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THE OSTEOLOGY AND RELATIONSHIPS OF *ARCHAEOMERYX*, AN ANCESTRAL RUMINANT[1]

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INTRODUCTION

The genus *Archaeomeryx* was first described by Matthew and Granger in 1925, upon the basis of a large series of teeth, skulls and portions of skulls, skeletal elements, and several associated skeletons, all of which had been discovered in the Upper Eocene Shara Murun formation of Mongolia by the Asiatic Expeditions of The American Museum of Natural History. In their original description, these authors gave a detailed diagnosis of the type species, accompanied by figures of the dentition. They also made a few remarks in this publication regarding the importance of this new form, as follows:

"This genus is of exceptional interest, as it appears to be an approximate ancestral type for the pecora. It has assumed the characteristic pecoran-traguline character of the united naviculo-cuboid, but it still retains the separate median pair and complete lateral pair of digits, the ulnar and fibular shafts are more primitive than in any pecora, the upper incisors are still retained, the premolars are of primitive pattern, the molars brachyselenodont. It lacks any of the various aberrant specializations which exclude all of the Eocene genera hitherto described from direct ancestry to the pecora and, as fortunately the principal osteological and dental characters are determinable from the exceptionally complete material, the affinities of the genus can be very satisfactorily appraised. So far as the higher ruminants are concerned, it affords tangible and very convincing proof of the theory of an Asiatic dispersal center."[2]

Beyond the original description of the genus, there has been very little notice taken of it in the literature, except for passing references in the course of general discussions dealing with ruminant evolution. Since, because of its relatively early age and its generally unspecialized habitus, this is

[1] Publications of the Asiatic Expeditions of The American Museum of Natural History. Contribution number 144.

[2] Matthew, W. D., and Granger, Walter, 1925. Amer. Mus. Novitates, No. 196, pp. 10–11.

one of the most important of the ruminants from an evolutionary standpoint, it has seemed advisable to make a detailed study of the genus as based upon the original materials, comparing it with other primitive ruminants in an effort to determine the actuality of its position as a possible structural ancestor for the pecorans. It is thought that such a detailed and comparative osteological description, together with additional figures, will give to palaeontologists and zoologists an increased appreciation and knowledge of this important form.

The illustrations were made by Mr. John C. Germann.

MATERIALS UPON WHICH THE PRESENT STUDY IS BASED

All of the specimens listed below were found in the upper Eocene Shara Murun formation, at Ula Usu, Mongolia. All belong to the type species, *Archaeomeryx optatus* Matthew and Granger, 1925.

Amer. Mus. No. 20311, type. Palate and mandible.
20312, palate and lower jaws.
20313, upper and lower jaws.
20314, upper and lower jaws.
20315, upper and lower jaws.
20316, portions of upper jaws; right M^{2-3}, left P^4–M^3.
20317, upper and lower jaws.
20318, upper and lower jaw fragments.
20320, articulated skeleton.
20321, skull and jaws, part of skeleton, lumbars, pelvis and part of hind limb.
20322, skull and jaws, pelvis and hind limbs with articulated feet, fore limbs and feet.
20323, miscellaneous upper and lower jaws and foot bones.
20324, miscellaneous upper and lower jaws and foot bones.
20325, miscellaneous upper and lower jaws.
Numerous teeth and skeletal elements, not numbered, representative of at least 38 individuals.

It may be seen that *Archaeomeryx optatus* is known from a considerable series of specimens, including literally dozens of dentitions. Thus it is possible to present a rather thorough study of the osteology of this animal and to attempt a reconstruction of the skeleton upon a solid foundation of factual evidence, with the one exception that in all cases the skulls are crushed, thereby making a restoration of the skull exceedingly difficult.

A REVIEW OF THE OSTEOLOGY OF *ARCHAEOMERYX OPTATUS*

Analysis of the Diagnostic Characters of *Archaeomeryx*

The description by Matthew and Granger, though brief, is remarkably complete, and there are but few important points in the anatomy of this genus to be added to what these authors have already so lucidly described. On the basis of the original description of the genus and the characters shown by the material at hand, a diagnosis of the generic type may be presented as follows.

Archaeomeryx optatus

1.—Of small size, approximately equal in this respect to the modern *Tragulus*.

2.—Skull hornless, with relatively small braincase, prominent occipital crest, and small orbit closed posteriorly. Mandible rather heavy.

3.—Dental formula 3/3, 1/1, 3/4, 3/3.

4.—Upper incisors well developed; upper canine of medium size; short post-canine diastema; three upper premolars; upper molars brachyodont, quadritubercular, with strong parastyle and mesostyle and well-developed internal cingulum.

5.—Lower incisors procumbent; lower canine incisiform and in series with incisors; first lower premolar caniniform and set apart by short diastemata from canine in front and from second lower premolar behind; lower premolars compressed and trenchant, the last with a well-developed inner cusp and a posterior basin; lower molars quadritubercular.

6.—Back rather long, with heavy vertebrae. Sacral vertebrae showing little fusion. Tail very long.

7.—Radius and ulna separate. Carpals separate. Metacarpals separate, the lateral toes being complete but somewhat reduced.

8.—Pelvis not fused to sacrum. Fibula reduced, only the proximal and distal ends being

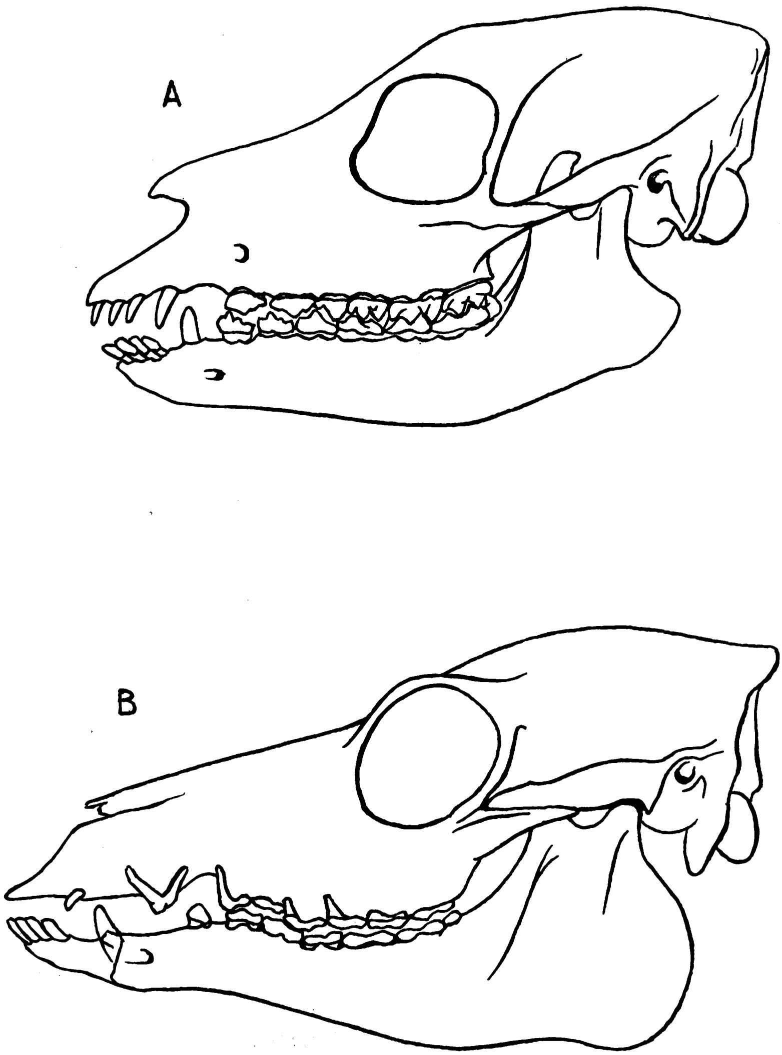

Fig. 1. Comparison of the restored skull and jaw of (A) *Archaeomeryx optatus* Matthew and Granger, based upon Amer. Mus. Ncs. 20311, 20320, 20321, 20322, with that of (B) *Hypertragulus hesperius* Hay, Amer. Mus. No. 7918, type. Drawing of *Hypertragulus* adapted from Frick, 1937. Lateral views, natural size.

retained. Astragalus completely artiodactyloid. Cuboid and navicular fused. Metatarsals separate, the lateral toes being complete but somewhat reduced.

The Comparative Osteology of *Archaeomeryx*

In this comparative review of the osteology of *Archaeomeryx*, the genus will be considered in the light of the resemblances and differences shown as it is compared with certain important genera truly representative of related families and subfamilies of traguloids.[1] Thus, *Archaeomeryx* will be compared so far as is possible with the primitive Eocene genus *Amphimeryx*, representative of the family Amphimerycidae.

[1] The basis for the classificatory terms here used will be elucidated on a subsequent page of this work.

In comparing it with the hypertragulids, the comparison will be largely with *Hypertragulus* itself, since this form is perhaps as typical as any member of the family. None of the protoceratids will be brought into this comparative study, because they are so highly specialized as to be of little concern to us in this connection. On the other hand, comparisons with the true Tragulidae will be necessary—with *Gelocus* as typical of the subfamily Gelocinae, and particularly with *Tragulus* itself, as a central type representative of the subfamily Tragulinae. In all of these comparisons, emphasis will be placed especially on the resemblances and differences between *Archaeomeryx*, *Hypertragulus* and *Tragulus*.

