible that so widespread a species should not have some local differentiation, and indeed a number of supposed subspecies or even distinct species have been designated, for instance *aurillardi*, *mexicanae*, and *pegazzinii*. These have, however, been based on characters such as vary among all populations of *terrestris*, and it has never, so far as I know, been established that there are real differences between the local populations,

as opposed to differences in form of individual tapirs that happened to be collected in one place or another. The sample here discussed is inadequate to prove the absence of local differentiation, but it suffices to cast the gravest doubts on current designations of supposed subgroups. Moreover, heterogeneous as it is, its variability is not unusually great for most characters and is quite consistent with the hypotheses of an essentially

is anteroposterior length and W is maximum transverse width. Except dm_2^1 and P_2^1 , all tapir cheek teeth have two distinct lobes, usually of different widths, and these were measured separately; W_A width of anterior lobe, W_P width of posterior lobe. (W =either W_A or W_P , whichever is greater.) Nasal breadth was taken across both nasals at their widest point. Nasal "length" is here an oblique measurement from the anterior tip of

TABLE 1
STATISTICAL DATA ON LINEAR DIMENSIONS OF DECIDUOUS MOLARS OF *Tapirus terrestris*

Variate	N	OR	SR	M	σ	V
dm^1 L	7	15.1-18.0	5.4	$16.19 \pm .31$	$.83 \pm .22$	5.1 ± 1.5
	7	13.4-15.8	4.0	$14.62 \pm .23$	$.62 \pm .17$	4.2 ± 1.1
dm^2 L	7	18.1-21.4	5.8	$19.45 \pm .34$	$.89 \pm .24$	4.6 ± 1.2
	7	16.0-17.6	2.3	$16.62 \pm .14$	$.36 \pm .10$	$2.2 \pm .6$
	7	17.8-21.3	6.5	$19.22 \pm .38$	$1.00 \pm .28$	5.2 ± 1.4
dm^3 L	7	18.3-21.4	5.6	$19.86 \pm .32$	$.86 \pm .23$	4.3 ± 1.2
	7	18.3-20.4	4.4	$18.99 \pm .26$	$.68 \pm .18$	3.6 ± 1.0
	7	17.3-21.0	7.2	$18.71 \pm .42$	$1.11 \pm .30$	5.9 ± 1.6
dm^4 L	9	20.0-22.8	5.6	$20.74 \pm .29$	$.87 \pm .21$	4.2 ± 1.0
	9	20.2-22.9	6.4	$20.95 \pm .33$	$.98 \pm .23$	4.7 ± 1.1
	9	18.0-20.7	5.6	$19.04 \pm .29$	$.86 \pm .20$	4.5 ± 1.1
dm_2 L	8	22.7-24.7	3.8	$23.39 \pm .20$	$.58 \pm .15$	$2.5 \pm .6$
	8	12.4-13.9	2.0	$13.28 \pm .11$	$.31 \pm .08$	$2.3 \pm .6$
dm_3 L	8	18.8-21.2	4.5	$20.24 \pm .25$	$.70 \pm .18$	$3.5 \pm .9$
	8	12.3-14.7	4.3	$13.24 \pm .24$	$.67 \pm .17$	5.1 ± 1.3
	8	12.6-14.0	2.7	$13.19 \pm .14$	$.41 \pm .10$	$3.1 \pm .8$
dm_4 L	8	20.1-22.2	5.7	$21.21 \pm .31$	$.88 \pm .22$	4.2 ± 1.0
	8	13.7-15.9	3.0	$14.58 \pm .17$	$.47 \pm .12$	$3.2 \pm .8$
	8	13.9-15.1	2.3	$14.32 \pm .12$	$.35 \pm .09$	$2.4 \pm .6$

similar (however individually variable) specific population all over tropical South America. For purposes of comparison the geographic heterogeneity of the sample may be more helpful than disadvantageous because the distribution is comparable with that of North American fossil tapirs.

The variates studied were chosen primarily for their usefulness in comparison with fossil materials. All cheek teeth, deciduous and permanent, were measured. L of the tables

the nasal to its postero-external angle, almost always a definite point above where the spiral groove turns onto the top of the skull. This unorthodox measurement was selected rather than a completely longitudinal dimension because it seems less affected by subjective factors and more functionally controlled than one involving the posterior nasal suture and can also sometimes be obtained on less well-preserved materials. For the same reason an oblique measurement from prosthion to the

nearest point on the orbital rim was finally used in preference to a facial measurement involving projection or some more or less subjective criterion. Other dimensions given are usual and self explanatory.

Skull dimensions of juveniles were also measured and studied, but not averaged with those of adults. For this purpose specimens with P_4^4 were counted as adult, although they

were counted as juveniles in order to be conservative.

The essential statistical data are given in the accompanying tables. Non-metrical characters were also studied, and some will be mentioned in subsequent discussions, but the full data on them cannot be given succinctly and are omitted. The statistics given are N , size of sample; OR , observed range (entered

TABLE 2

STATISTICAL DATA ON LINEAR DIMENSIONS OF PERMANENT UPPER CHEEK TEETH OF *Tapirus terrestris*

Variate		N	OR	SR	M	σ	V
P^1	L	17	14.6-17.7	6.4	$16.40 \pm .24$	$.99 \pm .17$	6.0 ± 1.0
	W	17	14.7-16.7	4.7	$15.31 \pm .17$	$.72 \pm .12$	$4.7 \pm .8$
P^2	L	17	16.1-18.9	3.8	$17.98 \pm .14$	$.58 \pm .10$	$3.2 \pm .6$
	W_A	15	17.0-20.3	4.1	$18.78 \pm .16$	$.63 \pm .11$	$3.4 \pm .6$
	W_P	16	17.7-22.3	7.1	$20.67 \pm .27$	$1.09 \pm .19$	$5.3 \pm .9$
P^3	L	16	17.1-21.2	6.3	$19.35 \pm .24$	$.97 \pm .17$	$5.0 \pm .9$
	W_A	15	20.4-25.5	7.5	$22.72 \pm .30$	$1.15 \pm .21$	$5.1 \pm .9$
	W_P	15	21.1-24.8	6.1	$22.74 \pm .24$	$.94 \pm .17$	$4.1 \pm .8$
P^4	L	14	18.3-21.7	7.8	$20.09 \pm .32$	$1.20 \pm .23$	6.0 ± 1.0
	W_A	14	22.6-28.1	10.5	$25.00 \pm .43$	$1.61 \pm .30$	6.4 ± 1.2
	W_P	14	21.1-26.2	10.1	$23.78 \pm .42$	$1.56 \pm .29$	6.6 ± 1.2
M^1	L	21	19.5-24.1	8.2	$21.09 \pm .27$	$1.27 \pm .20$	$6.0 \pm .9$
	W_A	21	21.9-26.8	8.0	$23.69 \pm .27$	$1.23 \pm .19$	$5.2 \pm .8$
	W_P	19	19.9-24.6	8.9	$21.43 \pm .31$	$1.37 \pm .22$	6.4 ± 1.0
M^2	L	15	21.4-26.2	8.9	$23.07 \pm .35$	$1.37 \pm .25$	5.9 ± 1.1
	W_A	15	23.4-29.0	9.5	$25.95 \pm .38$	$1.46 \pm .27$	5.6 ± 1.0
	W_P	15	20.7-26.0	11.0	$22.86 \pm .44$	$1.69 \pm .31$	7.4 ± 1.3
M^3	L	8	20.5-26.5	11.9	$22.64 \pm .64$	$1.83 \pm .45$	8.1 ± 2.0
	W_A	8	24.5-28.4	7.3	$25.85 \pm .40$	$1.12 \pm .28$	7.1 ± 1.7
	W_P	8	20.0-22.2	4.5	$20.94 \pm .24$	$.69 \pm .17$	$3.3 \pm .8$

do not necessarily have M_3^3 in place. It was found that no appreciable change in dimensions occurs after P_4^4 are in use. For instance, six skulls with P_4^4 but without M_3^3 average 351.5 mm. in length and seven with M_3^3 average 352.0 mm., a wholly negligible difference. In fact, specimens with $P_{2-3}^3 dm_4^4$ seem usually to be fully grown, or very nearly so, but these

by extreme measurements); SR , standard range from standard deviation (entered by span, see Simpson, 1941a); M , mean and its standard error; σ standard deviation and its standard error; V , coefficient of variation and its standard error. M , σ , and their standard errors were calculated by Dr. Anne Roe; the other statistics and the observed measurements are by me.

TABLE 3

STATISTICAL DATA ON LINEAR DIMENSIONS OF PERMANENT LOWER CHEEK TEETH OF *Tapirus terrestris*

Variate		N	OR	SR	M	σ	V
P ₂	L	14	20.1-22.8	6.2	21.14 ± .25	.95 ± .18	4.5 ± .8
	W	15	11.6-14.3	4.0	12.93 ± .16	.61 ± .11	4.7 ± .9
P ₃	L	15	18.1-21.1	6.3	19.65 ± .25	.97 ± .18	4.9 ± .9
	W _A	15	13.3-16.0	4.8	14.62 ± .19	.74 ± .14	5.1 ± .9
	W _P	15	14.9-17.1	4.0	16.02 ± .16	.62 ± .11	3.9 ± .7
P ₄	L	14	18.7-21.9	6.5	20.44 ± .27	1.01 ± .19	4.9 ± .9
	W _A	13	16.0-18.5	5.4	17.06 ± .23	.83 ± .16	4.9 ± 1.0
	W _P	14	16.5-19.1	5.2	17.80 ± .21	.80 ± .15	4.5 ± .8
M ₁	L	20	19.5-24.0	6.9	21.16 ± .24	1.07 ± .17	5.1 ± .8
	W _A	19	14.8-17.9	6.2	16.58 ± .22	.95 ± .15	5.7 ± .9
	W _P	20	14.5-17.0	4.7	15.57 ± .16	.73 ± .12	4.7 ± .7
M ₂	L	16	21.4-26.0	7.6	23.09 ± .30	1.18 ± .21	5.1 ± .9
	W _A	16	16.0-20.2	7.5	17.79 ± .29	1.15 ± .20	6.5 ± 1.0
	W _P	16	15.5-18.3	4.9	17.06 ± .19	.75 ± .13	4.4 ± .8
M ₃	L	7	21.4-28.4	14.4	24.29 ± .84	2.22 ± .59	9.1 ± 2.4
	W _A	7	16.4-20.0	7.6	18.31 ± .45	1.18 ± .32	6.4 ± 1.7
	W _P	7	15.3-17.7	5.8	16.36 ± .34	.89 ± .24	5.4 ± 1.5

TABLE 4

STATISTICAL DATA ON INDICES OF DECIDUOUS MOLARS OF *Tapirus terrestris*

Variate		N	OR	SR	M	σ	V
$\frac{100W}{L}$	dm ¹	7	85- 97	23	90.3 ± 1.4	3.6 ± 1.0	4.0 ± 1.1
	dm ²	7	95-101	10	98.9 ± .6	1.6 ± .4	1.6 ± .4
	dm ³	7	92-103	24	96.6 ± 1.4	3.8 ± 1.0	3.9 ± 1.1
	dm ⁴	9	99-106	13	101.0 ± .7	2.0 ± .5	1.9 ± .5
$\frac{100W_A}{W_P}$	dm ²	7	79- 93	24	88.7 ± 1.4	3.8 ± 1.0	4.3 ± 1.1
	dm ³	7	93-106	24	101.6 ± 1.4	3.8 ± 1.0	3.7 ± 1.0
	dm ⁴	9	105-113	15	110.0 ± .8	2.4 ± .6	2.2 ± .5
$\frac{100W}{L}$	dm ₂	8	53- 60	13	56.6 ± .7	2.0 ± .5	3.5 ± .9
	dm ₃	8	63- 70	17	66.2 ± 1.0	2.7 ± .7	4.1 ± 1.0
	dm ₄	8	65- 72	15	69.2 ± .9	2.4 ± .6	3.5 ± .9
$\frac{100W_A}{W_P}$	dm ₃	8	95-106	22	100.4 ± 1.2	3.5 ± .9	3.5 ± .9
	dm ₄	8	96-105	19	101.8 ± 1.0	2.9 ± .7	2.8 ± .7

TABLE 5

STATISTICAL DATA ON INDICES OF PERMANENT UPPER CHEEK TEETH OF *Tapirus terrestris*

Variate	<i>N</i>	<i>OR</i>	<i>SR</i>	<i>M</i>	σ	<i>V</i>		
$\frac{100W}{L}$	P ¹	17	85-106	40	93.3 ± 1.5	6.1 ± 1.0	6.5 ± 1.1	
	P ²	16	106-122	27	114.8 ± 1.0	4.2 ± .7	3.7 ± .6	
	P ³	15	110-127	31	118.7 ± 1.2	4.8 ± .9	4.0 ± .7	
	P ⁴	14	114-137	43	124.4 ± 1.8	6.6 ± 1.2	5.3 ± 1.0	
	M ¹	21	106-125	37	112.6 ± 1.2	5.7 ± .9	5.1 ± .8	
	M ²	15	105-119	23	112.7 ± .9	3.6 ± .7	3.2 ± .6	
	M ³	8	107-124	36	114.6 ± 2.0	5.6 ± 1.4	4.9 ± 1.2	
	$\frac{100W_A}{W_P}$	P ²	14	84- 95	27	89.5 ± 1.1	4.1 ± .8	4.6 ± .9
		P ³	15	93-106	21	100.0 ± .8	3.2 ± .6	3.2 ± .6
P ⁴		14	99-110	27	105.1 ± 1.1	4.1 ± .8	3.9 ± .7	
M ¹		19	108-118	24	111.1 ± .9	3.7 ± .6	3.3 ± .5	
M ²		15	103-123	25	113.7 ± 1.0	3.9 ± .7	3.4 ± .6	
M ³		8	118-133	27	123.6 ± 1.4	4.1 ± 1.0	3.3 ± .8	

TABLE 6

STATISTICAL DATA ON INDICES OF PERMANENT LOWER CHEEK TEETH OF *Tapirus terrestris*

Variate		<i>N</i>	<i>OR</i>	<i>SR</i>	<i>M</i>	σ	<i>V</i>
$\frac{100W}{L}$	P ₂	14	57– 69	25	61.3 ±1.0	3.9 ± .7	6.4 ±1.2
	P ₃	15	77– 85	12	81.7 ± .5	1.9 ± .4	2.3 ± .4
	P ₄	14	83– 90	16	87.0 ± .7	2.5 ± .5	2.9 ± .5
$\frac{100W_A}{W_P}$	M ₁	21	73– 88	26	78.9 ± .9	4.0 ± .6	5.1 ± .8
	M ₂	16	74– 81	14	77.2 ± .6	2.2 ± .4	2.9 ± .5
	M ₃	7	70– 81	23	75.7 ±1.3	3.5 ±1.0	4.6 ±1.2
$\frac{100W_A}{W_P}$	P ₃	15	82– 96	18	91.4 ± .7	2.7 ± .5	3.0 ± .5
	P ₄	13	92–100	18	96.0 ± .7	2.7 ± .5	2.8 ± .6
	M ₁	20	102–112	16	107.4 ± .6	2.4 ± .4	2.2 ± .3
$\frac{100W_A}{W_P}$	M ₂	16	99–110	21	104.2 ± .8	3.2 ± .6	3.1 ± .5
	M ₃	7	107–115	16	111.7 ± .9	2.5 ± .7	2.2 ± .6

VARIATION

The standard ranges and coefficients of variation in the accompanying tables give some idea of the absolute and relative variation, respectively, in *T. terrestris*.

In this geographically heterogeneous sample the linear dimensions of cheek teeth show variation that is quite usual for uniform mam-

malian races. The average coefficient of variation for the 56 tooth dimensions studied is 4.9, which is probably very near an average figure for functional teeth in homogeneous samples of mammals in general. In round numbers, *V* is from 3 to 6, inclusive, for 47 of the 56 measured dimensions. The least

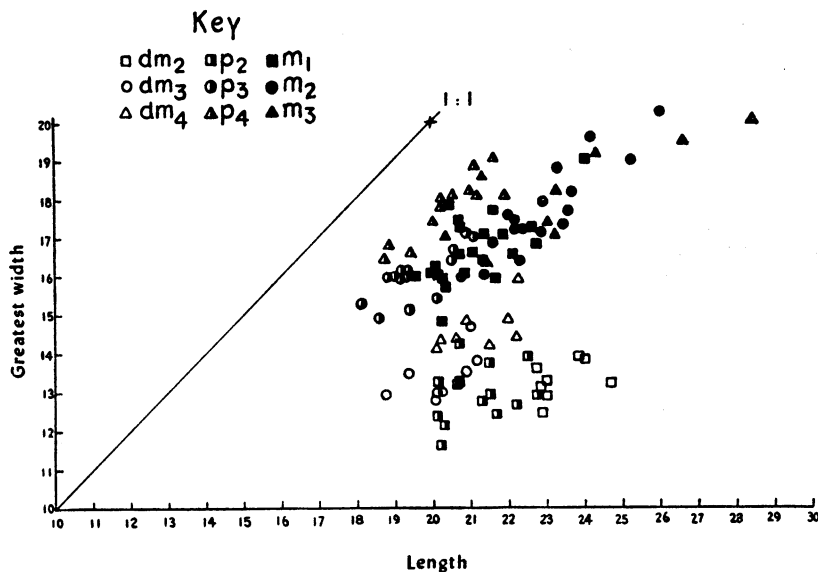


FIG. 1. *Tapirus terrestris*. Recent, South America. Graph of length and width in millimeters of lower cheek teeth.

variable dimensions ($V=2.2$ to 2.5) are anterior width of dm^2 , length and width of dm^2 , and posterior width of dm^4 . The most variable dimensions ($V=6.6$ to 9.1) are posterior width of P^4 , posterior width of M^2 , length and anterior width of M^3 , and length of M^3 . M^3 are the most variable single teeth.

