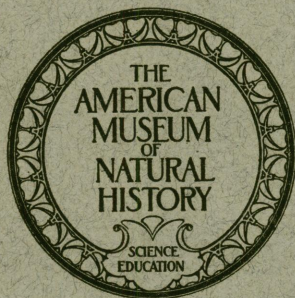


A STUDY OF *ORYCTEROPUS GAUDRYI* FROM THE ISLAND OF SAMOS

BY EDWIN H. COLBERT



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Article IV.—A STUDY OF *ORYCTEROPUS GAUDRYI* FROM THE ISLAND OF SAMOS

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INTRODUCTION

In 1923, Dr. Barnum Brown, of The American Museum of Natural History, having completed a series of extensive palaeontological field trips in northern India and in Upper Burma went to the Island of Samos at the east end of the Mediterranean Sea to collect fossil mammals in the Pontian beds exposed throughout the northern portion of the Island. As the result of a year's work in Samos an extraordinarily large and complete collection of Pontian mammals was procured and shipped back to the United States. This collection was made, and its release was effected through the coöperation of the Government of Greece, which by means of a special act allowed the fossils to be excavated and removed by Dr. Brown. The collection thus procured was so large that even now a considerable

portion of it is still unprepared, but as time goes on and the work of preparation slowly progresses, it becomes increasingly evident that the fossils constituting the collection offer an unusual opportunity, by reason of their completeness and their number, for the study of a characteristic Eurasiatic Pontian fauna. A few of the fossils in this collection already have been described. It is planned to continue the investigation of the collection to the best of our abilities during the next few years, and from time to time to bring out separate contributions describing unusual specimens or series of specimens, as the necessity for such publication arises. By a continuous publication of relatively small papers it is thought that the knowledge of this collection will be made more readily available than would be the case should such pub-

lication be deferred until a definitive monograph could be brought out. Indeed, since the collection is not as yet completely prepared, the method of description suggested above seems to be the only practicable means whereby the fossils contained in the collection can be made known. The papers already published describing Samos fossils in the American Museum collection are listed below. Consequently, this paper may be regarded as number three of what might be considered the "Samos Series" of American Museum Publications.

Previous Publications Dealing with the American Museum Samos Collection

- 1.—BROWN, BARNUM. 1927. "Samos—Romantic Isle of the AEgean." Nat. Hist., XXVII, No. 1, pp. 19–32.
- 2.—PILGRIM, GUY E. 1933. "A Fossil Skunk from Samos." Amer. Mus. Novitates, No. 663, pp. 1–15.

Orycteropus, the aard-vark, is at the present time confined to Africa, where it ranges from the northeastern, northwestern and central portions of the Continent to the Cape. During past geologic time, however, this genus was much more widespread than at present, for Pliocene fossils of *Orycteropus* have been found to the north in Central Europe and the eastern Mediterranean region (Pikermi, Samos, Maragha), and to the east in northern India. This animal, like so many Pliocene mammals of southern Eurasia, would seem to have "migrated" or extended itself into Africa at the end of the Tertiary, to become extinct in its former more northerly habitat.

Of the fossil aard-varks, *Orycteropus gaudryi* Forsyth Major is by far the best known species. Even so, this animal has until the present time been known for the most part from skulls, as is true of most of the other fossil species of *Orycteropus*. Therefore, the discovery by Dr. Brown at Samos of a relatively complete skeleton of *Orycteropus gaudryi*, and in addition a considerable series of skulls and jaws, offers for the first time an opportunity to increase greatly our knowledge as to the

Tertiary ancestors of the modern aard-vark.