The Skull

It is an interesting fact that the skulls of *Archaeomeryx*, *Hypertragulus* and *Tragulus* are all of about the same size; naturally, the same statement will hold for the skeletons, too. And judging from maxillae, mandibles and dentitions, the same is true for *Amphimeryx* and *Gelocus*. All of which means, of course, that in these several genera, representative of as many different subfamilies, the primitive ruminant or pecoran heritage has been retained so far as size is concerned. Evolution of most mammals from early Tertiary ancestors usually—although not always—has entailed an increase in size, and the mere fact that there has been no important growth increments in the various traguloids named above is in itself one indication of the slight amount of structural evolution that has taken place within these ruminants.

Archaeomeryx, *Hypertragulus* and *Tragulus*, all have hornless skulls—again a primitive heritage character for the ruminants. Because of the crushing of the specimens, nothing definite can be determined as to the size of the braincase in *Archaeomeryx*, but there is good reason to believe that it was about equal to the braincase of *Hypertragulus*.

In this respect, *Hypertragulus* and *Tragulus* are very similar to each other, which may be some indication that the modern chevrotain has stayed at about the "Oligocene level of intelligence" among the primitive ruminants. Continuing, the orbit in *Archaeomeryx* is seemingly smaller in proportion to the size of the skull than is the case in *Hypertragulus* or *Tragulus*, as might be expected when comparing an Upper Eocene genus with forms of a later date. An interesting character of *Archaeomeryx* is the apparent closing of the orbit posteriorly, showing that this advanced ruminant character probably was established at a very early date in the history of the suborder, even though in some later forms, such as *Hypertragulus*, the orbit tends to remain open posteriorly.

The horizontal ramus of the mandible in *Archaeomeryx*, though not so deep, is thicker and heavier than is the case with the rami of *Hypertragulus* and *Tragulus*.

These are the principal comparisons to be made in a consideration of the genera discussed above, further discussion being made impracticable because of the very crushed condition of the several known skulls of *Archaeomeryx*.

The Dentition

Archaeomeryx seemingly is unique among the pecorans in the possession of functional upper incisors. Matthew, in 1902, indicated by his text-figures a belief that the upper incisors might have been present in *Hypertragulus* and *Hypisodus*, while Frick, in 1937, indicated in some of his figures the possibility of a very small third incisor being retained in the premaxilla of the Hypertragulidae. Professor Scott, in his recent monograph of White River Artiodactyla (1940), mentions "minute alveoli" as being present in the premaxillae of *Hypertragulus*, and shows very clearly that there were very small, non-functional upper incisors present in the premaxillary alveoli of *Leptomeryx*. Since the complete premaxillae are not known in *Hypisodus*, the presence or absence of upper incisors, either functional or vestigial, is not known. It is quite evident, however, that in these Oligocene hypertragulids the upper incisors, when present are on the verge of being suppressed, so they cannot be considered as functional units in the dentition.

The upper canine is of medium size in *Archaeomeryx* as is the case in the more advanced *Hypertragulus*, but in both of these genera it is much smaller than in *Tragulus*. Therefore it seems logical to regard the large canines in the chevrotain as being due to a secondary enlargement, and not as basically primitive. The same probably is true of the primitive deer. The canine is internal cusp, seemingly a primitive character since this structure is well developed in the Uinta genus, *Leptotragalus*, but is reduced in *Hypertragus* and *Tragulus*. The fourth premolar is of the usual ruminant form, with an outer cusp and an inner crescent.

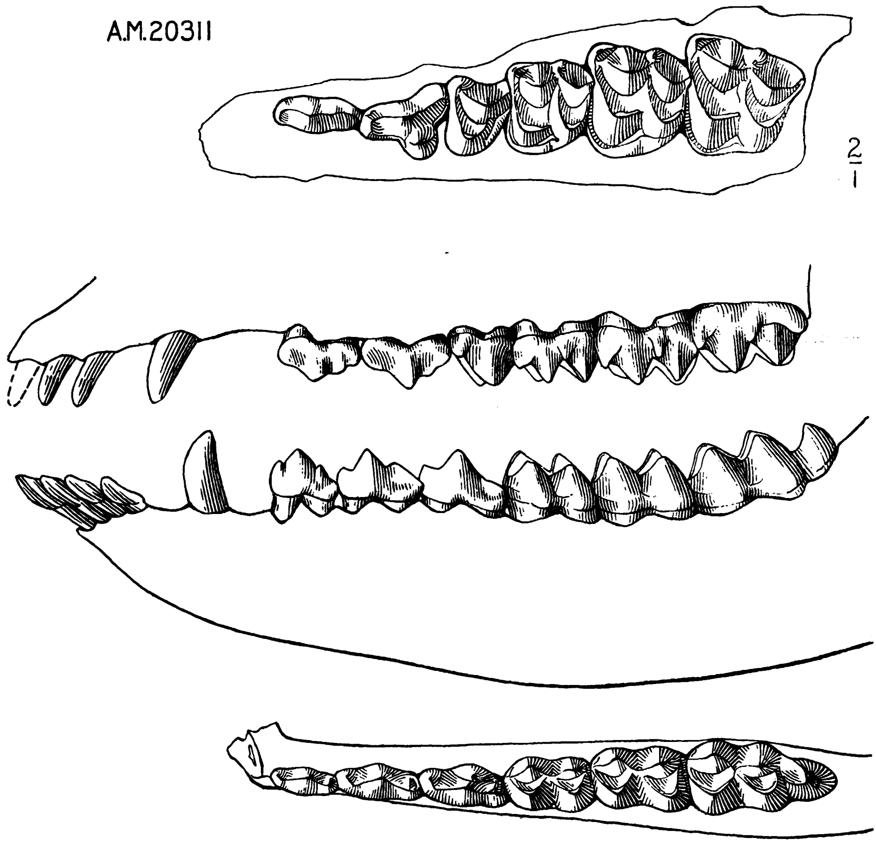

Fig. 2. *Archaeomeryx optatus* Matthew and Granger, Amer. Mus. No. 20311, type, upper and lower dentition. Revised from Matthew and Granger, 1925. Crown and external lateral views, twice natural size.

separated by a short diastema from the second premolar. Seemingly the first premolar had been lost in *Archaeomeryx*, in which respect, as in the case of the closed orbit, this genus is less primitive than the Oligocene *Hypertragulus*. The premolars on the whole closely resemble those of the New World hypertragulids. In the third member of the series there is a very large

The upper molars are quadricuspid as in the advanced ruminants, so that *Archaeomeryx* resembles *Hypertragulus* and *Tragulus*, and differs from *Amphimeryx* in which a protoconule is retained. It is unfortunate that our knowledge of *Amphimeryx* is not more complete, for the dentition suggests that this is probably a very primitive pecoran—probably more primitive than

Archaeomeryx if all the facts were known. On the other hand, the molars of *Archaeomeryx* are very brachyodont, as much as in any other ruminant, even *Amphimeryx*, and are distinguished by internal cingula and very heavy external styles—all of which suggest that in these respects, at least, *Archaeomeryx* is perhaps more primitive than *Amphimeryx*.

The lower incisors and the lower canine of *Archaeomeryx* show the usual ruminant character, being closely appressed and in series. These teeth are much more procumbent and more chisel-shaped than indicated in the type figure, resembling in this respect the same teeth in *Hypertragulus*. *Tragulus* is specialized beyond the condition just described in that the central incisor is much broadened, so that it is "shovel-shaped." The lower first premolar of *Archaeomeryx* is caniniform, and separated from the canine in front of it and the second premolar behind it by short diastemata. The presence of this caniniform tooth, a hypertragulid feature, is in distinct contrast to *Tragulus*, in which the first lower premolar is completely suppressed. As in the upper jaw, the last three premolars are clearly hypertragulid, especially P_4, in which there is a prominent cusp internal to the main cusp and a basined heel—structures duplicated in the P_4 of *Hypertragulus* but not to be seen in the more specialized, trenchant tragulid premolars.

The lower molars are quadricuspid and brachyodont, as might be expected. The heel of the third molar, as in the hypertragulids, is more primitive than it is in the tragulids in that its long axis is parallel to the long axis of the tooth, so that its rim is less crescentic than is the talonid of the modern tragulids.

The Axial Skeleton

The vertebral formula of *Archaeomeryx* is: cervicals—7, dorsals—13, lumbars—6, sacrals—2 or 4, caudals—numerous. The vertebral column is characterized by the large size of the individual elements composing it, the vertebrae, particularly the post-cervicals, being larger and heavier, and especially longer in comparison to the size of the animal, than is the case in the modern *Tragulus*, for instance. This means, of course, that *Archaeomeryx* had a relatively longer back than the recent tragulids, especially in the dorsal and lumbar regions, as might be expected in an earlier and a generally more primitive form. The difference is well illustrated by the ratio of the length of certain vertebrae to the molar series in *Archaeomeryx* and *Tragulus*.