In this sample the deciduous teeth are, as an average, less variable than their successors, and the premolars average less variable than the molars. The difference is not pronounced and might not obtain in the population as opposed to the sample. Still smaller differences in relative variation between longitudinal and transverse dimensions and between upper and lower teeth probably have no significance.

Another curiously suggestive fact as regards the sample, but also quite inconclusive as regards the population, is that if the terminal teeth are ignored, the least variable dimension of all the other lower cheek teeth is the posterior width (and the most variable is the anterior width), while in the non-terminal upper cheek teeth the posterior width is the most variable dimension in all but one case (P^3).

The various dimensions of single teeth tend to be positively correlated, and the ratio of these dimensions, proportions of the teeth,

tend to be less variable than the dimensions themselves. This would be expected, *a priori*, and would perhaps merit no special attention were it not for curious exceptions. The width: length ratios of dm^2 , P^1 , and P^2 (all anterior

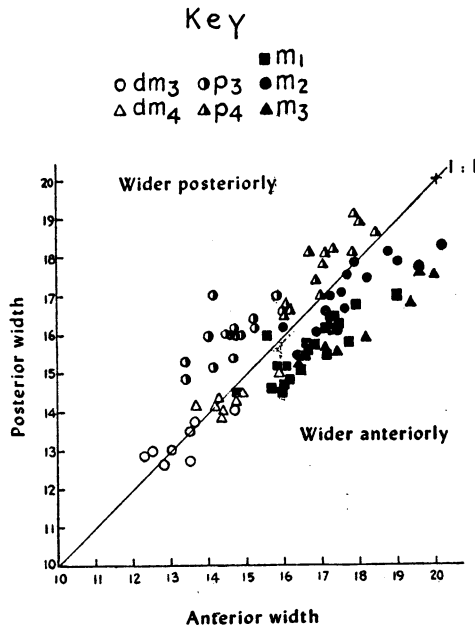


FIG. 2. *Tapirus terrestris*. Recent, South America. Graph of anterior and posterior widths in millimeters of lower cheek teeth.

cheek teeth) are distinctly more variable than the linear dimensions because these dimensions are only slightly correlated in these teeth. For instance, for P_2 the correlation coefficient of width on length is 0.23, a low sample value and one not necessarily indicating any correlation at all in the population (difference from zero is not statistically significant). For P_3 this coefficient is 0.67, a decisively significant positive correlation. In

proportions and the nature of the dental growth field, but such inferences cannot safely be based on a single species, and their consideration would lead too far afield for inclusion in this paper.

Variations in the skull have been less exhaustively studied, and only eight dimensions are considered. Five of these show normal variation for functional characters, with coefficients from 4.7 to 6.0, average 5.5.

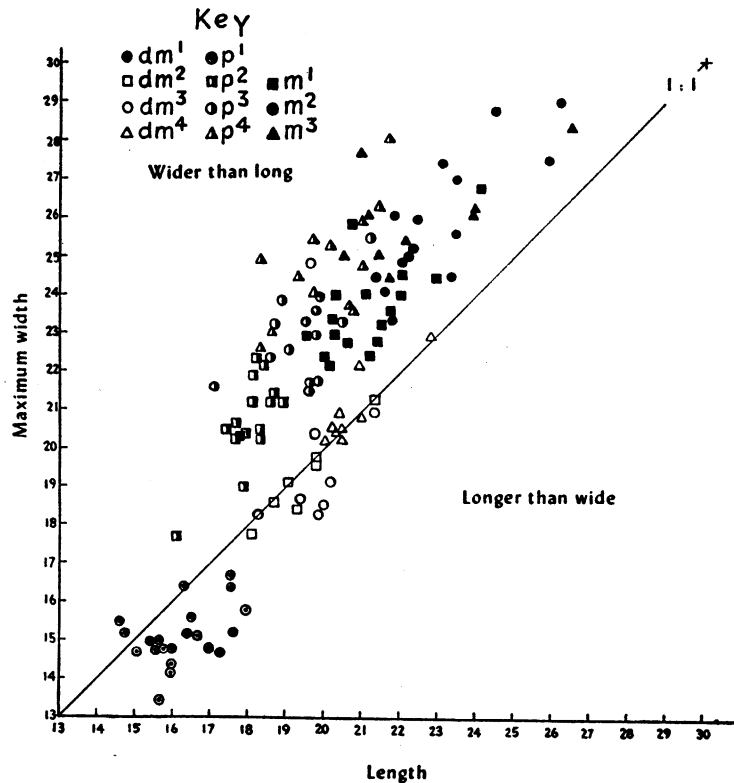


FIG. 3. *Tapirus terrestris*. Recent, South America. Graph of length and width in millimeters of upper cheek teeth.

other words, as a rule length and width (also anterior and posterior width) tend to vary together, but in dm_2 , P^1 , and P_2 (and possibly but not clearly a few others to less degree) length and width tend to vary independently. These teeth (particularly P_2 and P^1) are consequently extremely variable in proportions and in outline, and little dependence can be placed on these characters in taxonomy. Of still broader importance are possible inferences regarding genetic control of tooth

None of these can be considered unusually variable or constant. The dimensions of the nasals are, however, highly variable, and the length of the superior diastema is exceptionally so, $V=14.4$, the highest of any dimension measured in this species. This observation is important because differences in the diastema are striking in making comparisons and may be assumed to have more taxonomic value than should really be assigned to so variable a character. Moreover

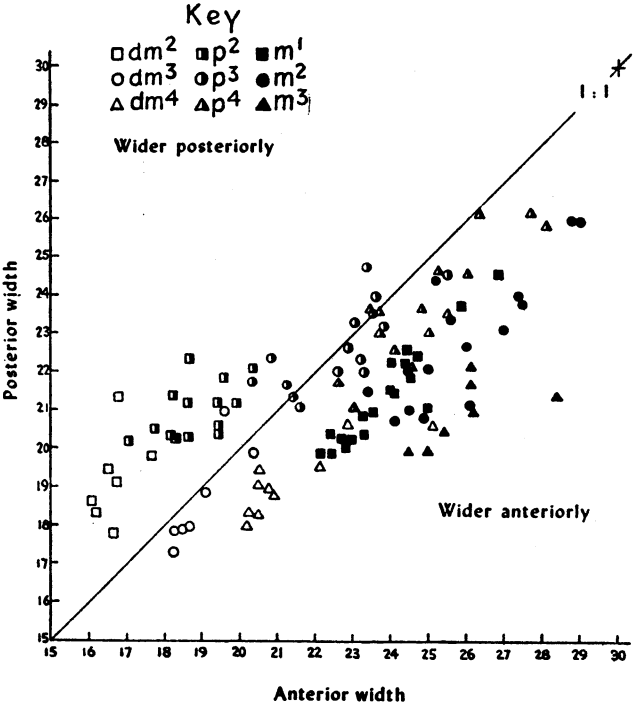


FIG. 4. *Tapirus terrestris*. Recent, South America. Graph of anterior and posterior widths in millimeters of upper cheek teeth.

the length of the diastema seems to have little dependence on general skull size or, within broad limits, on age.

Most of the skull dimensions are positively correlated in some degree, and although the proportions are rather variable the variation is less than for the component linear factors. The nasals again provide an exception. Their length and breadth vary with almost complete independence ($r = -.16$, with $N = 13$, very far from demonstrating any tendency

toward covariation). These nasal proportions are also striking superficial characters, and it is important to note that they are so extremely variable. Even in this small series of 13 specimens the index as here used varies from 71 to almost twice that, 138, and in the species as a whole variation from as low a value as 30 to as high as 150 may occur, that is, it is to be expected that extreme individuals of *Tapirus terrestris* can have the nasals only about one-third as wide as long (oblique

TABLE 7

STATISTICAL DATA ON LINEAR DIMENSIONS OF ADULT SKULLS OF *Tapirus terrestris*

Variate	N	OR	SR	M	σ	V
A. Prosthion-foramen magnum	13	308-375	121	351.7 \pm 5.2	18.6 \pm 3.6	5.3 \pm 1.0
B. Prosthion-choana	16	171-213	73	189.9 \pm 2.8	11.3 \pm 2.0	6.0 \pm 1.0
C. Prosthion-orbit	16	145-177	56	159.7 \pm 2.2	8.6 \pm 1.5	5.4 \pm 1.0
D. Sagittal crest-basisphenoid	13	117-140	50	128.8 \pm 2.1	7.7 \pm 1.5	6.0 \pm 1.2
E. Postauditory breadth	12	98-117	33	108.0 \pm 1.5	5.1 \pm 1.0	4.7 \pm 1.0
F. Oblique nasal length	13	50- 89	67	76.1 \pm 2.8	10.3 \pm 2.0	13.5 \pm 2.7
G. Nasal breadth	13	57- 74	34	66.6 \pm 1.5	5.3 \pm 1.0	8.0 \pm 1.6
H. Maxillary diastema	16	40- 62	46	49.4 \pm 1.8	7.1 \pm 1.2	14.4 \pm 2.5

TABLE 8
STATISTICAL DATA ON INDICES OF ADULT SKULLS OF *Tapirus terrestris*

Variate	N	OR	SR	M	σ	V
$\frac{100\text{ B}}{\text{A}}$	13	51 - 57	12	$53.7 \pm .5$	$1.8 \pm .4$	$4.0 \pm .7$
$\frac{100\text{ C}}{\text{A}}$	13	41 - 48	14	$45.1 \pm .6$	$2.1 \pm .4$	$4.7 \pm .9$
$\frac{100\text{ D}}{\text{A}}$	13	34 - 38	9	$36.5 \pm .4$	$1.4 \pm .3$	$3.8 \pm .8$
$\frac{100\text{ E}}{\text{A}}$	12	29 - 32	7	$30.8 \pm .3$	$1.1 \pm .2$	$3.6 \pm .7$
$\frac{100\text{ H}}{\text{A}}$	13	11.8- 17.4	11.3	$13.99 \pm .48$	$1.75 \pm .34$	12.5 ± 2.4
$\frac{100\text{ G}}{\text{F}}$	13	71 -138	117	90.0 ± 4.9	17.8 ± 3.5	19.8 ± 3.9

length) while at the other extreme they may be one and one-half times as wide as long.

It is now well established that in most mammals important skull proportions vary systematically with size, or in other words that relative growth of various dimensions is heterogonic. I have found little evidence that this is true in *T. terrestris*. The number of juveniles studied, only seven, does not suffice for absolute certainty, but if any real tendency toward heterogonic growth is present the heterogony must be slight. The only marked difference between very young and very old skulls is caused by the much higher sagittal crest in the latter. This, however, makes surprisingly little difference in the relative depth of this region, indeed no difference so far as our specimens demonstrate. The adult average index for depth from sagittal crest to basisphenoid against skull length is 36.5, and the average in the four youngest individuals measured is 36.3. The index for the very youngest available individual, almost new born, happens to be 37, very near the adult mean. The explanation of this apparent paradox is clear: the over-all or, so to speak, outside proportions of the skull remain approximately constant with growth, but the endocranial cavity increases

more slowly than the skull as a whole, the difference being made up by the increasing elevation of the sagittal crest.

With this exception, the juvenile tapir skull has all its proportions about as in the adult. The available skeletal material is insufficient for the necessary tests of trend in such variable characters, but the limb proportions also seem to remain approximately the same throughout life, which is unusual in an ungulate. It has been noticed more casually that young tapirs seem (except for the transitory pelage markings) more like miniature adults than is usual in mammals.

It is possible to find in the semi-popular literature (e.g., Brehm) or to hear from experienced tapir hunters most conflicting statements on sexual variation or dimorphism in this family. Regarding *T. terrestris* I have been told on one hand that the females average larger than the males, and on the other that the old males are decidedly larger than any females. Sexed skulls in the series available to me are too few to detect small differences in averages. There are only three sexed adult females, and these are quite near the averages for males in all cranial and dental characters. The largest animal in the series, an exceptional but apparently not

abnormal specimen for this species, happens to be male, but it differs as much from most of the males, including some individuals considerably older than this, as from the females. Obviously chance could well operate to make

this largest deviant male without there really being any tendency toward dimorphism. The evidence is that there is little if any osteological or dental difference between the sexes.

SOME DENTAL RELATIONSHIPS

Tapirs as a group are characterized by an unusually well-developed and long persisting deciduous dentition.¹ There is a fully functional dm^1 that is almost as large as its successor, P^1 . M^1 long function with the milk dentition. Dm^{2-3} are lost almost together and before M^2 come into use. Dm^4 then function for some time with the permanent dentition and are not lost until after M^2 have erupted, at which time the animals must be considered fully adult and very near or at their definitive size. We have one specimen of known age at death, 13 months, well grown (indeed above average size for the species) with dm^4 still functioning and M^2 not yet in place. M^3 do not reach occlusion until all the other permanent teeth are well worn.

It is now generally agreed that M^{1-3} in mammals should be considered members of the same set as the deciduous teeth and not as serially belonging with the permanent anteriors. The tapirs illustrate this fact not only by the eruptive sequence but also by the morphology. Thus in all respects M^1 differ from dm^4 in the same way and to about the same degree as dm^4 differ from dm^3 . On the other hand the transition from P^4 to M^1 is abrupt, despite the fact that P^4 are nominally molariform, and is different in direction and in degree from the transition from P^3 to P^4 . Moreover dm^4 have none of the characters commonly distinctive of the terminal member of a tooth series, and it is evident that the deciduous series does not functionally end at dm^4 .

In the tapirs, dm^1 - M^3 and, distinctly less perfectly, P^1 - M^3 are homodynamic series, the whole set functioning as a unit without any clear localization of function within the

cheek region, such as is almost universal in carnivores and occurs among many other mammals, even including some ungulates. In relatively undifferentiated series, such differentiation as does occur may be referred to a tendency, usually pronounced, toward what may be called terminalization: the most anterior and most posterior teeth are specially modified in accordance with their positions and do not intergrade in variation with their neighbors. This may accompany and be accentuated by reduction and loss at the ends of the series. In all the tapirs, fossil and recent, dm^1 and P^1 are completely lost and dm^2 and P^2 are fully terminalized, with some but not great reduction. Dm^1 and P^1 are more strongly affected than dm^2 and P^2 , and dm^3 and P^2 show slight terminalization. Although M^3 show little evidence of a trend toward functional dominance or usurpation of a disproportionate share of the adult dentition (compare the Proboscidea), they are remarkable in the tapirs for showing very little terminalization. They do show some narrowing and elongation of the posterior parts in comparison with M^2 , which is the most nearly universal characteristic of posterior terminalization, but this is slight, so slight that variant M^3 intergrade completely in morphology with M^2 .

Aside from the anterior terminalization and the functionally slight but non-intergrading differences between P^{2-3} on one hand and M^{1-3} on the other, the homodynamicity of tapir cheek teeth is well shown by the fact that ranges of variation overlap widely for any two adjacent teeth. As regards dimensions and proportions this is amply demonstrated by the accompanying statistical data. It is also true of morphological characters other than dimensions. The nearest thing to an exception is in the comparison of dm^3 with dm^2 and of P^3 with P^2 as regards anterior width and related characters. Here the sam-

¹ Ameghino (1911) believed that he had found a calcified pre-milk dentition in the recent tapir. The evidence is suggestive, but its interpretation is not absolutely certain. The specimens studied by me cast no light on this question, which is not further considered at present.

ples of *T. terrestris* do not intergrade, and only slight overlap would be expected in the population. The reason (that is, descriptively—it can hardly be claimed that the statement involves true causality) is that dm^2 and P^2 are slightly terminalized in correlation with the moderate relative reduction of dm^1 and P^1 .

All these relationships and tendencies seem

to be universal in the Tapiridae and exceedingly old in that family. They were fully established in the Oligocene (*Protapirus*) and probably earlier. The only essential change since that remote date has been increased molarization of the premolars, and even this is not striking because the premolars were already approximately molariform then and still are not perfectly so now.

DISTRIBUTION OF POST-PLIOCENE TAPIRS IN THE UNITED STATES

PLEISTOCENE TAPIRS have been found at about 50 localities in the United States. Most of the finds are fragmentary but are unmistakably tapirid. As elsewhere emphasized, the specific records are usually unreliable, and nothing definite can yet be said as to specific, and still less as to racial, distribution. It is to be expected that further discoveries will modify the pattern in detail, but the available data show well-defined peculiarities that are probably significant.