In his original type description of *Orycteropus gaudryi*, Major made the following statement:

"Le crâne de l'*Orycteropus Gaudryi* Major, de Samos, ne se distingue que par quelques caractères de peu d'importance de son congénère du Cap, abstraction faite de ses dimensions plus petites. Dans le pied postérieur, le premier et le cinquième métatarsien sont plus grands, relativement aux métatarsiens médians, que dans les espèces actuelles. Il semblerait donc que, dans cet ordre aussi, il y ait eu tendance à la réduction du nombre des doigts."¹

Since the discovery of *Orycteropus* at Samos the opinion of Major, cited above, has become quite prevalent, so that in the literature dealing with the tubulidentates it is generally stated that the differences between the fossil and the recent species are minor and unimportant. In the main, this idea may be true, but a detailed comparison of *Orycteropus gaudryi* with the recent forms has shown that in many respects there are distinct differences to be seen. Even though these differences are not great, they are numerous enough and developed to a degree sufficient to show the trends of evolution in the *Orycteropodidae* between Lower Pliocene and Recent times. In the following pages an attempt will be made to point out these differences, and the manner in which they demonstrate evolutionary developments in this family of peculiar mammals.

Therefore the purpose of this paper is to make a detailed comparison of the complete skeleton of *Orycteropus gaudryi* with the skeleton of the modern African *Orycteropus*, with the object of recording as completely as possible the resemblances and the differences between the Pliocene and the Recent types. Also the Samos species will be compared with other fossil species of the genus, and in addition with certain other extinct genera that seemingly are related to *Orycteropus* and its ancestors. Finally, measurements of the series of fossil *Orycteropus* skulls, jaws and teeth will

¹ Major, C. J. 1888. C. R. Acad. Sci., CVII, p. 1180.

be made, to see if possible the degree of individual variation within this extinct species.

The drawings of *Orycteropus* feet were

made by Mr. John C. Germann; those of the skull by Mr. Roger Bullard. The outline drawings and the charts were made by Mrs. Elsa Arnoux.

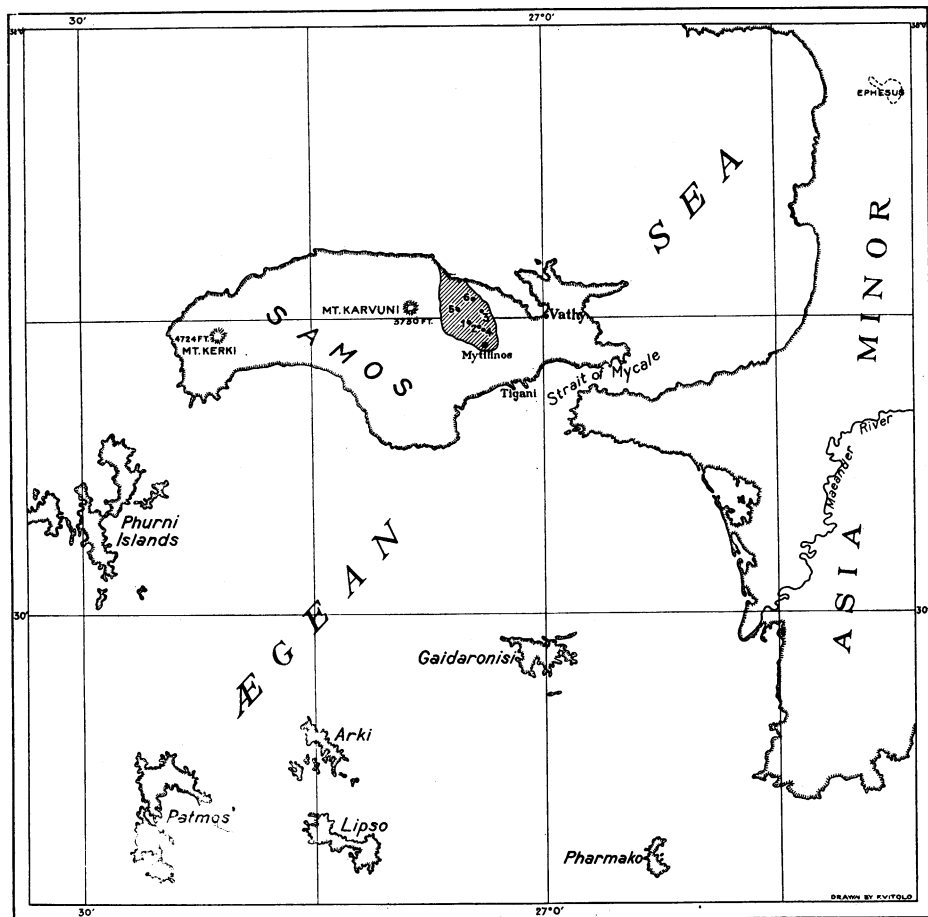


Fig. 1. Samos, near-by islands and the adjacent Turkish coast. The hatched area indicates the fossiliferous Pontian deposits; the numbers are those of the quarries. From Brown, 1927.