	Archaeomeryx	*Tragulus*
Ratio, $\frac{\text{length of fourth cervical}^{1}}{\text{length of molar series}} \times 100$	63	63
Ratio, $\frac{\text{length of tenth dorsal}}{\text{length of molar series}} \times 100$	77	56
Ratio, $\frac{\text{length of fourth lumbar}}{\text{length of molar series}} \times 100$	109	87

[1] Length of centrum.

Even though the fossil and the recent forms show a similarity of size in the cervical vertebrae, the extinct form is the more primitive in that the articular surfaces of the centra are more nearly vertical than in the modern genus, and likewise the neural arch and zyapophyses are seemingly slightly less expanded.

In the sacrum of *Archaeomeryx* the vertebrae are separate, for the most part freely articulating elements, whereas in *Tragulus* these are firmly fused into one solid structure, the result of evolutionary development over a long period of time. It is interesting to see that in one sacrum of *Archaeomeryx* the second and third vertebrae are fused, although the other members of the series are free. The number of sacral vertebrae in *Archaeomeryx* is difficult to fix definitely, due in part at least to the varying definitions as to what constitutes a sacrum in the mammals. In most systematic works the Artiodactyla are said to have four or five sacral vertebrae, a statement based upon the condition found in modern artiodactyls, in which there has been a considerable amount of fusion within the sacral region. If the sacrum be defined upon strictly morphological grounds, then the sacrum of a great majority of the mammals must be limited to the two anterior vertebrae that are actually connected with the ilia. In *Archaeomeryx* the first two sacral vertebrae show a direct connection with the ilia, and may thus be regarded as the true sacrals. It is quite evident that the two vertebrae following the second true sacral and occasionally fused might be regarded as sacrals, in which case they would be numbers three and four of the series. This condition may be compared with that of *Leptomeryx* in which there are five fused vertebrae, of which only the first two attach to the ilia, and with that of *Tragulus* in which a somewhat similar condition prevails. In the recent genus, the sacrum is complicated by the excessive secondary ossification that has taken place in the lumbar and pelvic regions, whereby there has been built a bony bridge from the tuber ischii to the posterior "sacrals," thereby firmly connecting the back of the sacrum with the ischii. This ossification has involved the inclusion of another vertebrae in the sacrum, so that there are in a way six "sacrals."

The greatest vertebral difference between *Archaeomeryx* and *Tragulus* is in the caudal region, for in *Archaeomeryx* the tail was quite long, while in the modern *Tragulus* it is very short. According to Scott, there was a short, slender tail in *Hypertragulus*. Naturally, the individual caudal vertebrae of the Eocene genus are elongated and rather heavy elements.

No remarks of consequence can be made as to the ribs and sternum in *Archaeomeryx*.

The Appendicular Skeleton

The Fore-Limb

The scapula in *Archaeomeryx* is not well preserved, but from the various fragments available, this element would seem to show no particularly distinctive features.

The humerus, so far as can be determined, is very similar to the same element in *Hypertragulus* and in the recent *Tragulus*, both as to size and as to form.

The radius and ulna bear about the same proportional relationships, so far as length is concerned to the humerus as is the case with *Hypertragulus* and *Tragulus*. These two bones in *Archaeomeryx* are distinctive in not being coossified, thereby showing in this genus a more primitive stage of phylogenetic development than do most of the later and more advanced ruminants, including *Hypertragulus* and *Tragulus*. Also, the ulna shows a lesser degree of reduction of the shaft than does the same element in *Hypertragulus* and *Tragulus*, being in this respect similar to the ulna of *Leptomeryx*.

In the manus there are four digits, all separate. The lateral metacarpals are relatively heavy, in which respect they are rather closely comparable to the same elements of *Hypertragulus*. Indeed, so far as can be determined the entire manus of *Archaeomeryx* is rather closely comparable to the manus of *Hypertragulus*. It is not possible to determine for certain the number of toes in the manus, because of the crushed condition of the material, but it would seem that the pollux probably was suppressed, in which case the Mongolian genus would be more advanced than *Hypertragulus*, in which there are five digits in the fore-foot.

The Hind-Limb

The pelvis of *Archaeomeryx* is of the usual pecoran type; that is, it does not show the specializations seen in the pelvis of *Tragulus*, where in the males especially, there is a neomorphic structure in the form of a longitudinal bridge of bone on either side, connecting the fused sacral vertebrae with the dorsal portion of the ischium. In *Archaeomeryx* the pelvis is relatively strong and heavy, with flaring ilia, the inner surfaces of which articulate with the large first two sacral vertebrae. The pubes are long, being almost as long as the ischia, bounding ventrally on each side the elongated obturator foramen. The ischia are expanded posteriorly and on each is a prominent tuber ischii and ischiatic spine, evidently to serve in part for the attachment of strong biceps and semimembranosus muscles.

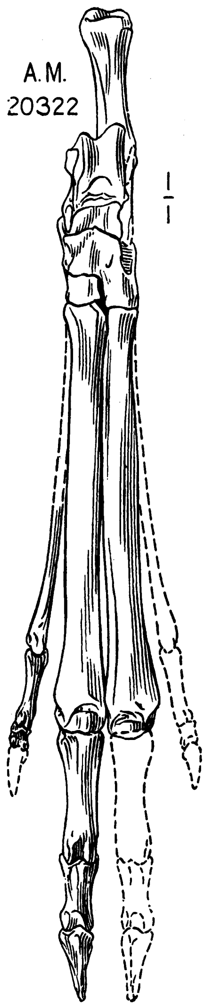

Fig. 3. *Archaeomeryx optatus* Matthew and Granger, Amer. Mus. No. 20322, left pes. Dorsal view, natural size.

The femur of *Archaeomeryx* is actually and relatively large, seemingly more so than in either *Hypertragulus* or *Tragulus*. This would indicate strong hind-quarters and an elevated lumbar and pelvic region—primitive ruminant characters that are retained in the modern *Tragulus*.

The tibia of *Archaeomeryx* is a heavy bone, proportionately heavier than the same bone in *Tragulus*. Its relative length as compared with the femur would seem to be about the same as in *Hypertragulus* and the chevrotain.

In the original description of *Archaeomeryx* Matthew and Granger mention proximal and distal vestiges of a fibula, but these do not appear in any of the material at hand. From the development of the fibular facets on the tibia, however, it would appear that such vestigial elements were present, and in all probability were not connected by a bony shaft.

The pes in *Archaeomeryx* is at once distinguished by the separate third and fourth metatarsals, a primitive condition that is relatively rare among other ruminants, but which is found in *Hypertragulus* and *Hypisodus*. The lateral digits are well developed, but comparatively smaller than the lateral digits in the fore-foot of the same animal, as is in keeping with the principle that the pes in hoofed mammals usually is more specialized than the manus. These lateral toes in *Archaeomeryx* are similar in development to those of *Hypertragulus*, and certainly somewhat larger proportionately than the same toes in *Tragulus*. In the Mongolian genus the cuboid and navicular are fused to form a single element, but the ectocuneiform is separate, a condition similar to that found in the hypertragulids, but more primitive than that characteristic of the Tragulidae and most of the more advanced ruminants, in which the ectocuneiform also is fused to the cuboid-navicular block.

The foregoing discussion may be summarized in outline form as shown below.

THE RELATIONSHIPS OF *Archaeomeryx*

Matthew and Granger placed *Archaeomeryx* in the Hypertragulidae, a position that was accepted by Scott by inference on page 507 of his great monograph of White River artiodactyls. "Except for one genus from the Eocene of Mongolia, the family is of exclusively North American distribution. . . ."[1]

In another part of this same work, however, Scott denies the hypertragulid affinities of *Archaeomeryx*, as follows: "By Matthew and Granger, who described and named the genus, *Archaeomeryx* is referred, I think improperly, to the Hypertragulidae,

[1] Scott, W. B., 1940. Trans. Amer. Philos. Soc., N.S., XXVIII, Pt. IV, p. 507.

	Hypertragulus	*Archaeomeryx*	*Tragulus*
Size	Small	Small	Small
Skull	Hornless	Hornless	Hornless
	Braincase rel. small	Like *Hypertragulus*	Braincase somewhat enlarged
	Sagittal crest	Sagittal crest	Reduced sagittal crest
	Orbit small	Orbit small	Orbit somewhat enlarged
Mandible	Comparatively heavy	Comparatively heavy	Lighter
Dentition	U. incisors vestig.	U. incisors functional	U. incisors suppressed
	U. canine small	U. canine small	U. canine enlarged
	Post-canine dias. short	Diastema short	Diastema elongated
	Cheek teeth brachyodont with large styles.....		Cheek teeth slightly taller, styles reduced
	Lower incisors of equal size..................		Central incisor broad
	Lower canine incisiform......................		Lower canine incisiform
	First lower premolar caniniform..............		P_1 suppressed
	P_4 with internal cusp and post. basin..........		P_4 compressed, trenchant
Axial Skeleton	Back comparatively long, esp. lumbars........		Back shortened
		Four sacrals..........	Five sacrals, fused
		Tail very long........	Tail short
Appendicular Skeleton	Radius-ulna fused	Radius-ulna distinct	Radius-ulna distinct
	Metacarpals distinct	Metacarpals distinct	Mc. III–IV fused
	Five toes in manus	Four toes in manus	Four toes in manus
	Fibula complete		Fibula reduced
	Cuboid-navicular fused	Cuboid-navicular fused	Cuboid-navicular-ectocuneiform fused
	Metatarsals distinct	Metatarsals distinct	Mt. III–IV fused

the only supposed member of that family which has, hitherto, been found outside of North America."[1]

Matthew and Granger were fully justified in assigning *Archaeomeryx* to the Hypertragulidae, as is evident upon the basis of the osteological characters presented in the original description of the genus or in the preceding pages of this present work. In order to summarize and clarify its hypertragulid relationships, a brief discussion regarding this question will be presented at this place.