The great majority of known finds are in the southeastern quarter or third of the United States, from central Texas, southern Oklahoma, and Missouri to Florida on the southeast and Pennsylvania on the northeast. Three general types of environment are indicated: along and near the Gulf and Atlantic coastal plains, Texas to South Carolina; a central lowland zone, Oklahoma to Ohio; and an Appalachian mountain and hill zone, Tennessee to Pennsylvania. The whole area now has at least 20 inches mean annual rainfall and most of it two to three times that. Presumably during the Pleistocene the average rainfall was at least as high and probably higher. All the occurrences are south of the margin of continental glaciation.¹ The sequence of eight finds in Missouri, Indiana, Kentucky, Ohio, and Pennsylvania closely paralleling the undulating drift margin is striking. It is most unlikely that this is explicable by the ice, itself, as a barrier because such northern advance of the tapirs was almost certainly interglacial. The exact correspondence is probably a coincidence. It is also possible that the most northern extension of the tapirs was pre-Illinoian and that the most northern burials were destroyed by the Illinoian and later advances. Some of the southern occurrences, however, are almost certainly post-Illinoian and some probably post-Pleistocene. In a broader way, the absence of tapirs in more northern deposits doubtless indicates that they were confined to the relatively warm parts of the continent.

¹ A possible exception is Big Bone Lick, barely within the glaciated area, usually recorded as the type locality of *Tapirus haysii* but probably in error.

Another, much smaller area of fossil tapir distribution is along the Pacific coast, one find in Oregon and seven reported from California. These occurrences are very fragmentary, and the scarcity of tapirs in the California collections is striking in view of the fact that tapirs were present and that so many large Pleistocene collections have been made. The probable explanation is that the tapir habitat was principally in the wet mountain valleys, the faunas of which are poorly sampled in the known fossil deposits, and that tapirs only occasionally strayed into the relatively arid and open lowlands. The few known occurrences are, in fact, in or very near what were well-watered hills in the Pleistocene. The most exceptional occurrences are those at Rancho La Brea, near San Pedro, and near San Diego. These minor fragments can easily be understood as strays from the more congenial mountains north of these localities.

The occurrence near Cape Blanco, Oregon, just below 43° north latitude, is the most northern now known, but does not indicate that the tapirs invaded a cold climate. This is far south of the ice margin in this longitude, and the Pleistocene temperatures there, like the recent temperatures, were probably similar to those around latitudes 38°–40° on the east coast. No colder climate is indicated than for a number of the eastern occurrences at lower latitudes.

In the enormous area that used to be called the Great American Desert, the arid stretch from approximately the 101st meridian to the Sierra Nevada, only two finds of fossil tapirs have been made, and these are far south, almost on the Mexican border, one near El Paso and the other in southern Arizona. It is probable that tapirs were always rare and usually absent in the desert regions and in the semi-arid and mostly treeless plains, even during the relatively wetter Pleistocene. The El Paso occurrence (Richardson, 1907) was in outwash from the Franklin Mountains, and with heavier rainfall than at present the environment would not be prohibitively unlike those apparently favored by the other

North American tapirs. The Arizona occurrence, which is being described by Dr. E. H. Colbert, is decidedly anomalous in the light of recent tapir ecology and of the evidence of Pleistocene distribution elsewhere. The specimens are only a few water-worn tooth fragments, but they are unmistakably tapirid.

A tapir almost certainly could not survive in this region today, and even the evidence

supposed that this particular sort of tapir—unidentifiable from the fragmentary remains—was adapted to more arid conditions than the others known.

The accompanying map (fig. 5) strikingly illustrates the coincidence of known Pleistocene tapir distribution with the region south of the continental glaciers and near or within the present line of 20-inch mean annual rain-

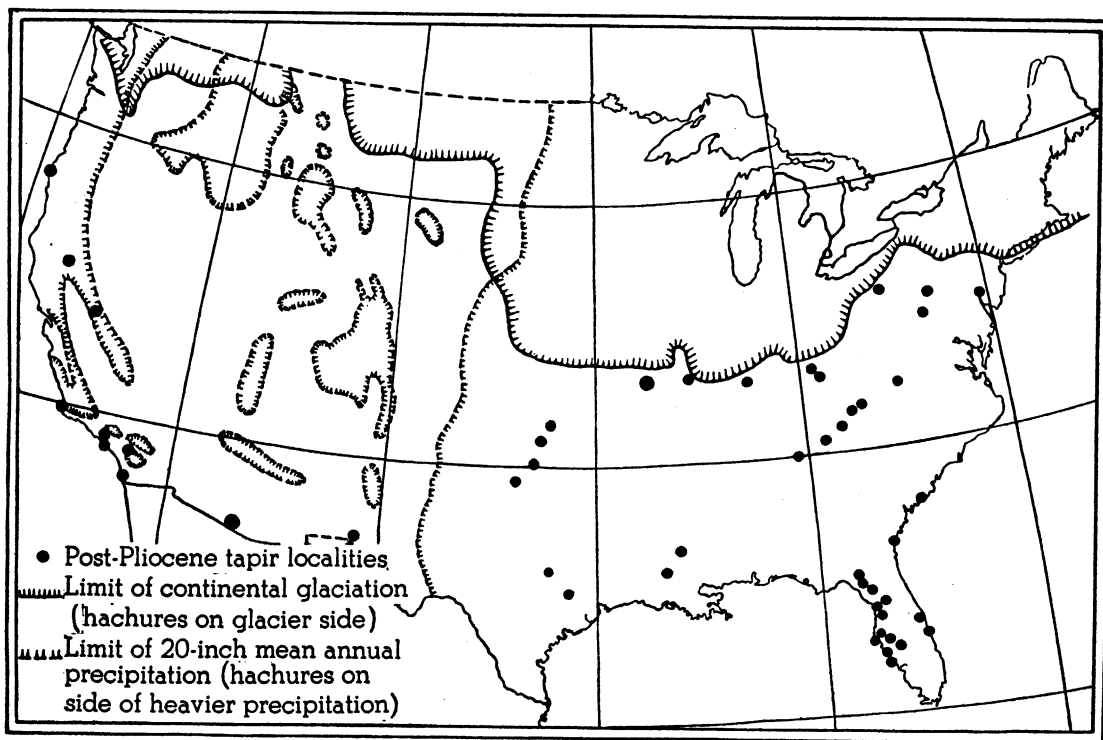


FIG. 5. Known occurrences of post-Pliocene tapirs in the United States. The present 20-inch precipitation lines and the Pleistocene glacial margin are indicated to show how nearly they define fossil tapir distribution. The ringed locality to the right of the center of the map is Enon, Missouri, type locality of *Tapirus excelsus*, described in this paper. The ringed locality in the southwest is the anomalous Arizona occurrence reported by Colbert, as discussed in the text.

of greater rainfall when this fossil fauna was alive does not suggest conditions fully suitable for tapirs. The associated animals are more consistent with semi-arid prairie country, and no more propitious environment is likely to have occurred for long distances in any direction. There must, however, have been permanent surface water, and perhaps gallery vegetation provided conditions tolerated by tapirs. The occurrence is marginal and was probably exceptional even if it be

fall. It is not suggested that Pleistocene rainfall was the same as recent, but the broad pattern was probably similar, at least in interglacial times. Recent tapirs occur almost exclusively in tropical rainy and humid mesothermal climates (of Köppen's system), and fossil North American tapirs are found mainly in areas that are now, and probably were when they lived here, humid mesothermal. The rare exceptions have been noted.

Data are insufficient for discussion of the

temporal distribution of tapirs in the United States. They doubtless occupied parts of this region continuously from the Pliocene to early post-Pleistocene. Changes in distribution would be expected, such as restriction to more southern areas during glacial advances, but the finds are too few and most of them are too insecurely dated for such changes to be followed. Tapirs were still present in the

United States when man entered North America, and the association has been established with reasonable certainty in southern Arizona, southern Oklahoma (Frederick), and Florida (Vero, Melbourne). These localities are all relatively far south and may indicate that tapirs had then disappeared in the middle latitudes that they had once occupied, but this is purely speculative at present.

REVIEW OF SOME PREVIOUSLY KNOWN NORTH AMERICAN PLEISTOCENE TAPIRS

NO ATTEMPT IS HERE MADE to reclassify and revise all the Pleistocene tapirs recorded from North America. Many of the specimens are inadequate for exact identification, most of the scattered originals have not been examined by me at first hand, and the published data are not always sufficient or strictly comparable. Attention will be directed mostly to

occurrences on which proposed new species have been based and, particularly, to the only two finds so far made that give a reasonably good idea of group, rather than purely individual, characters (the Seminole Field and Port Kennedy occurrences), both restudied from the specimens.

TAPIRUS VEROENSIS

SKULL

Tapirus veroensis was named and described by Sellards (1918) on the basis of an excellent skull (type), a fragment of lower jaw, and isolated teeth from the Pleistocene of Vero, Florida. Until the discovery in Missouri, recorded in the present paper, this was the only Pleistocene tapir skull known from America. Sellards' excellent account, with good figures, was concerned primarily with demonstrating that the specimen is not conspecific with any recent tapirs and that it belongs to *Tapirus* as opposed to *Tapirella* (assuming, as most zoologists have, that those are the two genera of recent tapirs). These conclusions were thoroughly established and cannot be questioned. It is, however, useful to extend comparisons more explicitly to the various recent species, rather than supposed genera, and to lay a somewhat wider basis for comparison. At this point reference is to the skull alone; the dentition will be discussed in the next section. This renewed study is based on Sellards' description and figures and an unusually good cast of the specimen, compared with series of recent skulls of *T. terrestris*, *indicus*, and *bairdii*+*dowi*, and a single skull of *T. roulini*.¹

As noted by Sellards, the skull is comparable to those of recent tapirs in general aspect and most details. The more striking

and potentially important distinctions are as follows:

1. The upper contour is nearly straight, the nasals nearly in the plane of the frontals. The most juvenile *T. terrestris* are similar, but adults are very different, with the frontals elevated above the nasals and tilted to rise toward the sagittal crest. In *T. bairdii* and *indicus*, nasals and frontals are nearly parallel, but the nasals are usually abruptly set down below the level of the frontals. This is variable, and *T. indicus*, especially juveniles but also some adults, may nearly approach *T. veroensis*. The condition in *T. roulini* is almost as in *T. veroensis*, and this character does not definitely separate those two species.

2. The sagittal crest is low, not arched, but single, the temporal muscles meeting at the midline without an intervening table. Again this resembles the juvenile, but not the adult, character of *T. terrestris* and again is almost exactly as in *T. roulini*. Both *T. bairdii* and *indicus* have a double crest, with a flat table between the sharp margins of the temporal origins. In *T. indicus* the table is narrower and to that extent it is nearer *T. veroensis*. In *T. bairdii* and *T. indicus* the narrowest part of the table is more posterior than the narrowest part of the single crest in *T. veroensis*.

3. Although the crest is thus single for part of its length, it separates posteriorly, and there is a large triangular table above the occiput. In *T. terrestris* this is scarcely or not developed. In *T. bairdii* and *indicus* the posterior part of the much more extensive

¹ Specimen kindly lent by the Yale Peabody Museum. It happens to be the same skull used by Hatcher (1896) in his classic study. It is fully adult, like the type of *T. veroensis*, and thus has some advantage over the immature *T. roulini* used for comparison by Sellards.

table is similar. *T. roulini* is most like the fossil, although the triangular table is a little smaller in the recent form, in the single specimens compared.

4. The dorsal part of the frontals, on the skull roof, is very broad, somewhat inflated, and flat on top. This is most distinctive from *T. terrestris* and *T. bairdii*. It is about intermediate between *T. roulini*, with the expansion somewhat less than in *T. veroensis*, and *T. indicus*, with the expansion somewhat greater.

5. The broad, shallow, spiral grooves, nearly meeting at the midline, are not exactly like those of any recent specimen seen by me, but this feature is extremely variable and the significance of differences in it is hard to judge.

6. The lateral grooves leading up to the spiral grooves are also broad and shallow, as is usual in *T. indicus*. In *T. terrestris*, *roulini*, and *bairdii*, as far as known to me, these grooves are always narrower and deeper.

7. There is a lacrimal pit and there is a flange or tubercle mainly on the frontal near the fronto-lacrimal suture. Sellards emphasized the lacrimal pit and seemed to imply that it is absent in the recent species. In my comparative materials, some suggestion of it occurs in all the recent forms, but it is smaller or less definite in all than in the fossil, which is most closely approached by some variants of *T. terrestris*. On the other hand, the tubercles may be more pronounced in *T. terrestris*, and this feature of the fossil is most nearly matched in *T. indicus*.

8. The ascending process of the premaxilla has a sharp, exposed, posterior projection ending about above the anterior end of P¹. In *T. terrestris* the projection is about equally sharp but more superomedial and, although quite variable, it seems always to end distinctly anterior to P¹. *T. roulini* is about like *T. terrestris* in this respect, although in the one available specimen the process extends farther back than is usual in *T. terrestris* and to that extent resembles *T. veroensis*. The condition in *T. indicus* includes variants almost exactly as in *T. veroensis*. In *T. bairdii* the end is less sharp and is decidedly anterior to P¹.

9. The dorsally exposed extension of the maxilla medial to the ascending process of

the premaxilla is well developed and has a sharp elevated or somewhat recurved edge. This, too, is like *T. indicus*. In *T. terrestris* and *roulini* there is normally no such exposure, or it may be present but small, and in any case the edge is smoothly rounded. As is well known, *T. bairdii* is very distinctive in this region, with the maxilla greatly produced upward to clasp the mesethmoid. The condition in *T. indicus* and *veroensis* could represent this in incipient condition.

10. As far as the fossil shows, the vertical plate of the mesethmoid is little ossified. The similarity to *T. indicus* listed under 9 strongly suggests that, when complete, the mesethmoid condition was also the same, with some ossification posteriorly, more than in *T. terrestris* or *roulini* but less than in *T. bairdii*.

11. The palate is more arched than in any recent skull available for comparison, but the difference in this variable feature is not very great.

12. There is a median tubercle at the posterior edge of the palate, and above this a median vomer plate rises abruptly, dividing the choanae. The tubercle is as in *T. indicus*, variable in *T. terrestris*, and absent in available *T. roulini*. Otherwise the region is about the same in these three species as in the fossil. *T. bairdii* is quite different.

13. The lambdoid crests are strong, well separated, and flare outward as well as backward. This is a well-marked distinction from *T. bairdii* or *T. terrestris*. *T. roulini* is intermediate, but more like *T. veroensis*. *T. indicus* is about like *T. veroensis* in this respect.

In summary, these structural features of the skull show marked distinction from *T. bairdii* and also, to less but still to unexpectedly great degree, from *T. terrestris*. Among the recent species, *T. roulini* and *T. indicus* most closely and about equally resemble *T. veroensis*. In some respects both are like the fossil, in some respects one is more like and in some the other is more like, and in some respects the fossil is intermediate. Although *T. veroensis* does not tend to tie in *T. bairdii* any more closely, it does tend to draw together *T. indicus*, *T. roulini*, and, through the latter, *T. terrestris* into a single species complex. *T. veroensis* represents another branch within the complex, and no

phylogeny can be established among these four essentially contemporaneous species—the less so because, as will later be noted, its dentition, unlike its skull, is nearer *T. terrestris* than *T. roulini* or *indicus*.

Sellards has also noted that the face and palate are shorter in proportion to total skull length in *T. veroensis* than in any of the recent species, but this depended on comparison of single specimens throughout, and further study indicates that these proportions are exceedingly variable. The difference may be real, but it is not reliable on the basis of present knowledge. For instance in *T. terrestris*, as given on another page, the mean palatal length:skull length index for 13 specimens is $53.7 \pm .5$ and the standard range is about 48–60. In *T. veroensis* the index is 52.5, and the difference is far from significant. I do not at present have adequate series to establish variation in proportions in *T. roulini* and *indicus*, the species that are most like *T. veroensis* in skull structure, but even the few available specimens show that their palatal:skull index, for instance, can be exactly as in the type of *T. veroensis*. There do not appear to be any really striking differences in over-all proportions, aside from minor dimensions closely related to the structural characters already reviewed.