MATERIALS UPON WHICH THIS STUDY IS BASED

The specimens in the American Museum Samos Collection were obtained by Dr. Brown on the northern side of the Island, north of the town of Mytilinos. It was from this portion of the Island that the material collected by Dr. Achille Stephani and described by Forsyth Major was discovered, and where the best Samos

collections subsequently have been made. According to Major¹:

"Les couches en question . . . traversent l'île presque de part en part, du nord au sud, à commencer par la côte septentrionale aux environs de Kokkari, ou j'ai constaté

¹ Major, C. J. Forsyth. 1892. "Le Gisement Ossifère de Mitylini," p. 3.

la présence des tufs volcaniques, jusqu'aux environs de Chora, près de la côte méridionale."

Dr. Brown secured the American Museum collection from six large quarries which he excavated, and which are indicated on the accompanying map by numbers. It is not possible to distinguish differences in age in the sediments exposed in these several quarries, and there is every reason to think that they represent a single, contemporaneous deposit, containing a unit fauna. The various specimens of *Orycteropus* described in the following pages were found in Quarries 1, 4 and 5, and the locality for each specimen is indicated in the numerical list. The horizon is Pontian, which is here considered as of lower Pliocene age.

MATERIALS

A. M. No. 20560, a skull, virtually complete but crushed somewhat laterally, with right P^2 , M^{1-3} , and left P^{1-2} , M^{2-3} . Also an associated left mandibular ramus with P_2 - M_3 . Samos, Quarry 5.

A. M. No. 20561, a skull, complete except for the tip of the muzzle and the occiput. Somewhat crushed, laterally. Containing in the dentition, right P^3 - M^3 and left P^4 - M^3 . An associated right mandibular ramus with P_2 - M_3 . Samos, Quarry 5.

A. M. No. 20562, a skull, virtually complete and uncrushed. With right P^2 - M^2 and left P^2 - M^3 . An associated left mandibular ramus with P_2 , P_4 - M_3 . In the skull the tip of the muzzle and the tympanic rings are lacking. Samos, Quarry 1.

A. M. No. 20563, a skull, complete except for the tip of the muzzle, but strongly crushed vertically. The third molars on each side are present. Also fragment of a left mandibular ramus without teeth. Samos, Quarry 5.

A. M. No. 20564, a skull, lacking the occiput, the zygomatic arches and the muzzle anterior to P^4 . Crushed laterally. With right M^{1-3} and left P^4 - M^3 . Samos, Quarry 5.

A. M. No. 20565, portion of an uncrushed skull, with the antorbital region back of the fourth premolar and the cranium, lack-

ing the occiput. Zygomatic arches missing. With right M^{1-3} and left M^{2-3} . Samos, Quarry 4.

A. M. No. 20694, an uncrushed skull, complete except for the tip of the muzzle, portions of the zygomatic arches and a part of the occiput. The tympanic rings are well preserved on both sides. With right P^1 - M^2 and left P^1 - M^3 . An associated mandible, complete except for the anterior portion of the symphysis, the right condyle and coronoid and part of the left angular process. With right and left P_2 - M_3 . Samos, Quarry 1.

A. M. No. 20756, fragment of a right maxilla with P^4 - M^3 . Also a left mandibular ramus, associated, with P_2 - M_2 . Samos, Quarry 4.

A. M. No. 22978, a right maxilla with P^4 - M^3 . Also right and left mandibular rami with right M_{1-3} and left P_2 - M_1 , M_3 . Samos, Quarry 5.

A. M. No. 22979, middle portion of a skull with the frontals and orbits, and right M^{1-3} and left P^4 - M^3 . Also a left mandibular ramus with P_1 - M_3 . Samos, Quarry 5.

A. M. No. 22980, a crushed skull, lacking the muzzle in front of the second premolars, the zygomatic arches and the occiput. With right P^2 , P^4 , M^1 , M^3 and left P^2 - M^3 . Samos, Quarry 5.