In its general size, *Archaeomeryx* is close to the characteristic hypertragulid genus, *Hypertragulus*, as has been noted by various authors. As in the hypertragulids, and the true tragulids for that matter, it is characterized by the raised hind-quarters, due to the relative great length of hind-limb elements as compared with those of the fore-limb. The dentition is typically hypertragulid, except for the fact that the upper incisors are fully developed. But the fact that these teeth may be present, though reduced, in some of the hypertragulids shows that there was some variability regarding this character within the family, dependent upon the stage of evolutionary development attained by particular genera. The caniniform lower first premolar in *Archaeomeryx* is a very characteristic hypertragulid character.

The general form of the skull of *Archaeomeryx*, is so far as can be determined quite similar to that in the hypertragulids such as *Hypertragulus*—a low, primitive skull with a centrally located orbit. The feet, too, are very similar in the genera being compared. As in *Hypertragulus*, the manus in *Archaeomeryx* has four separate digits (a small fifth toe persists in the American form) the lateral ones of which are of considerable size. In the pes the lateral toes are proportionately smaller, but the central metatarsals remain separate. The cuboid and navicular are in both genera fused into a single bone.

Archaeomeryx is possibly distinguished from *Hypertragulus* by its very long tail, but this is a point of difference of no great

[1] Scott, W. B., 1940. Idem, p. 603.

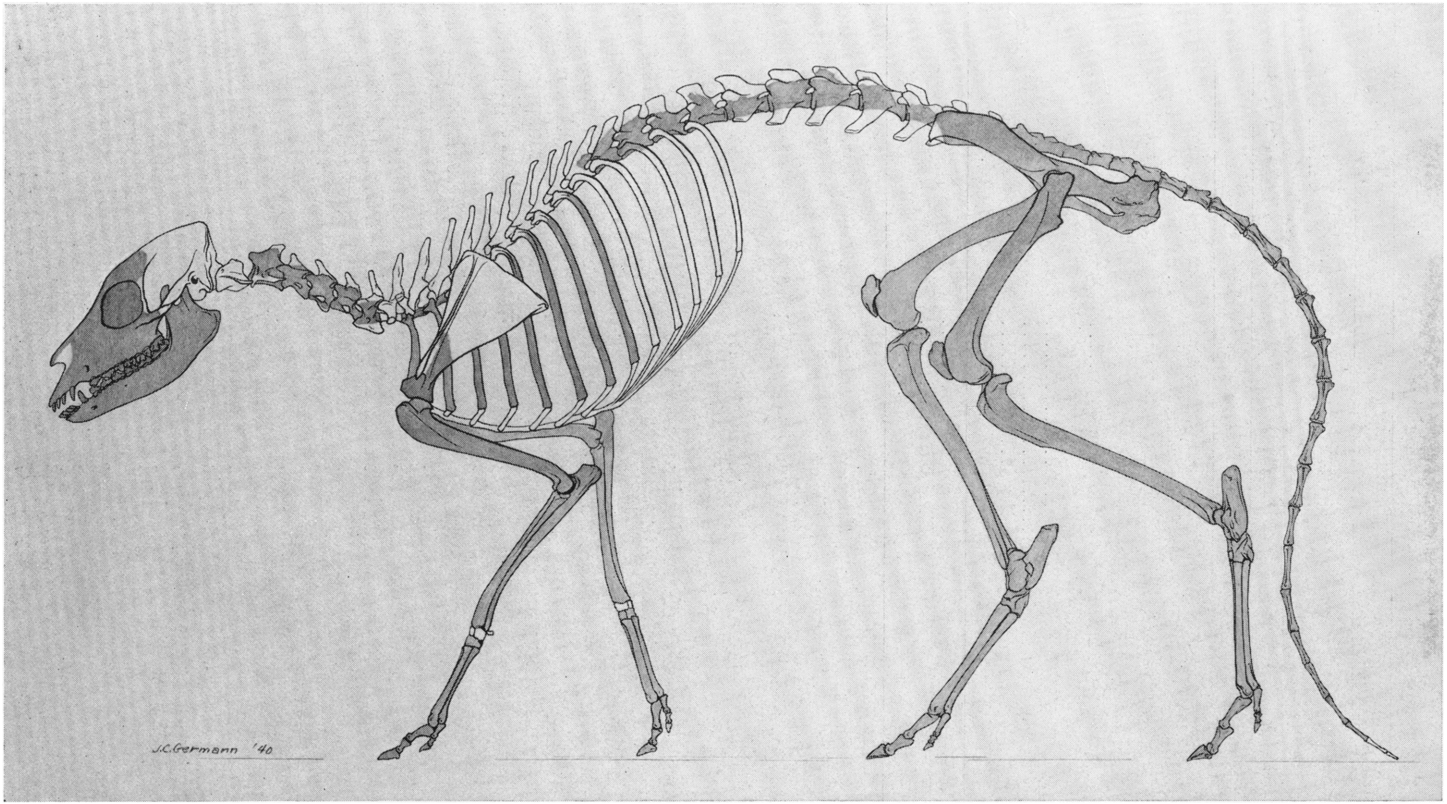

Fig. 4. *Archaeomeryx optatus* Matthew and Granger, restoration of skeleton based upon various specimens in the American Museum, as follows: Skull and jaw from Nos. 20321, 20322; teeth from Nos. 20311, 20322 and other specimens; cervical vertebrae and scapula from No. 20320; dorsal and lumbar vertebrae, sacrum and pelvis, limbs and feet from Nos. 20320, 20321, 20322; caudal vertebrae from various numbers. Lateral view, one-third natural size.