DENTITION

This study of the dentition of *T. veroensis* is based primarily on specimens in the Walter W. Holmes Collection from the Seminole Field near St. Petersburg, Florida, now in the American Museum. All specimens were found in a single area and *in situ* in the same bed of the Pleistocene Melbourne formation. Although the opposite extremes in the series differ as much as, or more than, adjacent extremes of quite distinct species, this unity of occurrence and the general nature of the distributions strongly support the view that a single species is sampled. Variation, although seemingly great when selected individuals are subjectively compared, averages somewhat less than in *T. terrestris*, as would be expected in a sample of one species more unified in geographic origin. The collection includes a palate with all cheek teeth, a right maxilla with P^4-M^3 , a left mandible with P_3-M_3 , and a large number of isolated teeth

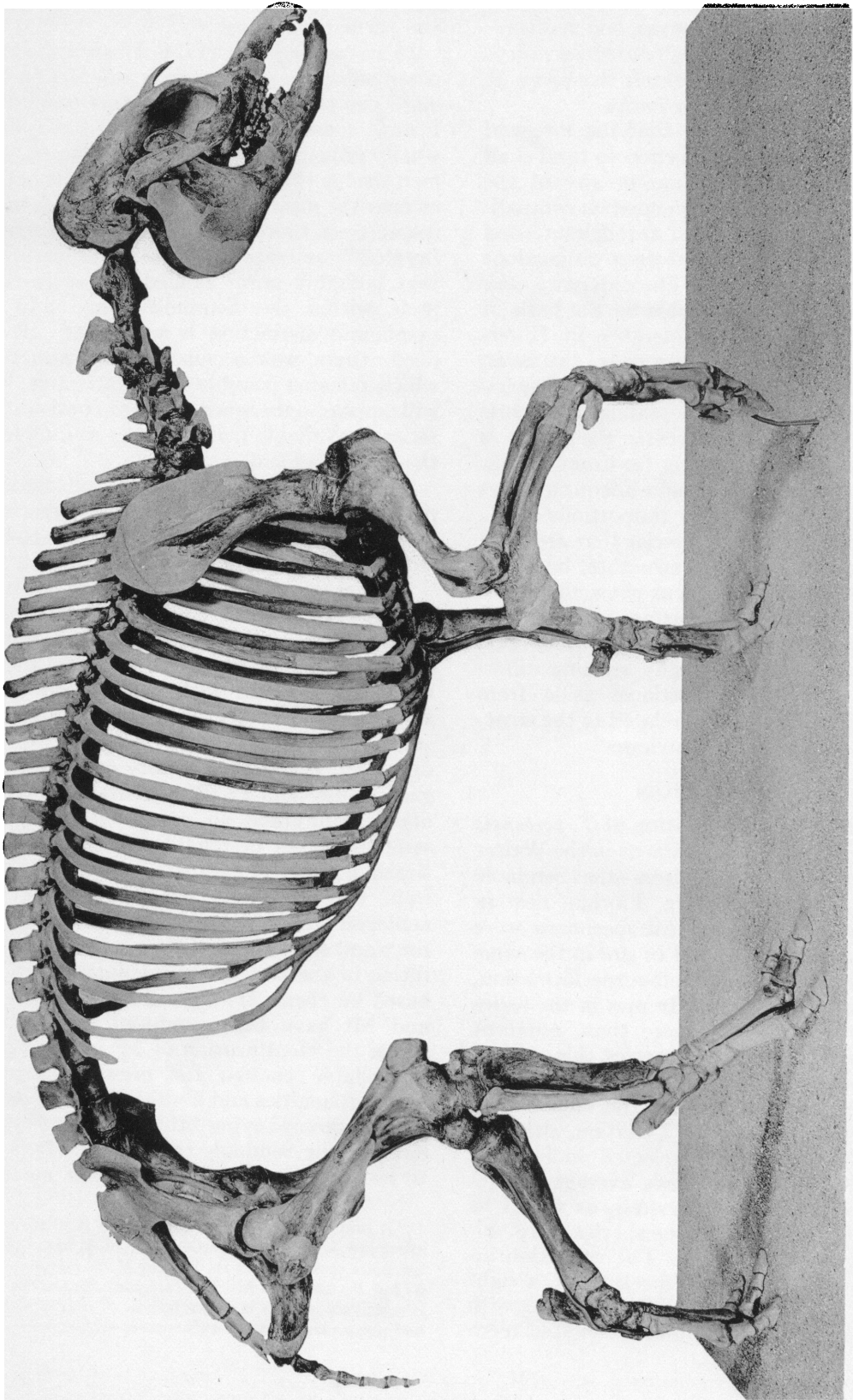
representing the whole dentition, deciduous and permanent.

In an earlier paper (1929) I based the supposed subspecies *T. veroensis sellardsi* on the more complete specimens of this collection. I now consider this action to have been wholly unjustified. Of course the single specimen that is the type of *T. veroensis* is not at or near the mean of the Seminole series in all respects—a thoroughly average or literally “typical” animal would be a monstrosity that probably never existed in nature—but it is within the Seminole range and no taxonomic distinction is warranted. If, indeed, there was a subspecific distinction, which remains possible but improbable, this will appear only when a large comparative series is available from Vero as well as from the Seminole Field.

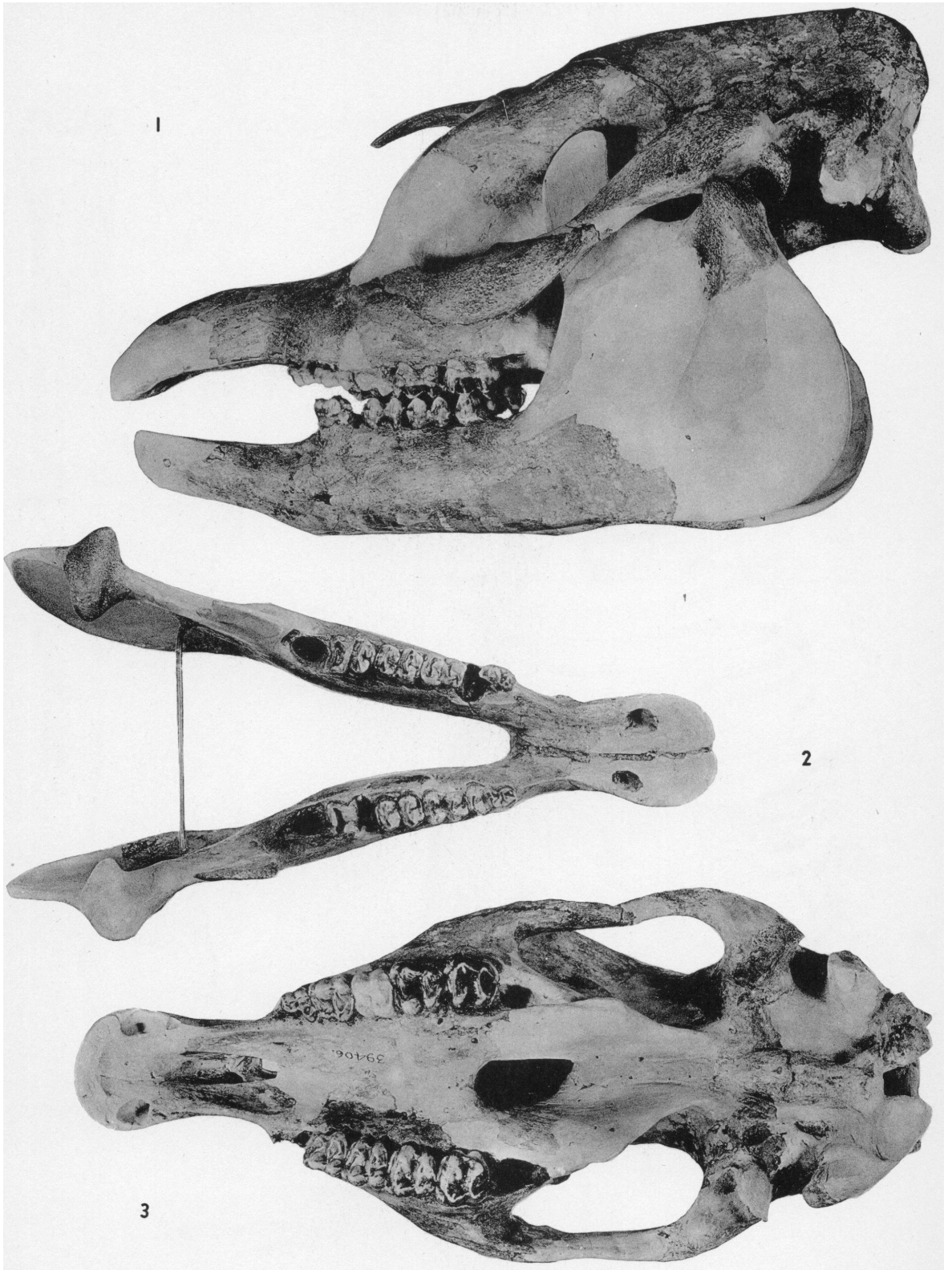
The type and associated Vero material as published by Sellards¹ have also been considered, but are omitted from statistical study for the sake of greater homogeneity.

The great difficulty of sorting isolated tapir teeth has been emphasized at various points in the present study. In the Seminole collection the lower teeth have been identified as to position with what seems to be sufficient probability, except that I cannot surely distinguish all dm_3 from P_3 . In the upper set, the same difficulty exists with regard to dm^1 and P^1 . P^2 is distinguished, but others intergrade so completely that the samples cannot be reliably sorted for statistical purposes. The molars are quite distinct from the premolars, but M^1 and M^2 are analogous to P^3 and P^4 in that some are distinct and some not and that subjective separation of the two would invalidate statistics based on them. It is possible that some M^2 and M^3 have been confused, but on the whole the identification of M^3 is believed to be reliable enough for present purposes. These difficulties and limitations are inherent in the accompanying tables (tables 9–11) of data on the Seminole tapir teeth. (It is also to be noted in all such cases that measure-

¹ It may be noted in passing that in the “paratype” lower jaw figured by Sellards, 1918 (pl. 4, figs. 1, 2), the teeth are probably not P_3 , P_4 , and M_1 as stated on page 63 but P_3 , dm_4 , and M_1 . The fact that the middle tooth is relatively narrow is characteristic of dm_4 in all tapirs and not a peculiarity of this species or specimen.



Tapirus excelsus, new species, type, A.M.N.H. No. 39406. Right lateral view of skeleton as mounted by Charles Lang. $\times 1/8$



Tapirus excelsus, new species, type, A.M.N.H. No. 39406. $\times 2/5$. 1, Left lateral view of skull and jaws (incisors not restored), as prepared by Albert Thomson; 2, superior view of lower jaws; 3, palatal view of skull



Tapirus excelsus, new species, type, A.M.N.H. No. 39406. $\times 3/5$. 1, Ventral view of atlas; 2, dorsal view of axis; 3, anterior view of preserved elements in left tarsus and metatarsus



1. *Tapirus excelsus*, new species, type, dorsal view of skull. Pleistocene, Missouri. A.M.H.N. No. 39406. $\times .37$

2. *Tapirus bairdii*, dorsal view of skull. Recent, Central America. A.M.N.H. No. 130104 (Dept. Mammals). $\times .40$



1. *Tapirus indicus*, dorsal view of skull. Recent, Malay Peninsula. A.M.N.H. No. 130108 (Dept. Mammals). $\times .40$
2. *Tapirus veroensis*, dorsal view of skull, cast of type. Pleistocene, Florida. $\times .34$



1. *Tapirus roulini*, dorsal view of skull. Recent, South America. Yale Peabody Mus. No. 11883. $\times .45$
2. *Tapirus terrestris*, dorsal view of skull. Recent, South America. A.M.N.H. No. 78519 (Dept. Mammals) $\times .45$

ments of isolated teeth tend to average slightly greater than if the teeth were in series in jaws; the resulting bias appears, however, to be so small relative to other sources of variation that the results are not importantly falsified.)

The dentition of *T. veroensis* as a whole closely resembles that of *T. terrestris* except in average size and variable details. There also appear to be no constant structural differences from *T. bairdii*. In the most distinctive qualitative dental character in *Tapirus* (*sensu lato*), the molarization of P^1-2 , *T. veroensis* seems to have almost the same modal condition and variation as in the species mentioned, more progressive than *T. indicus* or, more distinctly, *T. roulini*. (Note that the skull of *T. veroensis*, on the contrary, is more like these latter species than like *T. terrestris* or *bairdii*.)

In the type of *T. veroensis* there is a distinct basal tubercle on the outer face between paracone and metacone, above the ectoloph, on P^1-M^2 and more vaguely on the other upper cheek teeth. All the upper cheek teeth have a distinct basal tubercle between protocone and hypocone at the inner end of the median valley. Among the Seminole specimens none has so distinct an external tubercle and only a few have it faintly indicated. This is variable but often present in *T. terrestris* and *T. bairdii*. It would be orthodox to give taxonomic weight to this difference between the Vero type and the Seminole specimens (as I formerly did), but it is more probably only another case of a type's being somewhat atypical. The inner tubercle is often present in Seminole specimens (also in *T. terrestris* and *bairdii*) but is markedly variable as the following data show:

TEETH	TUBERCLE ABSENT	SMALL	DEFINITE TUBERCLE
		SWELLING OR INDEFINITE TUBERCLE	
dm^{2-4}	0	3	9
P^2	0	1	5
P^{3-4}	4	4	3
M^{1-2}	1	4	2
M^3	1	2	6

In describing tapir species, emphasis has also frequently been placed on presence or absence of similar tubercles between the

crests on the lower cheek teeth, but this character, too, is highly variable in all species and is distinctive only as an average, if at all. In the Seminole specimens the tubercles are often present on dm^{3-4} and P^3-M^3 , but they are always small, often absent, and it may be purely subjective whether the usual convexity in this region is called a tubercle. The tubercles, when present, may be on the inner or the outer side or on both. There is some tendency for them to be more common or prominent on the inner than the outer side, but this, too, is variable. The data are not to be taken very seriously because of the subjective element, but a census of 33 teeth sufficiently unworn to show the tubercles if present gave 11 with no tubercles, 2 with outer tubercle only, 8 with inner tubercle only, and 12 with both.

None of the upper cheek teeth has a definite, sharp external cingulum but some in each position, generally fewer than half, have a rounded basal swelling that is cingulum-like.

The character of the ectoloph crest, suggested by Olsen (1940) as a distinction between *Tapirus* (*Tapirella*) and *Tapirus* (*Tapirus*), cannot be clearly determined on most of the teeth because of wear. In the few teeth that show this character, the crest is less notched than is usual in *T. terrestris*, more than usual in *T. bairdii*, but probably within the range of both. Even in this limited material the variation is striking. For instance, in the three available unworn last upper molars, on one the crest runs almost evenly sloping downward to the metacone near, but not quite at, its apex, on another the crest is notched near the middle and rises again nearly to the metacone tip, and on the other the crest ends distinctly before reaching the metacone and there is a sharp, deep cleft between it and the metacone.

In all the dimensions of the teeth, *T. veroensis* averages larger than *T. terrestris* or *T. bairdii*. I do not have reliable averages for *T. indicus*, but it is probable that it, too, has smaller teeth than *T. veroensis* as a whole, although a few dimensions may reach the same average as the Florida fossils. On the other hand, the observed ranges of variation of dimensions of *T. veroensis* teeth overlap those of *T. terrestris* with only five exceptions (among 46 dimensions compared): W_1P_3 ,

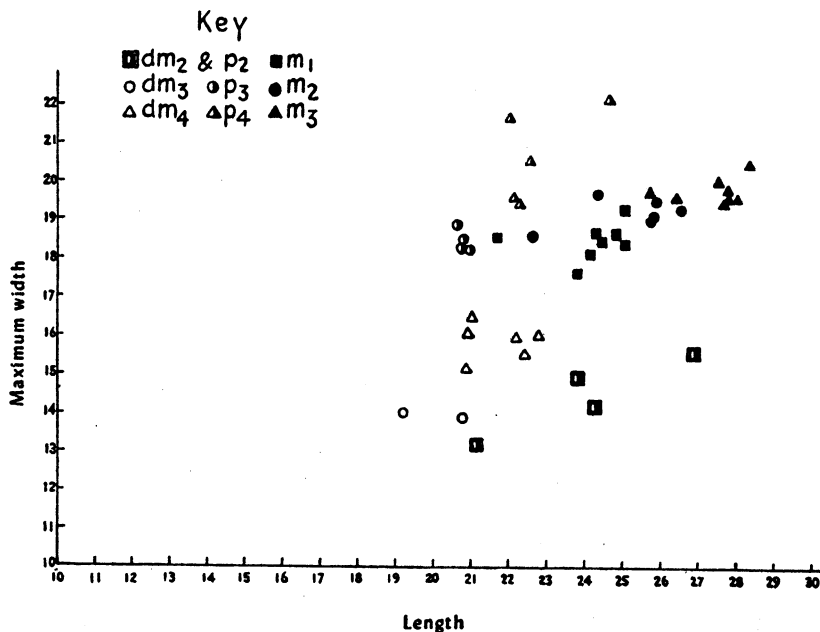


FIG. 6. *Tapirus veroensis*. Pleistocene, Seminole Field, Florida. Graph of length and width in millimeters of lower cheek teeth.

$W_P P_3$, LP_4 , $W_P P_4$, and $W_A dm^2$. Even in these five cases the lack of overlap is almost surely due to chance in small observed series; the standard ranges overlap and so, beyond much doubt, did the dimensions in the actual populations. In proportions, too, the ranges

overlap widely and in this case, as opposed to the absolute dimensions, no statistically significant differences in mean values have been found.

In short, neither qualitatively nor quantitatively have I found any way of distinguish-

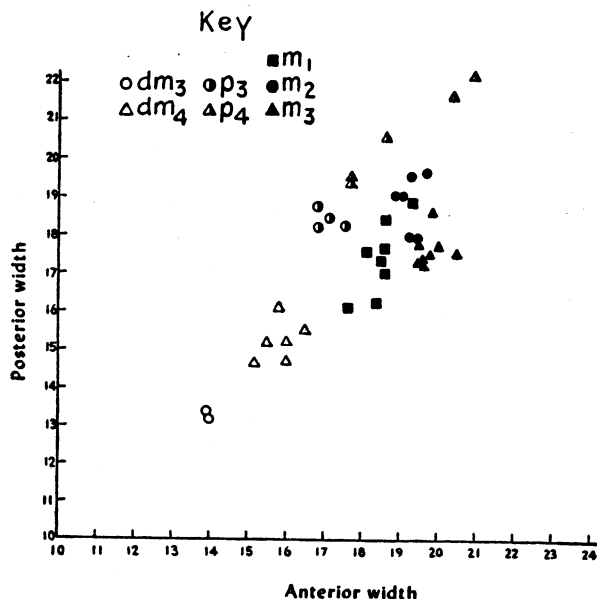


FIG. 7. *Tapirus veroensis*. Pleistocene, Seminole Field, Florida. Graph of anterior and posterior widths in millimeters of lower cheek teeth.