A. M. No. 20702, a left mandibular ramus containing P_3 - M_3 . Samos, Quarry 1.

A. M. No. 20800, a right mandibular ramus, containing P_3 - M_3 . Samos, Quarry 4.

A right mandibular ramus with P_1 - M_3 , no data.

A. M. No. 22976, a left tibia and left pes. Samos, Quarry 5.

A. M. No. 22762, a relatively complete skeleton, lacking the skull. This was the only associated skeleton found by Dr. Brown in the Samos deposits. It is composed as follows:

A complete series of presacral vertebrae, in many cases, however, lacking the neural spines and/or the transverse processes.

The first two sacral vertebrae.

Ten caudal vertebrae, in various states of preservation, and nine chevrons.

Portions of eight right ribs and five left ribs.

The right scapula complete, and the left scapula, lacking the superior and anterior borders.

The right humerus.

The right radius and ulna, the latter lacking its distal portion.

The left radius and ulna, the latter lacking its proximal portion.

The right fore-foot, lacking most of the

carpus, the second metacarpal and three ungual phalanges.

The left fore-foot, lacking certain carpal elements, a number of proximal and median phalanges and all of the ungual phalanges.

The right femur.

The right tibia and fibula, the latter lacking a portion of the shaft.

The distal articulations of the left tibia and fibula.

The right and left hind-feet, each almost complete.

Samos, Quarry 1.

THE COMPARATIVE OSTEOLOGY OF *ORYCTEROPUS GAUDRYI**Orycteropus gaudryi* COMPARED WITH THE MODERN AARD-VARK

The Skull, Mandible and Dentition

The obvious comparison to be made in a detailed study of the osteology of *Orycteropus gaudryi* is that between the fossil species and the modern forms of Africa. For this purpose, a skeleton of *Orycteropus erikssoni* has been selected, especially because this is a large form, and thus shows the greatest possible contrast with the fossil species. In this connection, however, other species of the modern *Orycteropus*, all of which are rather similar in osteological features, have been considered. Throughout this series of comparisons between the extinct and the recent *Orycteropus* the differences due to a progressive increase in size since Lower Pliocene times must be taken into account. In other words, any striking differences noted between the Pliocene and the recent forms must be looked at with the realization that there has been an increase in size of considerable magnitude during the interval between the presence of *Orycteropus gaudryi* in southeastern Europe and Asia Minor and *Orycteropus* of various species living at the present time in Africa. If this fact be kept constantly in mind comparisons will be facilitated, and differences will be in many if not most cases logically explained. It is the increment in size between Lower Pliocene and Recent times that forms the basis of evolutionary development within the genus *Orycteropus*.

The skull of *Orycteropus gaudryi* is approximately one-third smaller, linearly, than the skull of the large *O. erikssoni*. The recent *O. capensis* (*O. afer*) is almost exactly intermediate in size between the two above-named species in its linear dimensions. Consequently these three species¹ form an excellent graded series,

¹ In a consideration of the modern *Orycteropus*, the question of species is difficult of solution. Some authorities would recognize several species, others only one, of which the "species" might be considered as races or varieties. Generally speaking, the modern aard-vark shows the following types, whether these be "species," "subspecies" or "races."

a.—*Orycteropus capensis*—*O. afer*, South Africa, the type of the genus.

in which the differences due to a progressive increase in size may be readily studied, from the smaller, through an intermediate to the larger form.

Orycteropus erikssoni, and to a lesser *O. capensis*, show certain differences from *O. gaudryi* consequent upon their increasingly larger size and the factors involved in growth during a general size increase. Thus the muzzle of the fossil form tapers sharply from the fronto-nasal suture to the tip of the snout. The taper in the modern forms is much less pronounced, particularly in the larger of the two species being utilized for comparative purposes, due to transverse growth correlative with size increase. Closely related to this broadening of the anterior portion of the muzzle, is the transverse expansion of the palate between and anterior to the premolars. Thus, in *O. gaudryi* the cheek teeth and the alveolar ridges in front of the anterior premolars converge rather markedly from back to front. In *O. capensis* this convergence is less marked than in the fossil species, while in *O. erikssoni* the cheek teeth and the alveolar ridges in front of the premolars are virtually parallel.