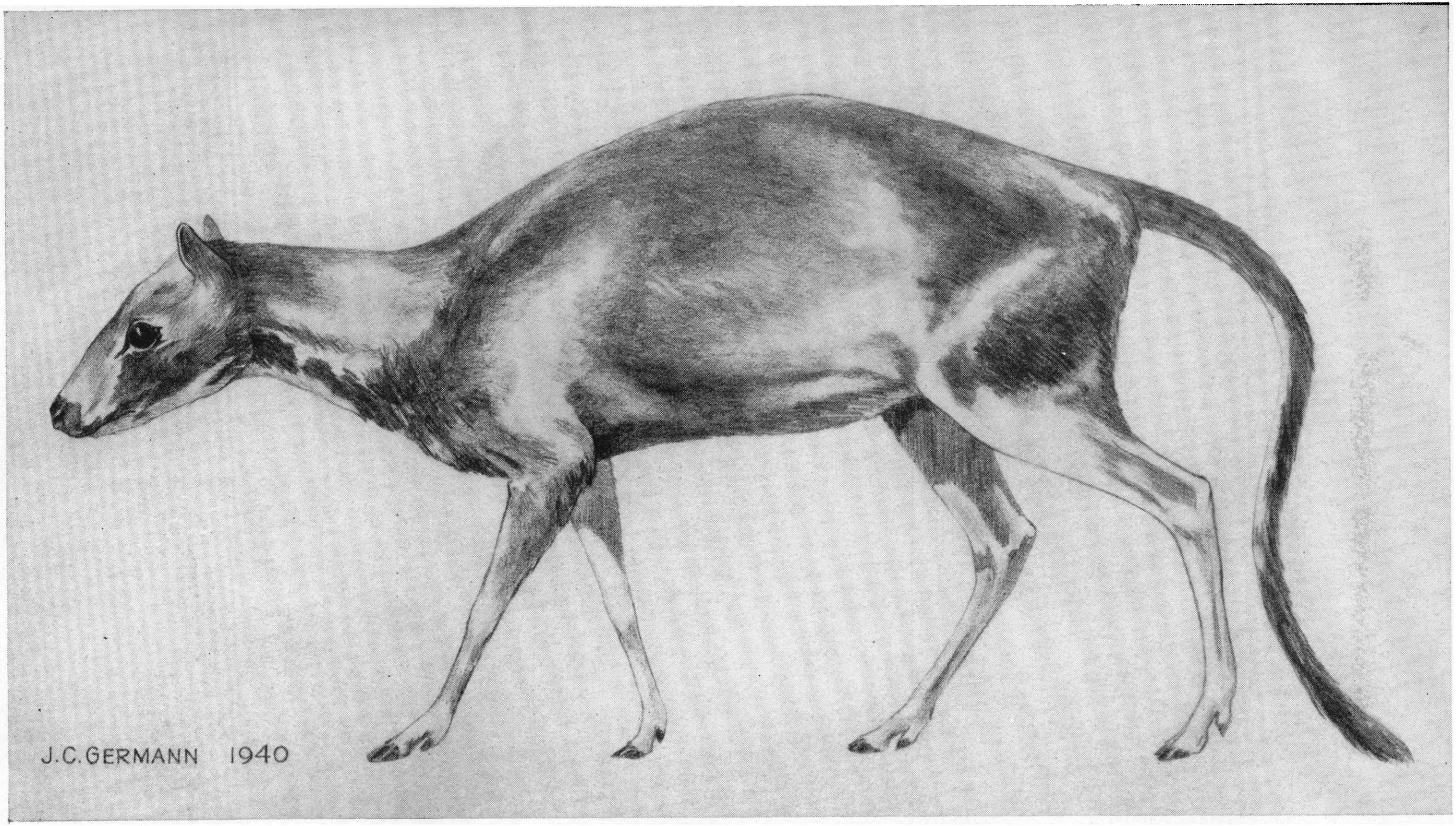

Fig. 5. *Archaeomeryx optatus* Matthew and Granger. Restoration of animal in the flesh. Based upon the restored skeleton as shown in figure 3, and upon analogies with the modern *Tragulus*. Lateral view, one-third natural size.

importance, and certainly cannot be used for excluding the Mongolian genus from the family Hypertragulidae. Unfortunately, there seems to be no very definite information as to the length of the tail in *Hypertragulus*. In *Leptomeryx* the tail evidently was rather short, as might be expected in a form of its general evolutionary stage of advancement.

Consequently, there are numerous arguments favoring the inclusion of *Archaeomeryx* within the Hypertragulidae, and none of importance that would exclude it from this family. As for its general habitus, the Mongolian genus is seemingly rather close to *Hypertragulus*. It is more primitive in the large upper incisors, the separate radius and ulna, and probably in the very long tail. It is less primitive in certain skull characters, such as the closed orbit, as compared with the open orbit in *Hypertragulus*, and in the general structure of the manus.

Table of Measurements, Ratios and Indices

	(1) *Hypertragulus calcaratus* P.U. 14543	(2) *Archaeomeryx optatus* A.M. 20322	(3) *Tragulus javanicus* A.M. 14128
Skull, length, pmx-cond.	85	90e	91
Skull, preorbital length	(41)	37e	40
Skull, postorbital length	(43)	52e	51
Skull, width postorb. constr.	22	..	29
Skull, occiput-basal width	26	..	30
Skull, vert. dia. orbit	(14)	16.5	29
Mandible, length	75	70	74
Mandible, depth at P_2	10.5	9	7.5
Mandible, depth at M_3	14	11	11
Mandible, height of condyle	27	26	28
I^1, ant.-post. dia.	..	..	..
I^2 ant.-post. dia.	..	1.1[1]	..
I^3 ant.-post. dia.	..	1.3	..
C ant.-post. dia.	3	2.2	4
P^1 ant.-post. dia.	4	..	..
P^2 ant.-post. dia. × trans. dia.	3	5.9 × 2.9	6 × 2.8
P^3 ant.-post. dia. × trans. dia.	5	6.3 × 3.5	5.5 × 3.9
P^4 ant.-post. dia. × trans. dia.	4	4.5 × 5.1	4.4 × 4.8
M^1 ant.-post. dia. × trans. dia.	5	5.0 × 6.0	4.4 × 5.5
M^2 ant.-post. dia. × trans. dia.	5	5.5 × 7.0	5.6 × 6.3
M^3 ant.-post. dia. × trans. dia.	7	6.0 × 7.1	6.4 × 6.5
M^2—height	4	4.0	4.0
I_1 trans. dia.		2.0	3.8

[1] Upper teeth and lower I-c from A.M. 20321.

	(1) *Hypertragulus*	(2) *Archaeomeryx*	(3) *Tragulus*
I_2 trans. dia.	..	1.8	0.9
I_3 trans. dia.	..	1.8	0.8
C ant.-post. dia.	..	2.1	1.7
P_1 ant.-post dia.	2	2.3	..
P_2 ant.-post dia. × trans. dia.	3	5	5.8 × 2.0
P_3 ant.-post dia. × trans. dia.	3	6.2	6.0 × 2.3
P_4 ant.-post dia. × trans. dia.	4	5.6	5.4 × 2.6
M_1 ant.-post dia. × trans. dia.	(5 × 3.5	5.8	4.9 × 3.4
M_2 ant.-post dia. × trans. dia.	6 × 4.5	6.1	6.1 × 4.2
M_3 ant.-post dia. × trans. dia.	9 × 5)[1]	10.0	8.8 × 4.1
M_2 height	..	..	4.5
Upper premolar series, length[2]	12	16.5	16.0
Upper molar series, length	17	18	16.8
Lower premolar series, length[3]	13.5	19	16.7
Lower molar series, length	19.5	22.5	19.8

[1] From A.M. 1341.
[2] Not incl. P^1.
[3] Not incl. P_1.

	(1) *Hypertragulus* (P.U. 14540)	(2) *Archaeomeryx*	(3) *Tragulus*
Length of cervical vertebrae	..	69e	66
Length of dorsal vertebrae	..	150e	113
Length of lumbar vertebrae	..	108	82
Length of sacral vertebrae	..	35	36[1]
Length of caudal vertebrae (approx.)	..	304e	50+
Scapula, height	54	60e	54
Humerus, art. length	68	72	65
Radius, art. length	58	65	58
Manus, extended length	54	76e	68
Metacarpal II, length	24	29[2]	36
Metacarpal III, length	29	35e	40
Metacarpal IV, length	26	35	39
Metacarpal V, length	22	..	35
Pelvis, length	97	96	90
Femur, art. length	80	90	80
Tibia, art. length	95	101	90
Pes, extended art. length	97	113	105
Metatarsal II, length	39	45	54
Metatarsal III, length	45	54e	58.5
Metatarsal IV, length	44	55	59
Metatarsal V, length	39	..	54

[1] Sacrum = 1st four fused vertebrae, i.e., True sacrals S1, S2 + Pseudo-sacrals S3, S4.
[2] From 20321.

	(1) *Hypertragulus*	(2) *Archaeomeryx*	(3) *Tragulus*
Ratio preorb. length/postorb. length	95	71	80
Ratio dia. orbit/length skull	16.5	18	32
Ratio U. premolar length/U. molar length	71	92	95
Ratio L. premolar length/L. molar length	70	84	85
Ratio cervical length/dorso-lumbar length	..	27	34
Ratio caudal length/dorso-lumbar length	..	118	(< 100)
Ratio humerus/radius	117	111	114
Ratio humerus/radius + manus	60	51	52
Ratio femur/tibia	84	89	89
Ratio femur/tibia + pes	42	42	41
Ratio metac. II/metac. III	83	83	90
Ratio metat. II/metat. III	87	83	92
Ratio manus/pes	56	67	65

An analysis of the ratios, based upon certain measurements of *Archaeomeryx, Hypertragulus* and *Tragulus,* may help to indicate to some extent the developmental trends in these three mammals. Thus the ratio of the preorbital to the postorbital length shows that the eye was most nearly centrally located in *Hypertragulus*—least so in *Archaeomeryx* (although in this latter genus the ratio is undoubtedly not very accurate because of the restoration necessary to bring the skull to a normal, uncrushed state). If a centrally located orbit is indicative of a primitive condition in the unspecialized ruminants, then *Hypertragulus* seemingly is least advanced in this respect. The orbit as shown by the ratios is proportionately small in both *Hypertragulus* and *Archaeomeryx,* which may mean that its much greater size in *Tragulus* is the result of a specialization taking place over a long period of geologic time.

Hypertragulus is distinguished from *Archaeomeryx* and *Tragulus* by the comparative shortness of both its upper and lower premolar series (not counting the first premolar) as compared with the molar series, the last two genera being close to each other with respect to this feature.

In the comparison of the ratios of limb elements, it may be seen that *Hypertragulus* is more primitive than the other two genera by reason of its relatively longer humerus, as compared with the lower fore-leg. But with regard to the length of the femur as compared with the lower portion of the hind-leg, all three genera are closely comparable.

Hypertragulus and *Archaeomeryx* resemble each other in a comparison of lateral toes with median toes, and curiously enough in both of these genera the lateral toes have undergone more relative reduction than have the same elements in the modern tragulid.

Finally, *Hypertragulus* may be distinguished from the other two genera by the shortness of its manus, as compared with its pes. In this respect, *Archaeomeryx* and *Tragulus* are rather closely comparable.

From this, it would seem that *Hypertragulus* is primitive in various skeletal proportions as compared either with *Archaeomeryx* or *Tragulus*—a conclusion that is borne out to some extent by the expression of certain qualitative characters, such as the presence of a pollex, the open orbit and the like. *Archaeomeryx* seems to show a mixture of quantitative characters, in some respects being like the more primitive *Hypertragulus,* in others like the more advanced *Tragulus,* yet as has been shown in preceding pages, the Mongolian form is especially primitive with regard to various qualitative characters, particularly the presence of three functional upper incisors, an inner cusp on the third upper premolar and a complete lack of fusion of the median metatarsals. Consequently its position must be determined only after a careful survey and a balancing of all of the characters considered in their relationship to each other.