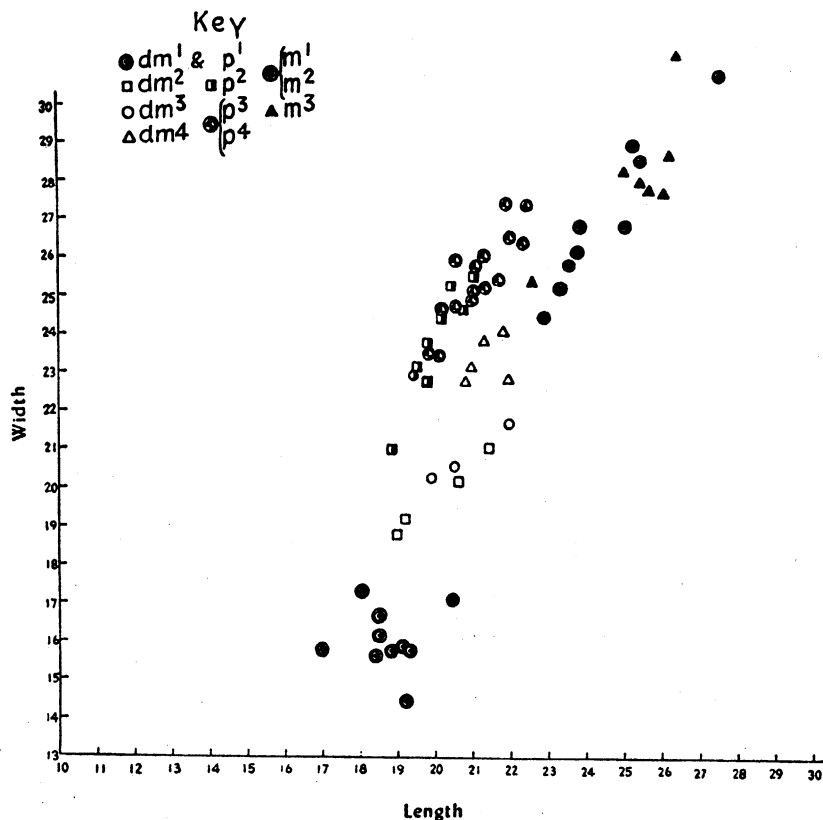


FIG. 8. *Tapirus veroensis*. Pleistocene, Seminole Field, Florida. Graph of length and width in millimeters of upper cheek teeth.

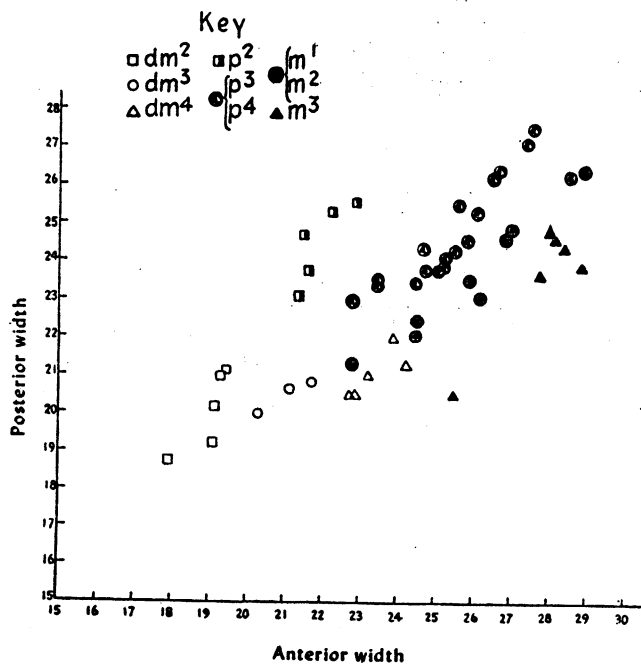


FIG. 9. *Tapirus veroensis*. Pleistocene, Seminole Field, Florida. Graph of anterior and posterior widths in millimeters of upper cheek teeth.

TABLE 9

SOME STATISTICAL DATA ON DIMENSIONS OF TEETH IN *Tapirus veroensis* FROM THE SEMINOLE FIELD, FLORIDA

Variate		N	OR	SR	M	σ	V
dm ₄	L	6	20.9-22.8	19.17-24.23	21.70 ± .32	.78 ± .23	3.6 ± 1.0
	W _A	6	15.2-16.5	14.50-17.16	15.83 ± .17	.41 ± .12	2.6 ± .8
	W _P	6	14.6-16.1	13.60-16.84	15.22 ± .20	.50 ± .14	3.3 ± 1.0
M ₁	L	8	21.7-25.0	20.87-27.42	24.14 ± .36	1.01 ± .25	4.2 ± 1.0
	W _A	8	17.6-19.3	17.00-19.92	18.46 ± .16	.45 ± .11	2.5 ± .6
	W _P	8	16.1-18.9	14.41-20.44	17.42 ± .33	.93 ± .23	5.3 ± 1.3
M ₂	L	6	22.6-26.6	20.83-29.52	25.17 ± .55	1.34 ± .39	5.3 ± 1.5
	W _A	6	18.9-19.7	18.41-20.16	19.28 ± .11	.27 ± .08	1.4 ± .4
	W _P	6	18.0-19.7	16.69-21.16	18.92 ± .28	.69 ± .20	3.6 ± 1.0
M ₃	L	8	25.7-28.3	24.72-30.04	27.38 ± .29	.82 ± .20	3.0 ± .7
	W _A	8	19.5-20.5	18.84-20.78	19.81 ± .11	.30 ± .08	1.5 ± .4
	W _P	8	17.4-18.6	16.43-18.89	17.66 ± .14	.38 ± .10	2.2 ± .5
P ²	L	7	18.5-20.8	17.05-22.30	19.67 ± .31	.81 ± .22	4.1 ± 1.1
	W _A	7	19.3-22.9	17.53-24.99	21.26 ± .43	1.15 ± .31	5.4 ± 1.4
	W _P	7	21.0-25.5	18.42-28.79	23.60 ± .60	1.60 ± .43	6.8 ± 1.8
M ³	L	7	22.4-26.0	21.30-28.82	25.06 ± .44	1.16 ± .31	4.6 ± 1.2
	W _A	7	25.5-31.4	23.08-33.52	28.30 ± .61	1.61 ± .43	5.7 ± 1.5
	W _P	6	20.4-24.8	18.78-28.38	23.58 ± .61	1.48 ± .43	6.3 ± 1.8

ing some variants of *T. veroensis* from some variants of *T. terrestris* or of *T. bairdii* on the basis of teeth alone, although the more nearly typical specimens can be so distinguished,

and the skulls are, of course, distinguishable at a glance. This complete intergradation in tooth characters of species that are, nevertheless, surely distinct emphasizes the stereo-

TABLE 10

SOME STATISTICAL DATA ON PROPORTIONS OF TEETH OF *Tapirus veroensis* FROM THE SEMINOLE FIELD, FLORIDA

Variate		N	OR	SR	M	σ	V
100 (max. width)	dm ₄	6	69- 79	61.7- 85.0	73.3 ± 1.5	3.6 ± 1.0	4.9 ± 1.4
	M ₁	8	74- 86	64.9- 88.7	76.8 ± 1.3	3.7 ± .9	4.8 ± 1.2
	M ₂	6	73- 86	61.9- 92.6	77.2 ± 1.9	4.7 ± 1.4	6.1 ± 1.8
	M ₃	8	70- 77	65.0- 79.4	72.2 ± .8	2.2 ± .6	3.1 ± .8
	Length	7	112-125	107.4-132.3	119.8 ± 1.4	3.8 ± 1.0	3.2 ± .9
100 (ant. width)	M ³	7	108-121	101.2-125.8	113.5 ± 1.4	3.8 ± 1.0	3.3 ± .9
	dm ₄	6	98-109	93.0-115.1	104.0 ± 1.4	3.4 ± 1.0	3.3 ± 1.0
	M ₁	8	101-114	91.6-120.8	106.2 ± 1.6	4.5 ± 1.1	4.2 ± 1.1
	M ₂	6	99-108	89.9-114.5	102.2 ± 1.6	3.8 ± 1.1	3.7 ± 1.1
	M ₃	8	103-117	97.4-124.8	111.1 ± 1.5	4.2 ± 1.1	3.8 ± .9
Post. width	P ²	7	87- 92	84.1- 96.5	90.3 ± .7	1.9 ± .5	2.1 ± .6
	M ³	6	113-125	104.8-131.2	118.0 ± 1.7	4.1 ± 1.2	3.5 ± 1.0

typed nature of *Tapirus*¹ and also shows how unreliable may be the usual paleontological identifications from single teeth or dentitions.

Some of the numerical data are summarized in tables 9-11.

OTHER TAPIRS IN FLORIDA

Pleistocene or early post-Pleistocene tapirs are abundant in Florida. Fourteen localities are definitely recorded, and there is no doubt that tapirs have been found elsewhere without printed record. They may be expected in any of the many deposits containing post-Pliocene fossil mammals in Florida; such localities are so numerous as to be almost continuous over a great part of northern and central peninsular Florida. The relative abundance of tapir discoveries in Florida may be ascribed in part to the unusually widespread occurrences there of late fossil mammals in general and in part, it is probable, to the real abundance of tapirs in the former fauna of Florida.

The more important finds are those *in situ* in the Melbourne formation, as at Vero and the Seminole Field. Most of the other records are of uncertain associations and stratigraphic position, many of them from spoil-banks, phosphate mines, and reworked or dredged river deposits in which there is frequently a mixture of faunas, sometimes with remains of as many as five different ages occurring, or reported, as if they were associated.

Most of these Florida tapirs appear to be *T. veroensis*, or at least not to be clearly separable from that species, which was the characteristic tapir of Florida in Melbourne times. As already noted, this is the common and probably the only tapir in the large Seminole Field collection, and my former report of a separate subspecies of *veroensis* and of a second larger species from that field was unwarranted. I also now believe that the tapir reported as *Tapirus* cf. *haysii*

from the Saber-tooth Cave, Citrus County (Simpson, 1928), is inseparable from *T. veroensis*.

TABLE 11

NUMERICAL DATA ON SOME TEETH OF *Tapirus veroensis* FROM THE SEMINOLE FIELD, FLORIDA
(Dimensions of teeth not adequately sorted or too few for useful calculation of other statistics.)

Variate		N	OR	M
dm ₂ and P ₂	L	4	21.1-26.9	*
	W	4	13.2-15.6	*
dm ₃	L	2	19.2-20.8	20.00
	W _A	2	13.9-14.0	13.95
	W _P	2	13.2-13.4	13.30
P ₃	L	4	20.6-20.9	20.78
	W _A	4	16.8-17.6	17.12
	W _P	4	18.3-18.9	18.50
P ₄	L	5	22.0-24.6	22.72
	W _A	5	17.7-20.9	19.06
	W _P	5	19.5-22.2	20.72
dm ¹ and P ¹	L	11	16.9-20.4	*
	W	11	14.5-17.4	*
dm ²	L	4	18.9-21.3	19.95
	W _A	4	17.9-19.4	18.89
	W _P	4	18.8-21.1	19.82
dm ³	L	3	19.8-21.8	20.70
	W _A	3	20.3-21.7	21.03
	W _P	3	19.9-20.8	20.43
dm ⁴	L	5	20.3-21.8	21.08
	W _A	5	22.9-24.2	23.42
	W _P	5	20.4-22.0	21.04
P ³ and P ⁴	L	16	19.3-22.2	*
	W _A	17	22.8-27.6	*
	W _P	17	23.0-27.5	*
M ¹ and M ²	L	11	19.6-27.1	*
	W _A	11	22.8-30.9	*
	W _P	10	21.3-27.7	*

* Means in these cases would not be valid because non-homologous teeth are included.

¹ It has been argued that because the tapir dentition is stereotyped and also evolved slowly, such individual differences as occur are more likely to have taxonomic value. The data here presented show that the opposite is true. There is large intra-group variation throughout, despite the slowness of changes in modal conditions, and the variation is much the same throughout the genus or family (inter-group variation is comparable to intra-group), so that individual differences are less, not more, likely to have taxonomic meaning.

It is, nevertheless, demonstrable that at least one other kind of tapir, and possibly more, occurred in Florida. The ecological or temporal distinctions from *T. veroensis* are not demonstrable from data now available, but some specimens are clearly distinct morphologically and others more doubtfully so. No specimen available to me warrants definite reference to a named species, but some may be noted to demonstrate the difference from *T. veroensis*. A.M.N.H. No. 23110 is a fragment of right lower jaw with the poorly preserved posterior end of M_2 and with M_3 complete but unerupted. It came to us in the W. W. Holmes Collection without locality record other than Florida. M_2 is 30.5 mm. in length, anterior width 21.5 mm., posterior width 19.6 mm., length:width index 70, anterior:posterior width index 110. The indices are almost average for *T. veroensis*, and the structure of the tooth

is not clearly different, but the dimensions are all somewhat greater than in Seminole Field *T. veroensis*, and there is virtually no chance that this tooth could be from the same population (P less than .001 for all three dimensions). The tooth is within the probable range of the Port Kennedy species usually called *T. haysii* but renamed *T. copei* on a later page, and the specimens may be tentatively referred to that species. This larger form must be rare in Florida. Even the teeth reported by Hay (1923, p. 207) as suggestive of *T. haysii* because of their large size do not appear to be outside the probable size range of *T. veroensis*.

Two other jaws in the Holmes Collection are nearer to *T. veroensis* but may represent distinct races, possibly temporal, of that species. A.M.N.H. No. 2311, collected by J. E. Moore south of Venice, probably not *in situ*, has M_{2-3} with the following dimensions:

	a. Length	b. Anterior width	c. Posterior width	100b/a	100b/c
M_2	24.9	19.4	18.7	78	104
M_3	24.7	18.6	17.0	75	109

M_2 is quite indistinguishable from *T. veroensis* and near the mean for the Seminole Field specimens, but M_3 is smaller than any of our specimens referred definitely to *T. veroensis*. It is barely within the standard range for the Seminole Field material and it could be from

the same population, but this is improbable. The size ratio of M_2 to M_3 is also probably unusually large for *T. veroensis*, although there are few specimens by which this ratio can be obtained for associated teeth.

TAPIRUS TENNESSEAE

This name was proposed by Hay (1920) on the basis of 10 separate teeth from Whitesburg, Tennessee, collected in 1885 by Ira Sayles. Hay did not say whether he considered these as representing a single individual, a point of prime importance in determining their places in the series. The assignment of one catalogue number, description of the species on the basis of the whole series as type, and absence of duplicates of homologous teeth might suggest individual association. On the other hand the conditions of collecting, the fact that other lots in the same collection (for instance, the horse teeth) are obviously scraps from several individuals, and the difficulty of fitting these into a single series comparable to most tapirs in wear and

other characters cast doubt on such association, and I suspect that at least two individuals may be present.

Hay's placing of the various teeth in the dental series is questionable, if not demonstrably incorrect. For instance, the tooth he calls P_3 has the posterior lobe considerably narrower than the anterior but, to my knowledge, this is never true of P_3 in any tapirid. Several of his other identifications are equally improbable. If these specimens are compared with the teeth that they most nearly resemble in *T. veroensis* and with which they are, I believe, most likely to be homologous, they all fall within the established or probable range of the Florida species as regards size and proportions. The other differences men-

tioned by Hay are also either equivocal or definitely present as variants in *T. veroensis*. For instance, he says the parastyle is smaller in *T. tennesseae*, but a large parastyle characterizes the molars of *T. veroensis*, and the parastyle region is broken and missing in the type molars of *T. tennesseae*. Or, again, Hay defines *T. tennesseae* by absence of external cingulum, but this is the normal condition of *T. veroensis*.

Since there seems to be nothing in Hay's description that really distinguishes his spe-

cies from *T. veroensis*, I consider *T. tennesseae* a possible synonym, essentially indeterminate at present, and properly ignored. A tapir found by me in the same region under similar conditions and with similar faunal associations is so nearly like Florida specimens of *T. veroensis* that its reference to that species is highly probable (Simpson, 1941b). Somewhat larger tapir teeth, referred to *T. haysii* because of their size, have also been found in Tennessee (see Hay, 1923, p. 209).

TAPIRUS HAYSII

Leidy (e.g., 1860) recognized two tapirs in the Pleistocene of the eastern states, distinguished by little but size. He called the larger *Tapirus haysii* and the smaller *Tapirus "americanus"* or *T. "americanus (?) fossilis"*, i.e., he did not distinguish it definitely from the living *T. terrestris*. Later authors also generally recognized two size groups in the same way, a larger *T. haysii* and a smaller not distinguished from *T. terrestris* until Selldars (1918) described a tapir of this size as *T. veroensis*. He implied that the small eastern tapirs in general had been incorrectly referred to *T. terrestris* and belong to his Florida species, which is probably true of most although not clearly proved. In the literature in general, the distinction of large *T. haysii* and the smaller species, whatever it be called, has been erratic and subjective, and the citation of one name or another is usually worthless as evidence of what tapir was actually present at a given locality. Specimens well within the size range of *T. veroensis* (or *T. terrestris*), or even below its average size have been called *T. haysii*, which seems to have become the popular name for tapir fragments not really identifiable, or at least not really identified.