Continuing this comparison, it is to be seen that there are prominent frontal lobes on the skull of *O. gaudryi*, at the anterior extremities of the frontal bones and immediately in front of the orbit. In *O. capensis* these lobes are still marked but less so than in the fossil form, due to a general enlargement of the fronto-nasal sinuses above the anterior ethmo-turbinals. Finally, in the large *O. erikssoni* the enlargement of the sinus space in the frontal region, consequent upon a general increase in the size of the animal, has been so marked that the two lobes, distinct in *O.*

b.—*Orycteropus aethiopicus*

Perhaps synonymous with *O. capensis*. This form, however, shows certain resemblances to the extinct, Pliocene types—in other words, it is seemingly more primitive as regards certain characters than is the Cape form.

c.—*Orycteropus erikssoni*, and *O. erikssoni faradjius*—Congo.

The largest of the aard-varks, and for this reason the most specialized in those characters resulting from evolutionary growth in size.

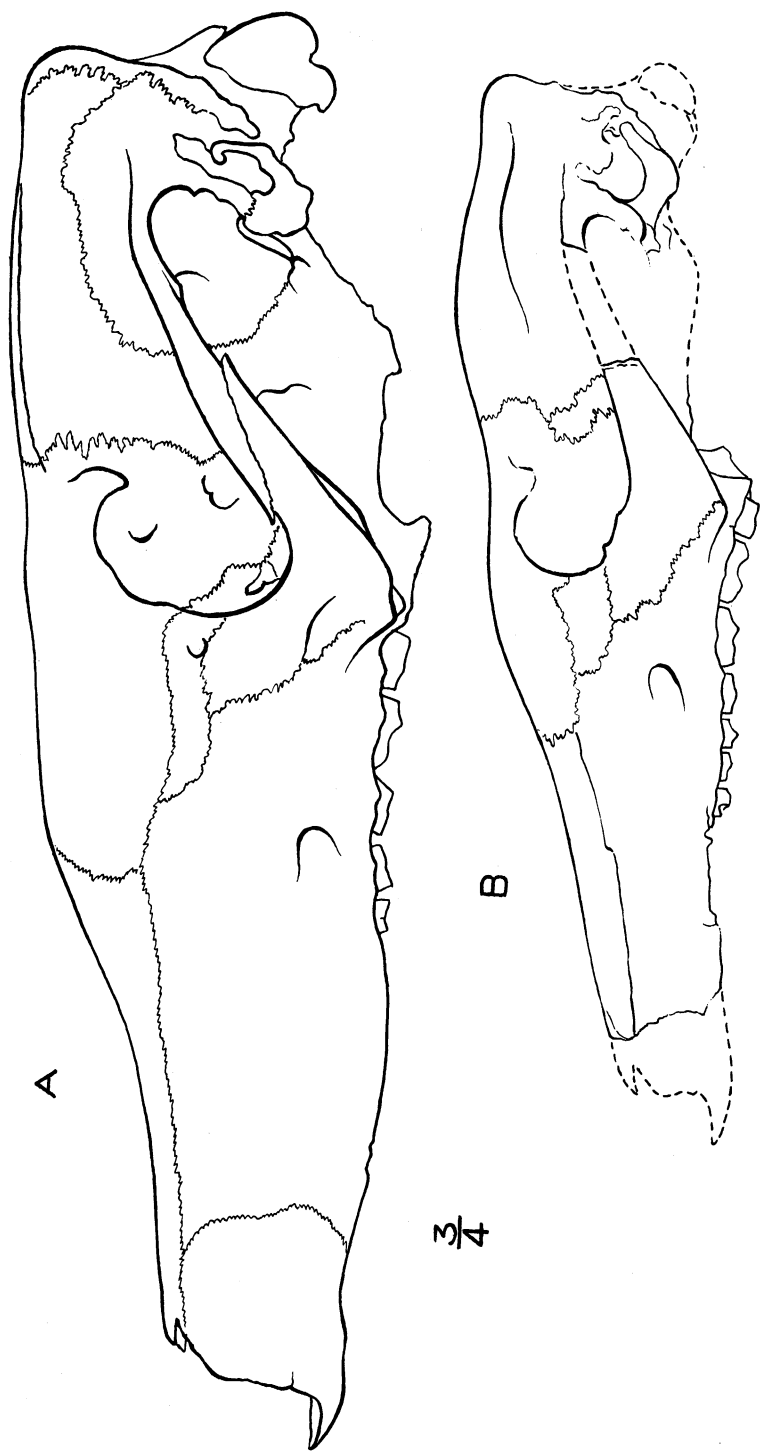


Fig. 2. The skull of (A) *Orycteropus eriksoni faradjius* Hatt, Amer. Mus. No. 51905, as compared with that of (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 20694. Lateral views, three-fourths natural size.