GENERAL DISCUSSION

The Classification and Phylogeny of the Ruminants

Matthew and Granger said that *Archaeomeryx* is of particular interest because "it appears to be an approximate ancestral type for the pecora," a statement based upon a careful consideration of the anatomical features of this Eocene genus, which have been outlined in the preceding paragraphs of this paper. In order that the position of the genus may be more thoroughly understood, it may be well at this place to review the taxonomic affinities of the various families of the "ruminants" thereby establishing a background that will be useful in an interpretation of the osteological study of *Archaeomeryx.*

Various authors have classified the artiodactyls, at best an extremely difficult task, with the result that the so-called ruminants have been accorded a variety of arrangements, some of which will be considered below. Perhaps a comparison of the several most important classifications of the ruminating artiodactyls (and their closely related forms) may be best presented by a

Scott 1940	Schlosser 1887	Zittel and Schlosser 1925	Osborn 1910	Stehlin 1910	Matthew 1929
		Bunoselenodontia			Ancodonta
	Anoplotheriidae	Anoplotheriidae		Anoplotheridae (sic)	Anoplotheriidae
	Anthracotheriidae	Anthracotheriidae		Anthracotheridae (sic)	Anthracotheriidae
		Dichobunidae			
Ruminantia		Selenodontia			
Tylopoda		Xiphodontidae			
		Caenotheriidae			Caenotheriidae
Oreodontoidea	Oreodontidae	Agriochoeridae	Oreodonta	Oreodontidae	Oreodontidae
Merycoidodontidae			Oreodontidae		
Agriochoeridae					
				Amphimerycidae	
				Ruminantia	
Cameloidea	Tylopoda	Camelidae	Tylopoda	Camelidae	Tylopoda
					Xiphodontidae
Camelidae			Camelidae		Camelidae
Hypertraguloidea	Dichobuniden		Tragulina		
Hypertragulidae	Caenotheriidae		Gelocidae		Pecora
Protoceratidae	Xiphodontidae	Hypertragulidae	Hypertragulidae	Hypertragulidae	Amphimerycidae
Tragulina	Tragulidae	Tragulidae	Tragulidae	Tragulidae	Tragulidae
					(+ Hypertragulidae)
Pecora	Gelocidae	Cervicornia	Pecora	Pecora	Cervidae
	(incl. Cervidae, Anti-	Antilocapridae	Giraffidae		Giraffidae
	lopidae, Bovidae,	Cavicornia	Cervidae		(+ Palaeomerycidae)
	Ovidae)		Merycodontidae		Antilocapridae
			Antilocapridae		Bovidae
			Bovidae		

chart. In this manner a comprehensive view of the essential points of the contrasting schemes of arrangement may be had in a convenient form.

Comparing and synthesizing these various classifications, it becomes apparent that there are two general schemes represented. In the first place, there is the classification of Scott, resting in part upon the tentative and partially expressed ideas of Rütimeyer. According to this idea, most of the North American "ruminants" of Tertiary times represent adaptive radiants of a great suborder Tylopoda. These are constituted in three general groups, the hypertragulids and their relatives, the camelids and the oreodonts. The ruminants having their origin in the Old World are the true tragulines, Tragulina, and the modernized types of the deer, giraffes and bovids, contained within the group Pecora.

As opposed to this, there is the classification formulated by Schlosser and elaborated by Osborn, Matthew and others, according to which the oreodonts are made a separate group, possibly of camelid, possibly of anthracothere relationships, while the group Tylopoda includes only the camelids and their immediate relatives. According to this scheme the hypertragulids are grouped with the "Old World ruminants"—the tragulids, deer, giraffids and bovids.

Scott's classification is based to a great extent upon his acquaintance with the important Uinta fauna, in which there is a large assemblage of primitive artiodactyls. This author has noted how, in tracing back the histories of the indigenous North American "ruminants," the hypertragulids, camelids and oreodonts, a distinct drawing together of these separate lines is seen in their upper Eocene representatives, intimating that at some period not so very much before the beginning of Upper Eocene times there was a common ancestor for all of the various branches of ruminant evolution. Therefore, upon the resemblances each to the other of the upper Eocene representatives of the several supposedly autochthonous Nearctic ruminant groups, Scott regarded them as belonging properly to a single suborder of the Artiodactyla, the Tylopoda.

The opposing scheme, on the other hand, is based upon the differences shown by the characteristic and somewhat more advanced members of the various ruminant groups, rather than upon the resemblances between their ancestral forms. Moreover, this classification is based entirely upon anatomical considerations, and does not take into account the distribution of the ancestral forms—seemingly an important criterion in Scott's arrangement.

There are advantages and difficulties in either of these two general taxonomic schemes, and the validity of either is dependent to a considerable extent upon the individual's philosophy as to the proper criteria of relationships in evolving mammals. Following the various ruminant groups back in geologic time we can see them converging toward each other as we approach the Eocene—as would, of course, be expected among a group of mammals having a common ancestor. In the Upper Eocene, especially in the Uinta fauna of North America, it is possible to see the close approach of many of the ruminant groups to each other, although even in the Upper Eocene ruminants, connected as they are by their resemblances, there already have been established the important diagnostic characters that mark them as members of the several families, of which they are the virtual progenitors.

What then are to be the criteria for a classification of the ruminants? Are certain families to be brought together because of the resemblances of their primitive Eocene representatives, or are they to be separated because of the differences of their post-Eocene, and one might say more characteristic genera? Does the evidence of the ancestral forms justify us in including the indigenous New World ruminants in one suborder, the Tylopoda? Is there to be a complete separation of the New World hypertragulids from the Old World tragulids? Perhaps it may help in this discussion to compare the diagnostic osteological characters of some of the fossil and recent ruminants.

In an evaluation of ruminant characters, it soon becomes evident that certain features are of particular value in comparing the families throughout the range of ruminant evolution, while other characters may prove to be of little use for this purpose. For instance, although antlers and horns are found only in the pecorans above the tragulids, their presence is not significant in separating the higher ruminants from the more primitive ones because they are of a secondary, sexual nature, and thereby subject to sexual dimorphism within a single species. A similar illustration of this is to be found in the development of the auditory bullae, which at first sight would appear to be useful for establishing family relationships, because in most of the primitive ruminants the bullae are hollow, while in many of the more specialized types they often show an interior cancellous structure. Yet in one family, the Tragulidae, both hollow and cancellous bullae are found, in forms that certainly must be very closely related to each other. (In "*Meminna*," perhaps the most primitive of the surviving tragulids, the bullae are hollow, while in *Tragulus*, and in the African *Hyaemoschus* as well, the bullae are cancellous.)

To further complicate this question is the fact that the "ruminant" artiodactyls (including those fossil forms which by a broad interpretation of the term may be included within this divison) show various characters or combinations of characters which connect them in different ways to each other. This is important, because it illustrates the inadvisability of relying too heavily upon a few characters, or upon restricted anatomical regions, such as the dentition alone or the feet alone, in attempting to determine relationships within the artiodactyl group. This fact was realized by Matthew, in 1929, who commented upon it as follows: "Study of the skeletons of the better known and later Artiodactyla shows that the characters of the front teeth and of the feet are quite as distinctive and important in determining the relationships as are those of the molars. The resemblances and differences in the foot characters appear to be quite as fundamental as those in the teeth and should be fully considered in working out the natural affinities. It appears to be necessary to evaluate the relationships first of those genera which are known from complete material and then to associate the imperfectly known genera as best we can."[1]

Therefore certain characters have been chosen for use in comparing the various families of ruminants, on the basis of their constancy within a family or within a series of families. These characters may be grouped into three large divisions (in no case is reliance placed completely on single characters), namely, those typical of the ancodont ruminants, those characteristic of the tylopodan ruminants and those developed in the pecoran ruminants.

In the ancodonts, as typified by the anthracotheres, there is a complete dentition, with the upper incisors well developed. The canines are of the generalized mammalian type and the anterior premolars are normal. The cheek teeth are selenodont and not elongated, while in all but the most advanced types the molars retain a protoconule. The feet are short and functionally four-toed, with a complete separation of all the elements. The tail is generally long.

In the tylopodans, as typified by the camels, the dentition may be complete or somewhat reduced; the reduction occurs in the upper incisors and the anterior premolars, but there is never a complete loss of the upper incisors. In the specialized types the lower canine becomes incisiform, while certain anterior premolars tend to become somewhat caniniform. The cheek teeth are selenodont and at a very early stage show a marked tendency toward elongation, with a correlative flattening of their ectolophs or buccal surfaces. The protoconule is characteristically absent. The feet are elongated, very much so in the later types, and they are precociously didactyl, with a fusion of the metapodials to form a "cannon-bone." Curiously enough, the cuboid and navicular remain separate. The tail is short.