The type of *T. haysii* is a single tooth presented to the Academy of Natural Sciences of Philadelphia by I. Hays in 1852 as coming from a canal in North Carolina. The name *T. haysii* was given by Leidy in the same year, but the species was not properly characterized until 1860 when Leidy described and figured it along with several other specimens referred to the species from diverse localities. At that time Leidy said that the type tooth

was "supposed to have been obtained from Big-bone-lick, Kentucky," without mentioning the contradictory earlier statement as to locality. It seems to me somewhat more probable that the tooth came from North Carolina, but it must be admitted that the locality is not now known and can never be established with any degree of certainty. It is much the most reasonable assumption that the specimen is from the Pleistocene, but even this is not absolutely certain, and of course it cannot be assigned to any particular part of that epoch.

Leidy believed the type of *T. haysii* to be M_2 , and this has been generally accepted, but it is probably incorrect. The chief differences between P_4 and M_2 in *Tapirus*, teeth otherwise remarkably similar, are: (a) with rare exceptions in which the widths are almost equal, M_2 has the anterior lobe wider than the posterior, and, with equally rare exceptions in which the widths are nearly equal, P_4 has the posterior lobe wider; and (b) with extremely rare possible exceptions, M_2 has the posterior lobe longer than the anterior, and P_4 has them equal or the anterior lobe longer. In both respects the type of *T. haysii* agrees with P_4 , and there can be little doubt that is its true homology. There is only the barest possibility that it is an aberrant M_2 .

The tooth has no structural peculiarities in comparison with other tapirs, and if it is definitive of a species this can only be on the basis of size and proportions. It is decisively too large to belong to any living species. It is above the known size range of P_4 in *T. veroensis*, although the difference is not so great that an extreme variant of that species

could not have the dimensions of the *T. haysii* type.

Later ideas of *T. haysii*, as far as they have had a concrete basis, have been derived less from the type than from the series of specimens from Port Kennedy (discussed elsewhere in this paper) referred to *T. haysii* by Cope. It is barely possible that the type of *T. haysii* is conspecific with the Port Kennedy species so called by Cope and all his successors, but it is improbable. The type is distinctly longer than any P_4 in the Port Kennedy collection and the difference is statistically significant.¹ It may, of course, turn out that the very homogeneous Port

Kennedy sample of P_4 is less variable than was its species as a whole and that the type of *T. haysii* is within the range of that species as it occurred over a wider area, but that is speculative. The fact is that this type is essentially indeterminate and that the species to which it belongs, and consequently the species properly called *T. haysii*, cannot at present be identified, in spite of the extensive use of this name in the literature.

(The possibility of fixing this widely used name by designation of a neotype has been considered but must be rejected. In this case none of the proper conditions for proposal of a neotype can be met.)

THE PORT KENNEDY TAPIR, *TAPIRUS COPEI*, NEW NAME

For the reasons just explained, the name *T. haysii* can no longer properly be used for the tapir represented in the collections from Port Kennedy, Pennsylvania, and this occasion is taken to provide a name for this form and to present basic data on the means and variation of its tooth dimensions and proportions.

TAXONOMY

Tapirus copei, new name

Tapirus haysii COPE and later authors, but not *T. haysii* Leidy, 1860.

TYPE: No. 178, Academy of Natural Sciences of Philadelphia. Palate with anterior teeth and left P^{1-4} and anterior part of M^1 .

HYPODIGM: Large series of specimens collected by Dixon and Mercer at Port Kennedy and now in the Philadelphia Academy, four partial upper jaws in addition to the type, seven partial lower jaws, and many separate teeth.

HORIZON AND LOCALITY: Pleistocene fissure deposit at Port Kennedy, Pennsylvania.

DIAGNOSIS: Essentially the species called *T. haysii* by Cope (1899) and most later authors. Larger than any recent species or than any other North American Pleistocene species except *T. merriami*. Significantly smaller than *T. merriami*. P^1 a large, robust,

relatively transverse and complex tooth with the protocone relatively far forward, a large, heavily ridged basin between this and the ectoloph. P^2 advanced in molarization, difference in anterior and posterior widths slight, protoloph fully developed.

DISCUSSION: The size of this species is in itself significantly different, as an average, from any other with which it is otherwise comparable, although a few tooth dimensions do intergrade with *T. veroensis*, and it is probable that extreme variant individuals, not groups, of all our defined Pleistocene species could be of nearly the same size. In its most nearly distinctive structural character, the molarization of the anterior premolars, this is the most advanced of our species in which this part is known, and is nearly comparable to the very large Chinese *Tapirus* (*Megatapirus*) in this respect. Here, again, the condition is approached and perhaps intergrades through extreme individuals in the other relatively advanced species *T. veroensis*, *T. terrestris*, and *T. bairdii*.

The type appears to have a remarkably long diastema, but this has probably been increased by crushing and is highly variable in the recent species, at least.

None of the more distinctive parts of the skull are known, and without these it is impossible to determine the closer affinities or phyletic position of the fossil. Its distinction as a species is nevertheless reasonably well established from the dentition alone,

¹ Aside from the structural details that make it unlikely that this type is M_2 , it is also outside the range of M_2 from Port Kennedy, most decisively in its higher ratio of length to width.

thanks to the presence of a series sufficient to allow fair estimation of averaged variant characters.

MEASUREMENTS

Data on the dimensions and indices of the

teeth are adequately summarized in tables 12-15. Homologous measurements of upper teeth are so few that standard statistics are not given, but these are supplied for the lower teeth.

PACIFIC COAST TAPIRS

Two kinds of tapirs have been named from California, both based on fragmentary material suggesting that the species are prob-

ably distinct but inadequate to reveal their closer affinities.

Tapirus haysii californicus was named by Merriam (1913) on the evidence of a single lower cheek tooth, judged to be M_2 . This is probably correct, but there is some chance that it is P_4 . Judging from the description and figures, the tooth is almost intermediate in the characters that distinguish P_4 and M_2 , although a little more like a variant M_2 . Combining measurements by Merriam and by Frick, the dimensions and indices are: L 25.3, W_A 17.8, W_P 17.5, $100 W/L$ 70, $100 W_A/W_P$ 102. This is significantly smaller than M_2 of *T. copei* (the species called *T. haysii* by Merriam). The ratio of width to length is also smaller than observed in the Port Kennedy sample of *T. copei*, but the difference is not statistically significant. The length is in the known range of *T. veroensis*, but the width is significantly less. The dimensions are all within the established range of M_2 in *T. terrestris*, but the width: length ratio is somewhat lower, not significantly. These characters also appear to be within the less well-established ranges for *T. bairdii*. The structural details noted by Merriam occur as variations in all these species.

Although Merriam rather curiously named this form as a subspecies of *T. "haysii,"* i.e., *T. copei* as it is now named, he correctly noted that it is distinct from that species and really nearer *T. terrestris* or *T. bairdii* in structure. It is impossible to say at present whether the tooth belonged to one of the latter two species or whether, as seems possible on zoogeographic grounds, it is a distinct form. In the latter case there is little chance that it is a subspecies of *T. copei*, and it may be known tentatively as *Tapirus californicus*.

In the same paper Merriam described associated M_1 - 3 from Cape Blanco, Oregon, as "*Tapirus* near *haysii californicus*." These teeth, too, are definitely smaller than those

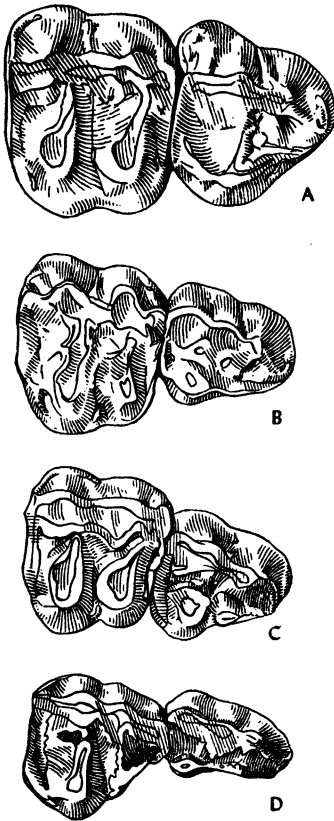


FIG. 10. Crown views of right P_1 - 2 in four species of Pleistocene and Recent tapirs. A, *Tapirus copei*, new species, Pleistocene, Port Kennedy, Pennsylvania, Academy of Natural Sciences of Philadelphia specimen, part of author's hypodigm; the variant shown is somewhat extreme, but the advanced molarization is characteristic of the species. B, *Tapirus veroensis* Sellards, Pleistocene, Vero, Florida, type, drawn from a cast. C, *Tapirus terrestris*, Recent, South America, A.M.N.H. (Dept. Mammals) No. 120996. D, *Tapirus roulini*, Recent, South America, Yale Peabody Museum No. 11883. All natural size.

TABLE 12
STATISTICS ON LOWER CHEEK TOOTH DIMENSIONS OF *Tapirus copei*, HYPODIGM

Variate	<i>N</i>	<i>OR</i>	<i>SR</i>	<i>M</i>	σ	<i>V</i>	
P₂	<i>L</i>	6	24.7–27.0	4.6	25.90 ± .29	.70 ± .20	2.7 ± .8
	<i>W</i>	6	15.5–17.6	4.3	16.57 ± .27	.67 ± .19	4.0 ± 1.2
P₃	<i>L</i>	9	23.0–25.1	4.3	24.22 ± .22	.67 ± .16	2.7 ± .6
	<i>W_A</i>	9	16.1–18.0	4.7	17.01 ± .24	.73 ± .17	4.3 ± 1.0
	<i>W_P</i>	9	17.8–20.2	4.4	19.19 ± .23	.68 ± .16	3.6 ± .8
P₄	<i>L</i>	6	24.1–24.9	1.7	24.60 ± .11	.26 ± .07	1.0 ± .3
	<i>W_A</i>	8	18.3–21.7	7.3	20.41 ± .40	1.13 ± .28	5.5 ± 1.4
	<i>W_P</i>	8	19.5–22.8	7.2	21.28 ± .39	1.11 ± .28	5.2 ± 1.3
M₁	<i>L</i>	6	23.4–27.0	7.1	25.53 ± .45	1.10 ± .32	4.3 ± 1.2
	<i>W_A</i>	7	19.8–22.9	6.3	20.83 ± .37	.97 ± .26	4.6 ± 1.2
	<i>W_P</i>	7	18.7–20.8	3.8	19.56 ± .22	.58 ± .16	3.0 ± .8
M₂	<i>L</i>	10	27.4–30.8	6.9	28.91 ± .33	1.06 ± .24	3.7 ± .8
	<i>W_A</i>	9	20.5–24.1	7.1	21.56 ± .36	1.09 ± .26	5.1 ± 1.2
	<i>W_P</i>	10	18.3–22.8	8.2	20.17 ± .40	1.26 ± .28	6.3 ± 1.4
M₃	<i>L</i>	6	30.1–31.5	3.8	30.78 ± .24	.58 ± .17	1.9 ± .5
	<i>W_A</i>	6	21.7–23.8	4.5	22.70 ± .28	.69 ± .20	3.0 ± .9
	<i>W_P</i>	5	19.2–20.5	3.3	19.84 ± .23	.51 ± .16	2.6 ± .8

of *T. copei* and probably have nothing to do with that species. They do not agree exactly with any known to me but in most respects are near, or in the possible range of, *T. veroensis*, *T. terrestris*, and *T. bairdii*. It is possible, and geographically probable, that they are the upper teeth of *T. californicus* or an allied

form. A broken upper tooth of similar size from Santa Maria, California, has been described by Stirton and Weddle (1929) but is too fragmentary to add much except an interesting locality record.

Since this paper was completed, but before going to press, Stock (1944) has described two

TABLE 13
STATISTICS ON LOWER CHEEK TOOTH INDICES OF *Tapirus copei*, HYPODIGM

Variate		<i>N</i>	<i>OR</i>	<i>SR</i>	<i>M</i>	σ	<i>V</i>
$\frac{100W}{L}$	P ₂	6	62– 65	8	64.0 ± .5	1.2 ± .3	1.8 ± .5
	P ₃	9	75– 83	16	79.2 ± .8	2.4 ± .6	3.0 ± .7
	P ₄	6	83– 93	29	87.5 ±1.9	4.5 ± 1.3	5.2 ±1.5
	M ₁	6	76– 91	34	81.8 ±2.1	5.2 ± 1.5	6.4 ±1.8
	M ₂	9	72– 83	20	74.9 ±1.0	3.1 ± .7	4.1 ±1.0
	M ₃	5	72– 78	15	73.8 ±1.0	2.2 ± .7	3.0 ±1.0
$\frac{100W_A}{W_P}$	P ₃	9	83– 94	22	88.9 ±1.1	3.4 ± .8	3.8 ± .9
	P ₄	8	91–100	17	96.1 ± .9	2.6 ± .6	2.7 ± .6
	M ₁	7	101–113	27	106.6 ±1.5	4.1 ± 1.1	3.8 ±1.0
	M ₂	9	100–115	37	107.7 ±1.9	5.7 ± 1.3	5.3 ±1.2
	M ₃	5	112–121	22	114.8 ±1.5	3.4 ± 1.1	3.0 ± .9

TABLE 14

DATA ON UPPER CHEEK TOOTH DIMENSIONS IN
Tapirus copei, HYPODIGM

Variate		N	OR	M
P ¹	L	3	22.4-24.9	23.8
	W	3	19.6-21.5	20.4
P ²	L	5	21.9-24.0	22.6
	W _A	4	25.5-26.5	25.9
	W _P	4	27.4-27.9	27.6
P ³	L	5	22.7-24.5	23.7
	W _A	4	27.0-29.5	28.6
	W _P	4	26.1-29.0	28.1
P ⁴	L	4	24.1-26.4	25.3
	W _A	4	29.9-31.8	30.6
	W _P	4	28.4-30.1	29.3
M ¹	L	5	25.8-26.4	26.1
	W _A	5	28.9-31.1	30.3
	W _P	4	25.8-27.9	27.3
M ²	L	5	27.3-29.7	28.1
	W _A	4	31.3-34.9	32.6
	W _P	4	28.0-31.5	29.7
M ³	L	5	26.8-29.2	28.2
	W _A	5	31.0-34.1	32.3
	W _P	5	26.5-29.0	27.8

isolated and imperfect tapir teeth, a probable M₂ from National City, San Diego County, California, and a probable P₄ from Los Angeles County. Stock referred the lower tooth to "*Tapirus haysii californicus*" and compared the upper tooth with the same supposed subspecies. It is a reasonable assumption, although of course not demonstrable, that these fragments are conspecific with *T.*

TABLE 15

DATA ON UPPER CHEEK TOOTH INDICES IN
Tapirus copei, HYPODIGM

Variate		N	OR	M
$\frac{100W}{L}$	P ¹	3	79- 96	86
	P ²	4	114-126	120
	P ³	4	113-126	120
	P ⁴	4	113-132	121
	M ¹	4	110-121	116
	M ²	4	108-125	115
	M ³	5	112-117	114
	P ²	4	92- 95	94
	P ³	4	100-103	102
$\frac{100W_A}{W_P}$	P ⁴	4	102-106	104
	M ¹	4	109-112	110
	M ²	4	105-112	110
	M ³	5	113-119	116

californicus, whatever the real status of that nominal species may be.

Tapirus merriami was named by Frick (1921) on the basis of a fragmentary jaw with imperfect M₁₋₂ from the Pleistocene of Bautista Creek, California. There is little doubt that the species is valid, because M¹, particularly, is significantly larger than established for any other defined North American species. As stressed by Frick, the discrepancy between anterior and posterior widths of M₂ is relatively great, and this is possibly distinctive from most other species but it is within the range for *T. copei*. On the basis of size and proportions, *T. merriami* is nearer to *T. copei* than to other known species, but this is not a reliable indication of phyletic relationship when dealing with such incomplete materials.

A NEW SPECIES OF TAPIR FROM MISSOURI

TAXONOMY

Tapirus excelsus, new species

TYPE: A.M.N.H. No. 39406. Juvenile skeleton consisting mainly of following elements, many of them damaged or incomplete: skull and jaws, all cervical vertebrae, 11 dorsals (numbers 1-11?), last lumbar, second sacral, four caudals (association uncertain), right and left scapulae, right and left humeri, right and left radii, right and left ulnae, left unciform, left pisiform, left patellae, right and left tibiae, left fibula, left astragalus, left calcaneum, left cuboid, left navicular, left ectocuneiform, left third metatarsal, left fourth metatarsal, two phalanges probably of left hind foot.

HYPODIGM: Type and a second, younger specimen, including three cervicals, ten dorsals, two lumbar, one sacral, right scapula, right humerus, left ulna, left radius, left scaphoid, left lunar, left cuneiform, part of pelvis, right femur, left astragalus, left calcaneum, right navicular, right ectocuneiform, right second, third, and fourth metatarsals, seven phalanges, and various fragments.

HORIZON AND LOCALITY: Pleistocene, near Enon, Missouri.

DIAGNOSIS: Most dental dimensions significantly larger than the average for the living species, *T. veroensis*, or *T. californicus* and smaller than *T. copei* or *T. merriami*. P¹ by observation (and P² by inference from P¹ and dm²) similar to *T. veroensis*, *terrestris*, and *bairdii*, more advanced than in *indicus* or *roulini* and less than the modal condition, at least, in *T. copei*. Skull structure and proportions basically like *T. veroensis* but markedly distinct in the separation of the nearly parallel temporal crests, with a broad intertemporal table between them. In this respect most like *T. bairdii*, but differing in the still broader table, weaker temporal crests, and much larger flat dorsal surface of the frontals.