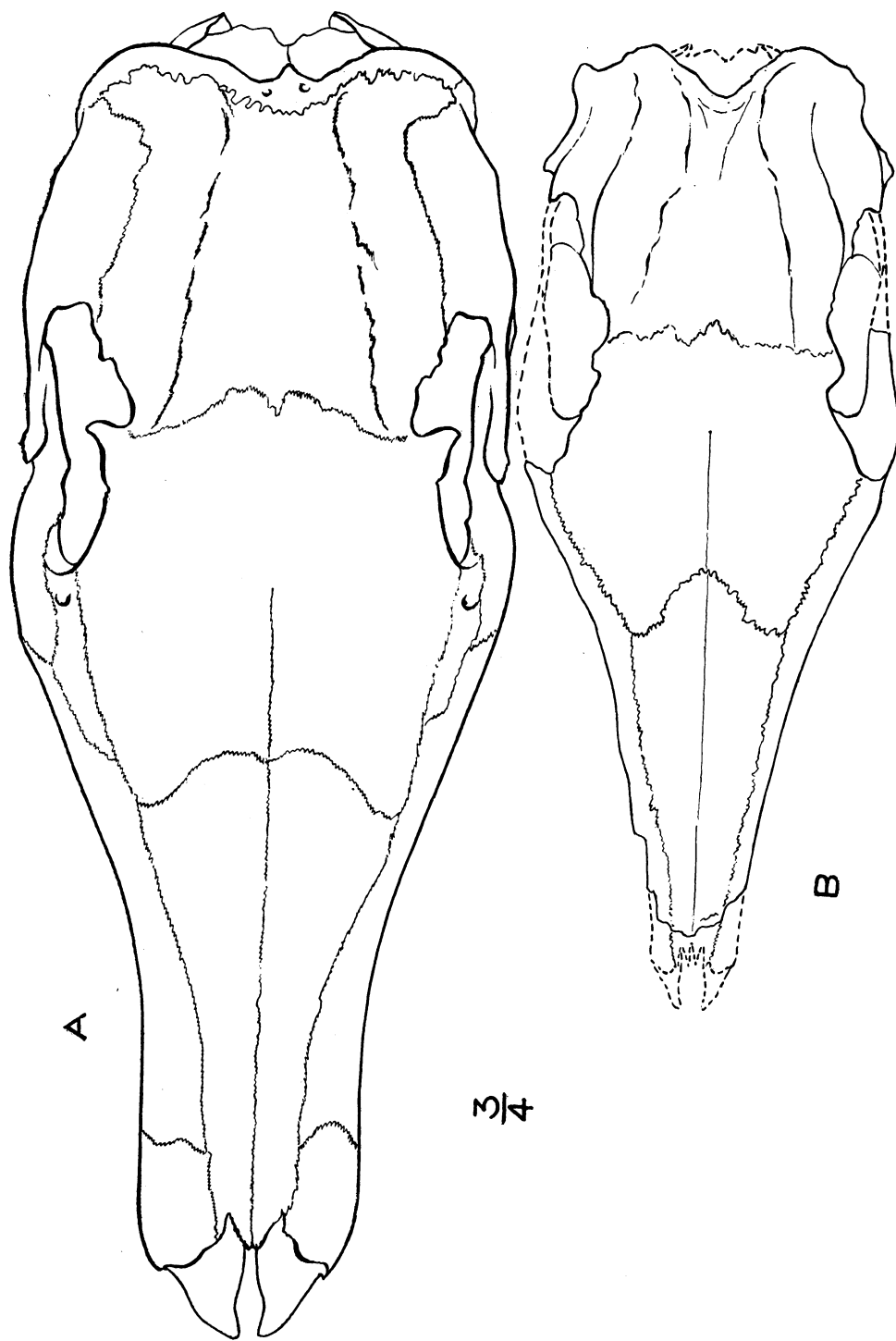


Fig. 3. The skull of (A) *Orycteropus eriksoni faradjius* Hatt, Amer. Mus. No. 51905, as compared with that of (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 20694. Dorsal views, three-fourths natural size.

gaudryi, have now become confluent, to form one large, swollen region, involving the posterior portions of the nasals and the anterior portions of the frontals. This change, progressing from *O. gaudryi* through *O. capensis* to *O. erikssoni* is reflected in the profiles of the tops of the skulls in these animals. In *O. gaudryi* there is a generally uninterrupted profile along the tops of the nasals, frontals and parietals, with a slight elevation caused by the frontal swellings. In *O. capensis* the frontal swellings are of sufficient size to cause a "dip" in the profile from the back portion of the nasals forward. Finally, in *O. erikssoni*, due to the great enlargement of the fronto-nasal sinuses, there is a large and decided "dip" or "stop" in front of the posterior portion of the nasal region.

As a result of the development of frontal sinuses, the cranial portion of the skull is raised somewhat in relation to the palatal-basiscranial line, so that in the recent *Orycteropus* the back portion of the skull is relatively higher as compared with the muzzle than is the case of the fossil. This is shown particularly by the angle of the zygomatic arch with the base of the skull, for in the recent form the posterior end of the arch has been pulled up so that the arch is steeper than is the case of the fossil.

The changes due to transverse growth during phylogenetic development are apparent, too, in viewing the top and back of the cranial region of the skull. In the recent aard-vark the temporal crests marking the dorsal limits of the temporalis muscles, are farther apart than they are in the fossil, due to the transverse growth of the cranium, the result of which is a slight amount of restriction of the temporalis in the recent form, as compared with the fossil. Correlated with this change on the top of the cranium is the change in shape of the lambdoidal crest, which in the fossil is broadly V-shaped when seen from above, the apex of the V being directed forwardly on the midline of the parietals, whereas in the recent form it has been "pulled out," so to speak, by the transverse expansion of the cranium and the occiput into a very shallow U-shaped line.