In the pecorans, as typified by the deer, giraffes, antelopes and the like, the dentition is always reduced by the suppression of the upper incisors, and usually the first upper and lower premolar. The lower ca-

[1] Matthew, W. D., 1929. Bull. Geol. Soc. Amer., XL, p. 406.

nine is always incisiform. The selenodont cheek teeth are not elongated and are always quadricuspid in the molars. The feet, moderately short in the more primitive types and elongated in the more advanced forms, are quadridactyl but functionally didactyl—since the lateral toes are always much reduced and of little use in locomotion. The median metapodials are fused, as are the cuboid and navicular in the pes. The tail is short.

The question concerning us at this place is how the "intermediate" groups may be fitted into the picture as presented above. It will be remembered that Professor Scott placed the oreodonts and hypertragulids in the Tylopoda, together with the true camels, because of their caniniform first lower premolars and their supposed American community of origin. Most authors have been inclined to place the oreodonts with the anthracotheres in the Ancodonta, and to link the hypertragulids more or less closely with the tragulids, which latter group is either within or closely allied to the Pecora.

The oreodonts are ancodont-like in that they never show a suppression of the upper incisors. In this respect they differ somewhat from the camels, for in the more advanced of these latter animals there is usually a suppression of certain upper incisors, although the process is never carried to completion. The upper canine in the oreodonts is large and characteristically caniniform, and as in most of the other ruminants the lower canine is incisiform and in series with the incisors. But the oreodonts are typified particularly by the enlarged caniniform first lower premolar which functions with the enlarged upper canine, a character that is found somewhat similarly developed in the hypertragulids, and to a lesser degree, in the camelids. On the other hand, the oreodonts are generally ancodont-like in the form of their cheek teeth, a point of some significance, particularly so in the case of the agriochoeres. There may be a protoconule in the more primitive types, but it is generally lost (except in the agriochoeres) in the more advanced forms. The feet in the oreodonts are quadridactyl, actually and functionally, with separate elements as in the ancodonts. The tail may be long or short.

Turning now to the hypertragulids, we see that these animals are on the whole pecoran-like as to the dental formula. In some of the primitive types, specifically *Archaeomeryx*, the upper incisors may be present, but generally these teeth are reduced to vestiges or completely suppressed. The lower canine is incisiform, while the first lower premolar is always caniniform, occluding with the upper canine when this latter tooth is of any appreciable size. This single character sets the hypertragulids apart in a very definite manner from the Old World tragulids. On the other hand, the hypertragulids are pecoran-like in the loss of the first upper premolar and in the development of the molars, which are quadricuspid, and short, and very similar in their general form and development to the same teeth in the tragulids and other primitive pecorans. The feet in the hypertragulids are also strongly pecoran, being quadridactyl but functionally didactyl, with the lateral toes reduced. In the hypertragulids, in decided contrast to the Pecora, the primitive condition of separate median metapodials holds, except in the most advanced forms. Like the pecorans, there is a fusion of the cuboid and navicular. The tail is long in the primitive types, such as *Archaeomeryx*, but shortened in the more specialized forms.

Whether or not the Old World tragulids are placed within the pecoran group or are separated as a distinct suborder is a matter of individual choice that does not affect the problem now under consideration. Within the categories as delineated above, the tragulids may be considered as primitive but characteristic pecorans, since they show the various features cited as typical of the Pecora. It is only when consideration is taken of more detailed features with which we are not primarily concerned, that the tragulids may be separated from the pecorans.

In conclusion, then, it may be said that a preponderance of oreodont characters link these animals with the typical ancodonts, while a preponderance of hypertragulid characters link these animals with the pecorans. The one character that links the oreodonts and hypertragulids with the camelids, as advocated by Professor Scott, is the caniniform first lower premolar. Should this character be accorded more weight than the other dental characters, plus the characters of the feet, plus the general habitus of the skeleton?

Turning now to the question of the Upper Eocene ruminants, particularly those from the Uinta formation of North America, we are confronted by the question as to whether they are more like each other than they are like the groups to which they were supposedly ancestral. This problem involves especially the genera *Leptotragulus*, *Protoreodon*, *Protagriochoerus* and *Protylopus*.

Leptotragulus certainly foreshadows very strongly the typical hypertragulids of the Oligocene. It is small, comparable to *Hypertragulus* in size, and in most respects its dentition is typically hypertragulid. Thus the upper molars are quadricuspid, brachyodont, with sharp crescents and large external styles. Indeed, the patterns of the cheek teeth, both in the upper and lower jaws, are strikingly similar in *Leptotragulus* and the hypertragulids. There is a strong internal cingulum. The lower canine would seem to be incisiform, while the lower first premolar, although still retaining two roots, is trending toward a caniniform shape. Even in this early form the diastemata between the cheek teeth and the anterior teeth, so characteristic of the hypertragulids, are present.

This genus is certainly different from *Protoreodon* and *Protagriochoerus*, which show distinct affinites with the Oligocene oreodonts and agriochoeres, respectively. Thus, in these genera, the upper molars show curved selenes diverging externally from the somewhat lingually placed protocone and paracone (especially in *Protagriochoerus*), as is characteristic of the "Oreodonta." The protoconule is still present, a character that is carried over into the later agriochoeres and some of the oreodonts. The lower canine is completely incisiform, while the lower first premolar is caniniform and considerably enlarged, as in the oreodonts. Moreover, in *Protoreodon* there are no diastemata between the teeth, another character that very strongly links it with the typical oreodonts, while in addition the shape of the mandible, with its considerably increased depth, is oreodont-like. The feet in *Protoreodon* are short and functionally quadridactyl, an oreodont character.

Protylopus, although showing the numerous primitive characters that might be expected in an Eocene ruminant, nevertheless displays its camelid affinites in a very certain fashion. The skull is long and low, both skull and dentition showing, even at this early stage, the lengthening so typical of the camels. Although the parastyle and mesostyle in the upper molars are still prominent, the ectoloph already shows a considerable amount of flattening, a trend of development continued in an ever-increasing degree in the later camels. Moreover, in this genus the anterior premolars above and below are much compressed from side to side, as in the later camels. The canine is tending to be incisiform, but the first lower premolar, though small, is not truly caniniform. Rather it is elongated and somewhat spatulate, a condition approaching that found in *Poëbrotherium*. In the occipital region there is a close appression of the paroccipital process and the bulla, quite as in the later camelids. Finally, the feet of *Protylopus* are strongly didactyl, with the side toes approaching closely the almost complete state of reduction that is found in the later camelids.

Therefore, on the basis of their important characters, it may be said with confidence that *Protoreodon* is an ancestral oreodont, *Protagriochoerus* an ancestral agriochoere, *Protylopus* an ancestral camel and *Leptotragulus* an ancestral hypertragulid. Moreover, the oreodont, camelid and hypertragulid characters of these Uinta genera are so strongly marked that one may be justified in saying that by Upper Eocene times the trends of ruminant evolution were established to such a point that the genera of this age were diverging away from each other towards the habitus of their various descendants in a most decided fashion. In other words, although the primitive heritage characters are still present in the Upper Eocene ruminants, it is

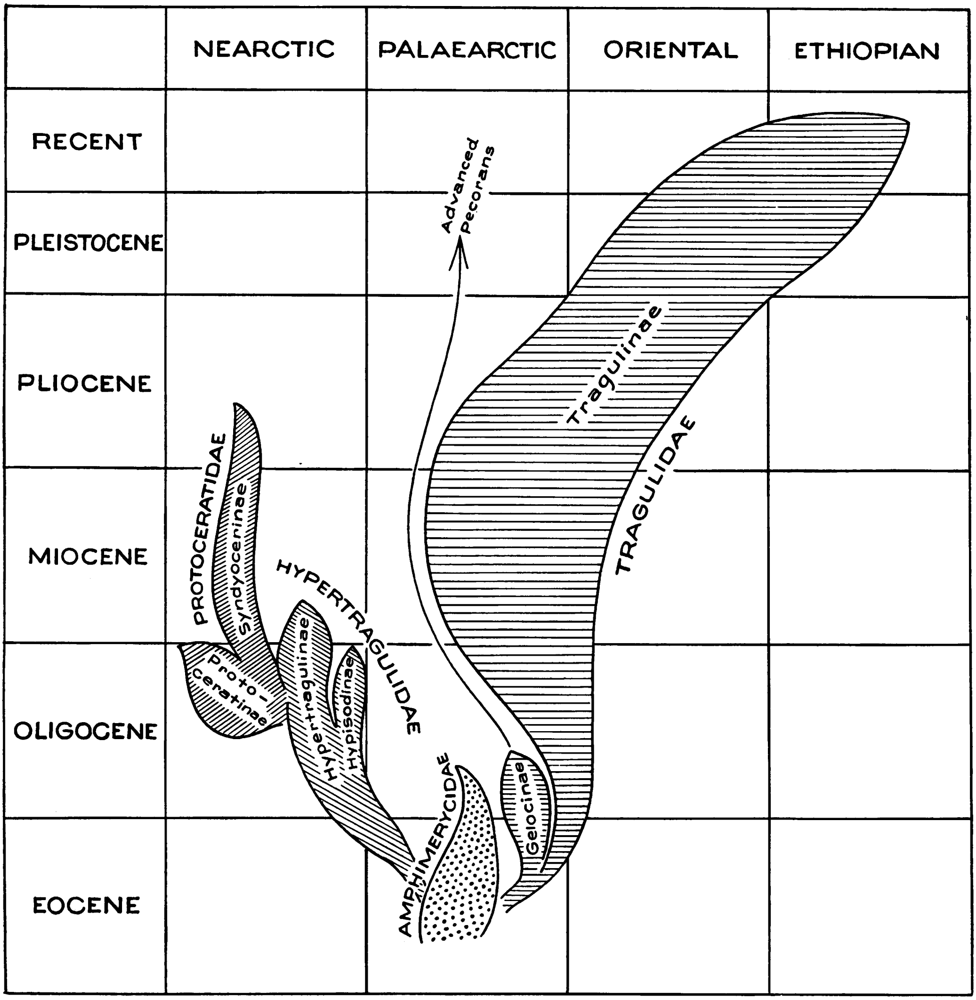

Fig. 6. Phylogeny of the primitive ruminants.

the beginning of their specialized habitus characters that make them distinctive as genera.