OCCURRENCE

These specimens were found in the course of mining for lead in Sullens Mine, a little over a mile southwest of Enon, Missouri, on Moreau Creek in Moniteau County, near

the border of Cole County. There had been an old mine at this locality, pre-Civil War by repute but (according to Mr. Grimes) probably of more recent date. With the recent rise in the price of lead, it was decided to reopen the mine, and a new sloping shaft or tunnel was sunk. This encountered a large sink-hole, approximately 40 feet in depth and 100 feet in diameter, below the surface aperture, which is considerably smaller. The overhanging roof would have made the hole an effective trap before it was filled, and this doubtless accounts for the accumulation of animal remains. The bones occur in blue clay, among fallen blocks of limestone, in the bottom of the hole. Above this bone- and mineral-bearing accumulation the hole had become nearly filled with earth.

The discovery of large quantities of fossil bones came to the attention of Mr. Loyd E. Grimes, Superintendent of Schools in nearby Eldon, Missouri, and of Mr. A. C. Burrill, Curator of the Missouri Resources Museum in Jefferson City. Some of the first bones removed (*Equus* cf. *complicatus*) were sent to the American Museum for identification in July, 1941. Mr. Burrill also brought the find to the attention of the University of Missouri, and Dr. M. G. Mehl of that institution subsequently made extensive collections on which he reported orally in 1942 to the Society of Vertebrate Paleontology and the Missouri Academy of Sciences, but a published account of which had not appeared when this paper was written.

After the completion of Dr. Mehl's work, mining operations continued to turn up fossil bones which were recovered *in situ* and in the dump by Mr. Grimes. These were sent to Mr. Burrill and by him forwarded to the American Museum of Natural History under an agreement that this Museum would prepare and identify the specimens which would then be divided between it, the Missouri Resources Museum, and the Eldon public schools. Among these new discoveries were the two partial tapir skeletons that are the principal occasion for this paper, as well as many horse and other bones to be mentioned more briefly. In the division of these materi-

als, the type tapir skeleton has been assigned to the American Museum, and the second, younger skeleton, as well as almost all the other (non-tapir) specimens were returned to Mr. Grimes after study.

ASSOCIATED FOSSILS

Only a partial list of the fossils recovered from this locality can be given at this time. The most complete representation is doubtless in the University of Missouri collection, and no attempt is made to anticipate the faunal study which will, it is hoped, be provided by Dr. Mehl and his colleagues. Mention will be made of only a few forms forwarded with the tapir skeletons and, in more general terms, of some others listed by Mr. Grimes and Dr. Mehl. In preliminary reports Dr. Mehl has mentioned horses, a mastodon, a sloth, frogs, and many large turtles. Mr. Grimes, in letters, also mentions these sorts of animals and adds that fish bones and what was believed to be a snake bone (not preserved) have been found.

The fossils sent to us with the tapirs are as follows:

TERRAPENE CANALICULATA HAY

Incomplete plastron and carapace. Identified by Dr. E. H. Colbert who adds that this extinct Pleistocene species has hitherto been known only from Florida. It is interesting from an ecological point of view that the fossil species is associated with tapirs both in Florida and Missouri.

PROBOSCIDEANS

There is a partial tusk that may be either mastodon or mammoth. There are also fragments of a very young mammoth, probably parts of one individual, including small skull fragments, a few parts of skeletal bones without epiphyses, and two third deciduous molars, one fragmentary and one nearly complete. Comparative materials do not permit the certain identification of such incomplete parts of so young an animal, but the specimen suggests *Paralephas* and could be *P. jeffersonii*, the common species of this region.

EQUUS CF. COMPLICATUS

There are two nearly complete lower jaws, much of four upper dentitions, and numerous

skeletal parts of several different individuals. All seem to be of one species, an *Equus* of moderate size. The teeth are slightly smaller than the type of *complicatus* and of course differ enough in detail to be distinguished nominally if this were desirable. They seem to be within the range of the common Hay Springs, Nebraska, horse often called *E. complicatus* and could also be within the range of several other supposed species, such as *E. niobrarensis* and others, many of which will probably prove to be individual or local variants of the *E. complicatus* group.¹

The association is typically Pleistocene, but the facies is peculiar and not quite like any other Pleistocene fauna known to me. The data here presented are too incomplete for very positive conclusions, but the great number of turtles (as reported by Mehl and others) and the apparent absence, certainly the relative scarcity, of artiodactyls are established, unusual features.

Neither the fauna nor the geological circumstances, so far as known to me, justify assigning this deposit to any more precise age within the Pleistocene.

DESCRIPTION

DENTITION

The preserved dentition of the type includes dm^1 (broken), dm^{2-4} , dm_2 (broken), and dm_{3-4} of the deciduous dentition (in most cases the teeth of both sides). M^1 is in place and well preserved on both sides. M^2 , unerupted, was preserved in its crypt on the right side and has been removed and kept separate for study. M^3 is not preserved. The permanent premolars, upper and lower, are present beneath the deciduous teeth, but the specimen was not endangered to expose them except right P^1 which was exposed sufficiently to determine its posterior width and general form. The anterior half of left M_1 is present,

¹ In my opinion the taxonomy of our Pleistocene horses has become so chaotic that the "species" and "identifications" in the literature are almost completely meaningless. Under these circumstances it serves no truly scientific purpose to label even excellent specimens by a current name, because the meaning of such a name is unknown and will remain so until some exceptionally able student with very abundant materials spends the months or years necessary to establish the real characters and variation of many properly unified samples of different ages and localities.

and M_2 can be seen, but not measured, in the crypt on both sides. The tip of the right permanent upper canine is visible, and there is a loose left second upper incisor probably of this individual.

Morphologically all the teeth are of the *T. terrestris-bairdii-veroensis* type, a complex in which, as already sufficiently emphasized, there seem to be no clear-cut or constant differences in dental morphology aside from size and proportions. In the character of the ectoloph of M^2 , emphasized by Olsen (1940) as distinguishing *T. terrestris* and *T. bairdii*, the type of *T. excelsus* can be closely matched in both those species and is about intermediate between their probable modal conditions. P^1 is within the range of each of the three species mentioned and is less advanced than is typical of *T. copei*, more than is typical of *T. roulini* or *indicus*.

As to minor variable characters possibly significant in modal condition (of course indeterminate from this single specimen) but not clearly distinctive in many individuals, all the cheek teeth are moderately rugose. Dm^{1-4} have basal swellings but no sharp external cingula, and the swellings are still less distinct on M^{1-2} . The parastyles are relatively large on all preserved upper cheek teeth and quite distinct on dm^2 . There are no external median tubercles such as occur on the type and some other, but not all, specimens of *T. veroensis*. On dm^{2-4} and M^{1-2} there are no internal cingula across protocone or hypocone, but there is a small sharp ridge across the inner end of the valley between those cusps and this forms a fairly definite intermediate tubercle, least distinct on M^2 . Dm_3 has a distinct internal intermediate tubercle and is rugose, but not definitely tuberculate, in the corresponding external position. Dm_4 has both internal and external tubercles well defined.

Tapirus excelsus is significantly larger in average dental dimensions than any living tapir. In comparison with *T. veroensis* the type teeth are above the average size for that species in all dimensions for which conclusive comparisons can be made. Due mainly to the paucity of material for full statistical comparison, this difference in size is not demonstrated to be significant in every case, but it is decisively significant for a few dimensions,

notably the two widths of dm_4 , and there can be little doubt that most of or all the teeth did average larger in *T. excelsus* than in *T. veroensis*, although clearly the ranges of the two overlapped for some dimensions. M^{1-2} are longer in *excelsus* than in *veroensis*, but the widths of the same teeth are within the observed range for *veroensis*. The width: length ratio is consequently lower in *excelsus*, but the difference is not clearly significant.

Comparison with *T. copei* is incomplete because it is mainly the deciduous teeth that are known in *T. excelsus*, and these are poorly represented in the hypodigm of *copei*. In the homologous dimensions that are available, *T. excelsus* is uniformly smaller than observed teeth of *T. copei* with the single exception of the length of M^2 which in *excelsus* is below the average for *copei* but in the observed range. The width of P^1 and all the dimensions of M^1 are near or beyond the level of significance, and there is little doubt that these teeth, at least, were smaller in the species *excelsus* (and not only in the type specimen) than in *copei*. The form of P^1 is also characteristically different in *excelsus*, more as in *veroensis*, although intergradation in the populations is possible. In spite of the limited material for direct comparison, *T. excelsus* is thus quite clearly distinct from *T. copei*.

It is a moot question whether some of the midwestern or eastern tapirs hitherto referred to *T. haysii* or other species may not belong to *T. excelsus*. This is probable, but cannot be conclusively demonstrated. The single tooth from Herculaneum, Missouri, referred by Olsen (1940) to *Tapirella* cf. *bairdii* may well belong to *T. excelsus*, although it is relatively shorter and wider than M^2 of the type and has the ectoloph somewhat less notched. The lower jaw from Frederick, Oklahoma, described by Hay and Cook (1930) as *T. haysii* is considerably larger and is more likely to belong to *T. copei* (= *T. "haysii"*) or an undescribed species. The palate from Chickasha, Oklahoma, described by Stovall and Johnston (1934) as *T. haysii* indicates an animal about the size of *T. excelsus*, but P^{1-2} seem, from the rather inadequate figure and description, to be nearer *T. copei* than other defined species. It is, however, rather futile to attempt exact identification of any of these scattered finds

from the available data, and this is unnecessary at present from a strictly taxonomic point of view.

The principal available metrical data on the teeth of the type of *T. excelsus* are given in table 16.

had not fused and do not make good contact with the skull but appear to have been stepped down slightly below the frontal level, much as in *T. bairdii* or *indicus*. The exact shape of the nasals, extremely variable in recent tapirs, is nearly matched in juvenile

TABLE 16
AVAILABLE DIMENSIONS AND INDICES OF THE TEETH OF THE TYPE OF *Tapirus excelsus*

	dm ²	dm ³	dm ⁴	dm ₂	dm ₃	dm ₄	P ¹	M ¹	M ²	M ₁
<i>L</i>	20.8	21.6	24.1	25.9	22.7	23.2	—	25.0	27.8	—
<i>W_A</i>	18.7	22.0	25.1	—	15.5	18.2	—	26.4	30.3	19.5
<i>W_P</i>	22.0	21.6	22.8	Ca. 17	16.5	17.7	17.1	25.1	26.6	—
$\frac{100W}{L}$	105	102	104	Ca. 66	68	78	—	106	109	—
$\frac{100W_A}{W_P}$	85	102	110	—	94	103	—	105	113	—

SKULL

The skull has been somewhat distorted and as received by us was broken into numerous fragments, probably as a result of the mining operations that uncovered it, and a considerable part is missing. The preserved fragments were carefully assembled by Mr. Albert Thomson and suffice for reasonable restoration of the whole skull. The more important deficiencies are the tips of the premaxillae, the ascending processes of the maxillae and the lacrimal region, and the pterygoid region. Most of the sutures are quite open, as they would be in so young an individual, but judging from recent tapirs the animal had nearly reached its definitive size. The probable skull changes to be expected in an animal of the same species fully adult would involve relatively insignificant increase in size, sharpening and perhaps some elevation of the temporal crests, some elongation of the palate, and possibly some ossification in the mesethmoid.

The dorsal contour is nearly straight, as in most tapirs of this age, but without the incipient arching already clear in *T. terrestris* at this stage. The post-nasal cranium appears more elongate in lateral view than in *T. bairdii*, and the lateral view of this region is most like *T. indicus* or *veroensis*. The nasals

T. terrestris and *bairdii* and probably is not distinctive from variants in the other species.

The temporal crests do not meet to form a single sagittal crest but are well separated, and between them is a broad table almost flat but slightly arched anteroposteriorly, with nearly parallel sides until the crests, here vague and rounded, diverge in the lateral frontal region. The aspect of this region happens to be the most clearly diagnostic single character among recent and, as far as it is known in them, Pleistocene tapirs, and it alone unmistakably distinguishes all the sufficiently defined species. The union of the temporal crests into a single sagittal crest or their separation by an intervening table is not changed by growth. In *T. terrestris*, although the height of the sagittal crest increases greatly with age, it is present and single from birth. In *T. bairdii* and *indicus* the temporal crests are separated (in characteristically different ways) throughout life. *T. excelsus* most resembles *T. bairdii* in this character, but differs in that the parietal table is relatively still broader (the broadest known in any tapir). The temporal crests are more rounded and less definite; this is in part an age character, but the crests seem normally to be sharper in *T. bairdii* of the same age.

The posterior part of the intertemporal

table is formed by the supraoccipital. In this specimen anterior to this part, between the posterior ends of the parietals, there are two clear interparietals. They are nearly symmetrical about the midline, a smaller in front of a larger, together forming a wedge between the parietals, nearly reaching the similar wedge formed by the frontals and projecting backward between the parietals. Such a posterior wedge may occur in any of the recent species but is not typical, or at least invariable, in any unless it be *T. roulini*, in which it occurs in the one skull studied by me. In no case seen by me is it formed by a separate interparietal, although some of the older skulls with a wedge look as if such an element might have been separate when they were very young. As is well known, interparietals may occur in a wide variety of mammals and are often quite sporadic and variable within a given group.

The dorsal surface of the frontals is extraordinarily large and especially broad, more than in *T. veroensis*, most suggestive of *T. indicus*, and in marked distinction from other species.

The spiral grooves are broad and shallow and meet at the midline as in the type of *T. veroensis* and often in *T. bairdii* and *T. indicus*, rarely or not in *T. terrestris* and *T. roulini*. The lateral grooves on the frontals are also broad and shallow, almost as in *T. veroensis* and to that extent like *T. indicus*, but less like the usual condition in other species. The lacrimal region below this is unfortunately lacking.

The ascending process of the premaxilla and the way that it is enveloped by the maxilla suggest *T. veroensis*, *T. indicus*, and *T. bairdii*, but the process ends somewhat farther from the first premolar than is usual in the first two and is sharper than is usual in the last. The dorsal exposure of the maxilla posteromedial to this and its sharp edge also suggest *T. veroensis* and *T. indicus*. There are no sharp, large ascending flanges such as clasp the mesethmoid in *T. bairdii*, even in a comparably juvenile stage before the mesethmoid has ossified.

The occiput is relatively narrower than in *T. veroensis*, and the lambdoid crests, although about equally protruding, heavy, and rounded, do not flare outward quite so much.

This is not exactly matched in any recent specimen compared, but is suggestive of *T. bairdii*.

As regards size and proportions, the skull restoration precludes complete accuracy, but is probably a sufficiently good approximation. The skull is very nearly of the general size of the type of *T. veroensis*, but as it is a juvenile and *T. veroensis* is based on an adult, the adult *T. excelsus* would attain greater size than the *veroensis* type. Allowing something for this difference in age (e.g., as regards the palate, which lengthens somewhat with age) and for slight individual variation, no probable difference of proportions is seen between the two types. The type of *T. excelsus* is generally within the size range for adult *T. terrestris* but is comparable only with the largest variant adults of the latter, and *T. excelsus* clearly reached greater adult size. The proportions are generally similar, but the cranium is notably broader and less deep in *T. excelsus* (and also in *T. veroensis*), whether compared with adult or with juvenile *T. terrestris*. The relative depth of the cranium is also less than the average for *T. bairdii*, although probably within its range. The relative width is almost at the mean for *T. bairdii* and is another special resemblance to that species.

Basic comparative measurements and indices are given in table 17.

POST-CRANIAL SKELETON

The type includes most of the important post-cranial elements, as enumerated above, and the second, younger specimen provides confirmation or variants of many characters and also includes a few bones (notably several carpals) not present in the type. Both specimens are juvenile, and comparison with adults might be seriously misleading. The available recent materials do not sufficiently exhibit the range of variation in the skeleton in a comparable stage of development, and comparison is mostly with single specimens, for which allowance must be made. The more striking differences, such as the shape of the odontoid process of the axis and the tarsal articulations of the metatarsals, have, however, been confirmed by check on several recent skeletons.

In spite of small differences in variable

TABLE 17

COMPARATIVE SKULL DIMENSIONS AND INDICES IN *Tapirus excelsus*, *T. veroensis*, AND *T. terrestris*
(The dimensions are those listed for *T. terrestris* on a previous page.)

Dimension or Index	Type, <i>T. excelsus</i>	Type, <i>T. veroensis</i>	Mean, <i>T. terrestris</i>	Large Juvenile <i>T. terrestris</i> , Same Age as <i>T. excelsus</i> Type
A	Ca. 370	379	351.7	355
B	Ca. 185	199	189.9	179
C	Ca. 175	174	159.7	152
D	114	113	128.8	131
E	127	122	108.0	102
F	71	—	76.1	64
G	64	Ca. 75	66.6	65
H	52	44	49.4	46
100B/A	Ca. 50	53	53.7	50
100C/A	Ca. 47	46	45.1	43
100D/A	Ca. 31	30	36.5	37
100E/A	Ca. 34	32	30.8	29
100H/A	Ca. 14	12	14.0	13
100G/F	90	—	90.0	102

details in every bone, the general characters of the skeleton are so like those of all living tapirs that a straight description is unnecessary and would waste space. The following notes are, therefore, comparative only and for the most part mention differences from the two most readily available and geographically near recent species, *Tapirus terrestris* and *T. bairdii*. The *T. terrestris* skeleton used for general comparison is of exactly the same physiological age as the type fossil, as indicated by tooth eruption, suture closure, and fusion of epiphyses. The *T. bairdii* specimen is a little older: dm^{1-3} have been replaced (dm^3 very recently), but M^2 has not erupted; on the tibia, for instance, the distal epiphysis has fused and the proximal epiphysis is beginning to fuse, while both are unfused in the fossil. This small age difference probably does not falsify comparisons in any essential way.