If this is the case, if the bulk of characters in the skull, teeth, feet and body point to the distinctness of the Upper Eocene genera constituting the oreodonts, camelids, hypertragulids and other ruminant families of that day, what is the value to be placed upon the caniniform first lower premolar, which has been used as a character pointing to the close relationship of the first three groups named?

A caniniform first lower premolar, in a greater or lesser degree, is not at all uncommon among the early Artiodactyla, as an examination of Eocene genera will show, and there is reason to think that such a structure might have been independently developed in various families belonging to this order. It is most highly developed in the Hypertragulidae and the oreodonts, as Scott maintained, while its expression in the camelids is considerably less pronounced than is the case in the two other families cited. But it is also found in certain primitive bunodont artiodactyls of dichobunid relationships, notably in the

European forms *Cebochoerus* and *Choeropotamus*, and perhaps in the Mongolian genus *Gobiohyus*—although in this latter animal the tooth in question is not so much caniniform as it is small, and single rooted. A similar small, single rooted P_1 was present in some of the American dichobunids, such as *Lophiohyus* and *Diacodexus*.

But to consider only those forms in which the first lower premolar actually functions as a canine in opposition to the upper canine, it is at once evident that the tooth has been derived independently in the European dichobunids as compared with the American Hypertragulids and oreodonts. For in the European forms it is generally doubly rooted, with an elongated base, as compared with the rounded, single-rooted tooth so characteristic of the oreodonts and hypertragulids. The caniniform P_1 in the oreodonts is of quite different form from that in the hypertragulids and this difference extends to the Eocene genera, *Protoreodon* on the one hand and *Leptotragulus* and *Archaeomeryx* on the other. In the hypertragulids the caniniform P_1 is invariably rounded in cross-section, sharply pointed and erect. In the oreodonts it is laterally compressed, with a strong ridge on the front and on the back surface, and it is generally rather procumbent. Whether these differences are to be regarded as divergences from a single origin, or as expressions of two independent origins is a question that in itself cannot be solved. But taking into account the numerous ancodont-like characters in the skull, dentition and skeleton of the oreodonts, and the numerous pecoran-like characters in the skull, dentition and skeleton of the hypertragulids, there is more than a faint reason to suspect the caniniform P_1 as being due to an independent origin in the two groups.

If the resemblances and differences discussed in the foregoing paragraphs are significant, then the hypertragulids may be regarded as an essentially New World branch of primitive ruminants, closely related to but somewhat divergent from the Old World Tragulidae. Indeed, the discovery of *Archaeomeryx* in Mongolia would seem to point to the probability of an eastern Palaearctic origin for the Hypertragulidae, perhaps in common with that for the Tragulidae. The Hypertragulidae may be a New World development of the ancestral pecoran stock, just as the Tragulidae are the Old World expression of this same stock. Having separated, the Hypertragulidae gave rise to the aberrantly specialized Protoceratidae, both families becoming extinct, while the Tragulidae were ancestral to the deer, giraffids and bovids, all of which groups proved to be extraordinarily successful.

With the above considerations in mind, the tragulines might be placed among the ruminants and related artiodactyls somewhat in the following manner.

Order Artiodactyla
- Suborder Ancodonta
  - Superfamily Anthracotherioidea
  - Oreodontoidea
- Suborder Tylopoda
  - Superfamily Cameloidea
    - Family Xiphodontidae
    - Camelidae
- Suborder Tragulina
  - Superfamily Amphimerycoidea
    - Family Amphimerycidae
  - Superfamily Hypertraguloidea
    - Family Hypertragulidae
      - Subfamily Hypertragulinae
      - Hypisodinae
    - Family Protoceratidae
      - Subfamily Protoceratinae
      - Syndyoceratinae
  - Superfamily Traguloidea
    - Family Tragulidae
      - Subfamily Tragulinae
      - Gelocinae
- Suborder Pecora
  - Superfamily Cervoidea
  - Giraffoidea
  - Bovoidea

CONCLUSIONS

1.—On the whole, *Archaeomeryx* is probably the most primitive ruminant (to use this word in its more restricted sense) of which the osteology is fairly completely known. It is not as primitive as *Amphimeryx*, in that this latter genus still retains a protoconule, which is lost in *Archaeomeryx*. However, so little is known of *Amphimeryx* beyond the dentition that it is not possible to gain any very adequate idea as to the general habitus of this animal.

2.—*Archaeomeryx* is a member of the family Hypertragulidae, and in most of its anatomical characters it is rather close to *Hypertragulus* itself. In certain characters, such as the development of the upper incisors and the possession of a very long tail, it is more primitive than *Hypertragulus;* in a few, such as the closed orbit and the four-toed manus, it is less so.

3.—Both *Archaeomeryx* and *Hypertragulus*, although resembling each other closely, also show many resemblances to the Old World *Tragulus* which because of their number and character would seem to be due to more than mere convergence. Most of the differences between these typical hypertragulids and *Tragulus* are of secondary importance in that they represent minor specializations that have taken place in the Old World form during the long geological period through which it has persisted. Such are the somewhat enlarged braincase and the enlarged orbit, complete loss of the upper incisors, enlargement of the median lower incisor, somewhat greater hypsodonty and reduction of styles in the cheek teeth, the relatively shorter lumbar section, the fused sacrum, the shortened tail, and fusions in the feet, specifically between the median metapodials and the cuboid-navicular-ectocuneiform in the tarsus. The one difference of great significance between the hypertragulids and the tragulids is the caniniform first lower premolar in the former, which is to be compared with a very small tooth in some of the fossil tragulids and a complete suppression of it in the recent genera. Undoubtedly the development of this tooth points to the early separation of the two families from a common ancestor, probably of late Eocene age, with the result that they followed separate but parallel courses of evolutionary development.

4.—Nevertheless, the numerous resemblances between the Hypertragulidae and the Tragulidae constitute strong evidence for the relationship of these families with each other, as descendants of a common ancestor. So it is that by looking at a modern *Tragulus* we are able to gain a fairly comprehensive idea as to the habitus of the ancestral pecoran of Eocene age. If *Archaeomeryx* could be restored and brought to life and placed beside a modern chevrotain, the two would look superficially very much alike, the main differences externally being in the somewhat longer back, the very long tail and the lack of a canine tusk in the Eocene genus. Other differences of taxonomic importance, such as the retention of the upper incisors and the caniniform first lower premolar in the fossil form, would not be noticeable.

5.—In any consideration of artiodactyl relationships it is necessary to consider the *sum* of characters that are of diagnostic importance, for single characters may be dangerously misleading when applied in this complex group of mammals. This is particularly true among the ruminants, where families may be combined in a variety of ways upon the basis of single characters. Therefore, upon the basis of as many characters as it is possible to use in a consideration of fossil and recent forms, it seems evident that the relationships of the hypertragulids are with the true tragulids and pecorans, rather than with the camels.

6.—It is quite probable that the ancestral pecoran lived in the Palaearctic region, possibly in Central Asia, a conclusion supported by the presence of the Amphimerycidae, the most primitive of the ruminant group, in Europe, and of *Archaeomeryx*, a very primitive type, in Central Asia. From the ancestral pecoran stock two early lines diverged, namely, those represented by the Hypertragulidae and by the Tragulidae. The Hypertragulidae, it would seem, at a very early stage in their history migrated from Asia into North America, where they flourished for a relatively short time and then died out, but leaving as their descendants the rather aberrant Protoceratidae, a group that also was destined to ultimate extinction. The Tragulidae, on the other hand, continued in the Old World, where they have been quite successful, not only in their own limited evolutionary development but in their legacy of specialized ruminants which now dominate the Holarctic mammalian faunas. At an early stage there was a division of the Tragulidae into two phylogenetic lines. One of these was that of the Tragulinae, which has continued to the present times with but little evolutionary change. The other was that of the Gelocinae, which at an early date showed a trend towards the habitus of the higher pecorans, and very probably was directly ancestral to the deer, giraffes and bovids.

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