VERTEBRAL COLUMN: The atlas is relatively much narrower, transversely, than in either *T. terrestris* or *T. bairdii*, and the transverse processes are squarer at the ends. The dorsal tubercle is large, but is not so elevated or pointed as in the specimens compared. The central aperture (neural canal plus cavity for odontoid) is pear-shaped, less circular than in *T. terrestris*; *T. bairdii* is

intermediate. The foramina on the ventral surface of the transverse process open into a large, sharply defined pit in *T. bairdii*; in *T. terrestris* this is less pronounced and in the fossil still less. This individual has an unusual anomaly, the vertebrarterial canal being completely absent on the right side. It is normal on the left side (also on all the following cervicals), and the atlas is otherwise symmetrical. The artery itself presumably was normal but somehow was pushed aside, rather than surrounded, by the expanding atlas of the embryo.

The odontoid process of the axis is sharply distinct from either recent species. It protrudes more strongly, making the centrum as a whole relatively longer, and it is narrow and peg-like. In *T. terrestris* it is wide and has a protruding, semi-cylindrical articular surface suggestive, in incipient form, of the spout-like process of the ruminants. *T. bairdii* is somewhat intermediate, but distinctly closer to *T. terrestris* than to the fossil. The more juvenile fossil specimen is also somewhat intermediate, but still definitely more like the type fossil than like *T. bairdii*. The neural canal is relatively lower and more triangular than in either recent species. The postzygapophyses differ from *T. terrestris*

and are more like *T. bairdii* in being relatively nearer together, with a definite, sharp notch between them.

This approximation of the postzygapophyses continues on the third to sixth cervicals, which also resemble *T. bairdii* in having the transverse processes relatively somewhat wider than in *T. terrestris*. The centrum is relatively larger, the arch relatively smaller, and the neural canal relatively more shallow than in either recent species. These discrepancies decrease backward, and the seventh cervical is more nearly a harmonious enlargement of that in the comparative recent species.

In the anterior dorsal region the transverse processes become relatively narrower (transversely), and the neural spines become relatively much higher than in either recent species. The capitular facets are very large. The notches for the spinal nerves are still open on the first six, or possibly seven, dorsals. In *T. terrestris* and *T. bairdii* of comparable age they are open only on the first dorsal. The type includes 11 dorsals, apparently in sequence. More posterior dorsals are preserved in the second, younger specimen and are much as in the comparative recent species.

The larger specimen has part of one and the smaller parts of two lumbar. They are not particularly distinctive, nor is the second sacral of the older specimen, the only one preserved.

There are four caudals that may belong to this animal, although they are heavier and less compressed dorsoventrally than corresponding caudals of the compared recent tapirs and have the transverse processes single rather than wing-like and more or less bifid.

SCAPULA: The scapula is decidedly shorter dorsoventrally and wider anteroposteriorly than in *T. terrestris*. Differences from *T. bairdii* are still more marked in these respects, and the latter also has the postspinous fossa relatively narrower than in the fossil.

FORE-LIMB: The humeri of *T. terrestris* and *T. bairdii* are almost alike except in size. The fossil differs from both in having the humerus relatively shorter and stouter and also, but less distinctly, in the sharper and more prominent external trochlear ridge.

The ulna is also stouter than in the recent species. Its proximal articular part is about as in *T. terrestris* and less oblique than in *T. bairdii*. The distal epiphysis, preserved only in the younger specimen, is relatively longer than in the recent species, as is that of the radius of the same individual. The proximal articular surface of the radius (both specimens) has the internal part larger, making the whole more triangular, than in the two comparative living forms.

Of the carpus, the type includes only unciform and pisiform, but the younger specimen has the scaphoid, lunar, and cuneiform. The scaphoid is more compressed in the dorso-palmar direction and has a much larger and more proximal palmar (third) facet for the lunar than in *T. terrestris*. *T. bairdii* is intermediate as regards this facet, but still less like the fossil in proportions.

The lunar is relatively narrower transversely and deeper proximodistally than in either recent species. The articulations are more like *T. bairdii* and differ from *T. terrestris*, aside from the scaphoid facet as mentioned above, in that the cuneiform facet does not extend so far in a palmar direction, and the unciform and magnum facets are in contact, not separated by a groove.

The unciform is about as in both recent species except for being relatively broader transversely. The pisiform is relatively deeper, proximodistally, than in either recent form but more like *T. bairdii*.

The only preserved bone distal to the carpus is the second metacarpal of the type. The proximal articulation is less quadrate and more oblique than in *T. terrestris*; *T. bairdii* is about intermediate. As in *T. bairdii* there is a well-developed internal facet (for the trapezium?).

PELVIS: The pelvis is nearly as in the recent forms but differs from both in being relatively a little deeper, with a less elongate but deeper (dorsoventrally) obturator foramen, and with a somewhat less straight upper contour.

HIND-LIMB: Like the humerus but in lesser degree, the femur is relatively short and stout. The three trochanters agree fairly well with *T. bairdii*. All three are somewhat more produced and deflected in *T. terrestris* of comparable age. The scar below the third tro-

chanter (mainly for origin of the gastrocnemius muscle) is very deep and wide in the fossil and sharply bounded above, a development more nearly approached in our specimens of *T. bairdii* than in *T. terrestris* but distinctive from both.

The patella is wider and shallower (anteroposteriorly) than in the recent species.

The proximal end of the tibia is deeper anteroposteriorly and narrower transversely than in *T. terrestris* and more, but not exactly, like *T. bairdii*. The bone does not otherwise differ noticeably in the three species, except for size.

The fibula of the type lacks both epiphyses. The distal end of the shaft appears to have been more expanded than in either recent form and sharply crested as in *T. bairdii*.

The calcaneum has all its processes relatively heavy and produced. The proportions are rather more like *T. bairdii* than *T. terrestris*, for instance in the stout tuber and projecting sustentaculum, but still are distinctive, as in the greater projection of the distal end. The astragalus is not very distinctive but resembles *T. bairdii* in having a somewhat shorter neck than in *T. terrestris* (like some other resemblances and differences possibly a mere function of gross weight).

The cuboid is relatively wider transversely than in *T. terrestris* and has all its processes somewhat more prominent. *T. bairdii* is, again, somewhat more like the fossil.

The external cuneiform has a well-developed facet for the fourth metatarsal. Such a facet is also present in *T. bairdii* but is smaller. In *T. terrestris* (several specimens) it is absent and, on the contrary, the third metatarsal is in contact with the cuboid. (In *T. indicus* the fourth metatarsal is in contact with the ectocuneiform.) This striking mechanical difference in feet otherwise so closely similar is remarkable in such nearly allied species. It might seem to indicate a major difference in evolutionary trend and hence to merit higher taxonomic value than I am inclined to give it. It could however, be caused by a genetically slight difference in tarsal growth pattern, and homologous differences are known in closely allied genera, if not species, of other perissodactyls, e.g., among titanotheres.

Except for this difference in tarsal articulations, the third and fourth metatarsals, preserved in the type, are not particularly distinctive, except that the proximal plantar process of the fourth is more produced than in either recent form.

GENERAL COMPARISONS: Table 18 gives characteristic dimensions throughout the skeleton of the type and the log differences of the corresponding dimensions of the two recent skeletons used for detailed comparisons. The log differences, and hence the various proportions, are also shown graphically in figure 11. (For method of construction and interpretation see Simpson, 1941c.) The three specimens, doubtless also the three species, have much the same build, yet the detailed proportions of these dimensions, and of others not plotted here, differ throughout. In this regard there is no clear-cut preponderance of resemblance between any two of the three. In the comparisons of the diagram, the two recent specimens differ about equally from the fossil and resemble each other slightly more than either resembles the fossil, but this difference is so small that no conclusion should be based on it. The only safe statement from these data is that all three are about equally distinctive.

The various proportions of individual bones, as far as clear and possibly significant, have been mentioned. In a more general way some of the more striking distinctions brought out by these measurements may be briefly noted. The skull is longer relative to the skeleton in both recent specimens, but this may mean only that the fossil skull has been restored a little too short. The disproportionate length of the axis results mainly from the different structure of the odontoid process. The cervical centra are relatively large and the dorsal spines are relatively much longer in the fossil, but other observed differences in vertebral proportions are small and probably not significant. In general the limbs of the fossil tend to be somewhat shorter and heavier, but in a somewhat irregular way as regards proportions of individual bones.

The average log difference between the fossil and the specimen of *T. terrestris* of the same age is 0.136, which indicates that the linear dimensions of the fossil are about 1.37 times those of the recent animal (its bulk

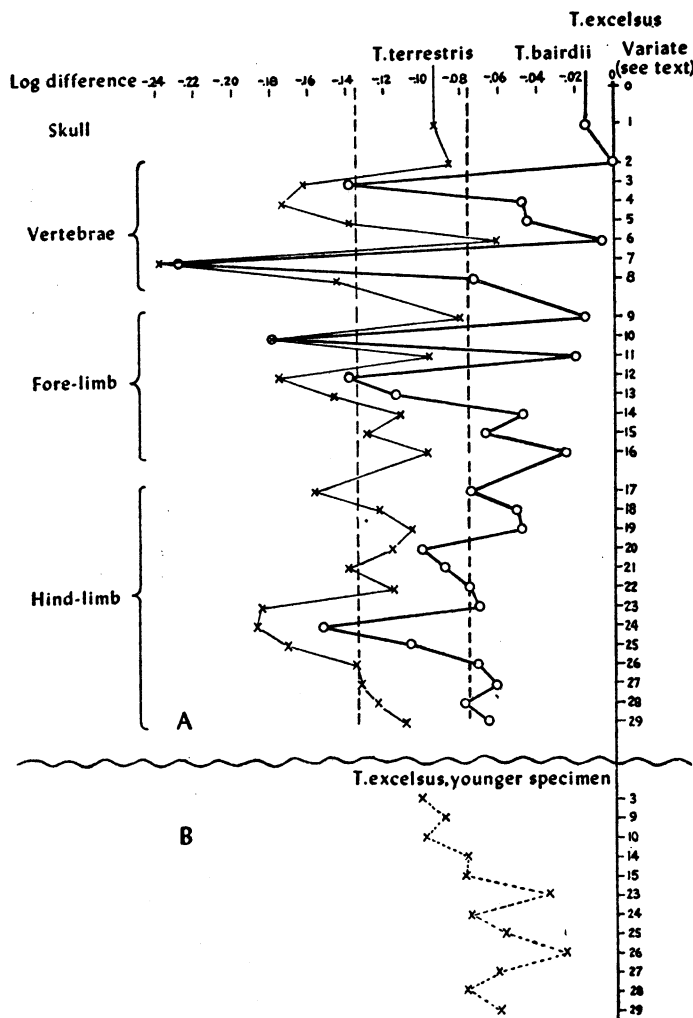


FIG. 11. Log difference graph (ratio diagram) of skeletal dimensions of *Tapirus excelsus*, new species, and compared recent species. Differences in logarithms of the measured dimensions are entered on the abscissal scale at the top of the diagram. Variates are numbered to the right, corresponding with the numbers and specifications used in table 18. In both A and B the continuous line to the right (zero on the log difference scale) represents the type of *T. excelsus*. A, *T. excelsus*, type, compared with skeletons of *T. terrestris* and *T. bairdii*; the broken vertical lines represent the mean log differences for these two comparative specimens. B, *T. excelsus*, type, compared with a second, younger specimen of the same species.

and weight in life would thus be something over two and one-half times as great). The average log difference from the specimen of *T. bairdii* is 0.076, making the linear ratio about 1.19 (and the bulk ratio about 1.7). Since the specimen of *T. bairdii* is a little older, a greater discrepancy at the same age is indicated. The fossil is probably near or above the maximum size for *T. bairdii* and

almost certainly well above that for *T. terrestris*.

Comparison of the type with the smaller juvenile found at the same place reveals essential agreement in morphology, as would be expected, within the limits imposed by marked difference in age and size. The proportions (e.g., fig. 11) agree better than do those of either fossil alone compared with

TABLE 18

	Dimension	A.M.N.H. No. 39406 (Absolute Value in Millimeters)	<i>Tapirus</i> <i>terrestris</i> (Log Difference)	<i>T.</i> (<i>Tapirella</i>) <i>bairdii</i> (Log Difference)
1	Length of skull (prosthion-foramen magnum)	Ca. 375	-.094	-.015
2	Width of atlas	139	-.086	.000
3	Length of centrum of axis	77	-.163	-.139
4	Width of 4th cervical	97	-.174	-.047
5	Width of 7th cervical	91	-.139	-.045
6	Width of 6th dorsal	69	-.061	+ .006
7	Oblique height of spine of 7th dorsal	144	-.239	-.229
8	Width of 2d sacral	96	-.143	-.073
9	Maximum dimension of scapula	260	-.080	-.015
10	Least anteroposterior width of shaft of scapula	53	-.180	-.180
11	Length of humerus	251	-.097	-.020
12	Least diameter of shaft of humerus	33	-.177	-.139
13	Width of distal end of humerus	77	-.147	-.114
14	Length of ulna without epiphyses	245	-.112	-.047
15	Length of radius without distal epiphysis	201	-.130	-.067
16	Length of 2d metacarpal without distal epiphysis	89	-.098	-.025
17	Anterior rim of acetabulum to posterior end of ischium	184	-.158	-.075
18	Maximum diameter of obturator foramen	73	-.123	-.050
19	Length of femur	324	-.106	-.049
20	Least diameter of shaft of femur	34	-.117	-.101
21	Width of distal end of femur	87	-.141	-.089
22	Length of tibia	280	-.117	-.076
23	Length of calcaneum	112	-.186	-.071
24	Depth of shaft of tuber of calcaneum	37	-.188	-.153
25	Length of astragalus	64	-.172	-.107
26	Width of body of astragalus	52	-.136	-.072
27	Length of metatarsal III	128	-.134	-.062
28	Width of shaft of metatarsal III	24	-.125	-.079
29	Length of metatarsal IV	112	-.110	-.067

either of the recent species, as expected, yet show some discrepancies. These may be in part individual deviations, but are probably in some degree also due to age. Although both juvenile, the two fossils are separated by a period of most rapid growth. Despite the youth of the type, comparison of recent tapirs indicates that it had probably nearly reached adult size and would have grown slowly thereafter had it lived, while the smaller animal must still have been growing rapidly. Some difference in details is inevitable from this factor alone.

As the preceding comparisons showed, the fossil also differs from either recent form in characters of descriptive morphology, within the narrow limits of the rather stereotyped

tapir structure. On a tabulation of each point, not much greater resemblance to one recent species rather than the other is indicated. Nevertheless in a few details, especially of limb and foot structure, of possibly greater significance, there does seem to be slightly closer agreement with *T. bairdii*. As regards phylogenetic relationships, this tendency is not of clear-cut meaning and must be viewed with a certain reserve.

AFFINITIES

Although *Tapirus excelsus* is a clear-cut, distinctive species when all its known anatomy is taken into account, it simply rings another set of changes on the differential characters unevenly distributed throughout

the genus *Tapirus* (including *Tapirella* and *Acrocodia*), resembling now one, now another species and of course basically like all in the great majority of its structural features. Its most nearly unique character is the great expansion of the intertemporal and frontal table, and this is only an extreme of a tendency clearly established in *T. bairdii* and *T. indicus*.

The only fossil species for which there is a broad basis for comparison is *T. veroensis*. *T. excelsus* and *T. veroensis* appear to be rather closely related, perhaps more closely to each other than to any recent species, as suggested by similarity in most features of skull and dentition. The dentition shows little difference except in size, and the skulls are nearly alike except in the arrangement of the temporal crests, which is, however, a strong and important difference. In many or most of the characters differentiating *T. excelsus* and *T. veroensis*, *T. excelsus* tends to resemble *T. bairdii*. In the skeleton also (where sufficient

basis for comparison with *T. veroensis* is lacking) special resemblances to *T. bairdii* (but also some differences) have been noted. Yet *T. excelsus* lacks the most distinctive single character of *T. bairdii*, the peculiarity of the mesethmoid region that has induced many students to place that species in a separate genus.

Thus *T. excelsus* stands rather close structurally to *T. veroensis* on one hand and to *T. bairdii* on the other. *T. veroensis*, in turn, has been shown to have special resemblance to *T. roulini* on one side and *T. indicus* on the other. Further, *T. roulini* is clearly rather close to *T. terrestris*. The whole is an intricate complex in which each defined group represents a different specific line with different segregations of fluctuating characters. Vertical grouping into a smaller number of phyletic lines or horizontal grouping into other than monotypic genera seems to be impossible except in a way so subjective as to be unacceptable.

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