Looking at the back and basiscranial regions of the skull, the principal changes due to an increase in size are the broadening and flattening of the glenoid, the transverse expansion of the basicranium and similarly of the occiput. These changes during the increase in size, with the resultant differences between the three species, as described above, are obvious and need no further elucidation. In addition, it would seem that the condyles are not only actually but relatively broader in the recent form than they are in the fossil.

Certain other differences between *Orycteropus gaudryi* and the recent aard-varks have been pointed out by Forsyth Major and by Andrews. The first of these authors considered that there was a difference in the size and form of the lacrymal bone in the fossil and recent species, describing this element as being larger, and more fully exposed on the facial region in the fossil than in the recent forms. Andrews has shown, however, that the difference seen by Forsyth Major actually does not exist, and the present material upholds Andrew's contention. Among the series of *O. gaudryi* skulls at hand, no essential difference can be seen from the recent species in the size and shape of the lacrymal bone.

Andrews called attention to the fact that the mastoid in *O. gaudryi* is less prominent than it is in the recent species, while the tympanic ring is round in the fossil form, as compared with a somewhat oval-shaped ring in the recent animal. On the basis of the series of skulls in the American Museum, these differences would seem to be valid, although in each case the difference between the fossil and recent species, as cited by Andrews, is at best slight. On the other hand, a supposed difference in the size of the postorbital process of the frontal between the fossil and recent aard-varks, described by Andrews, appears from a study of more complete material to be non-existent. Andrews, dealing with a single skull of *O. gaudryi*, thought the postorbital process to be relatively larger in the fossil than in the recent species. The series of skulls at hand shows this character to be variable in the fossil form, so

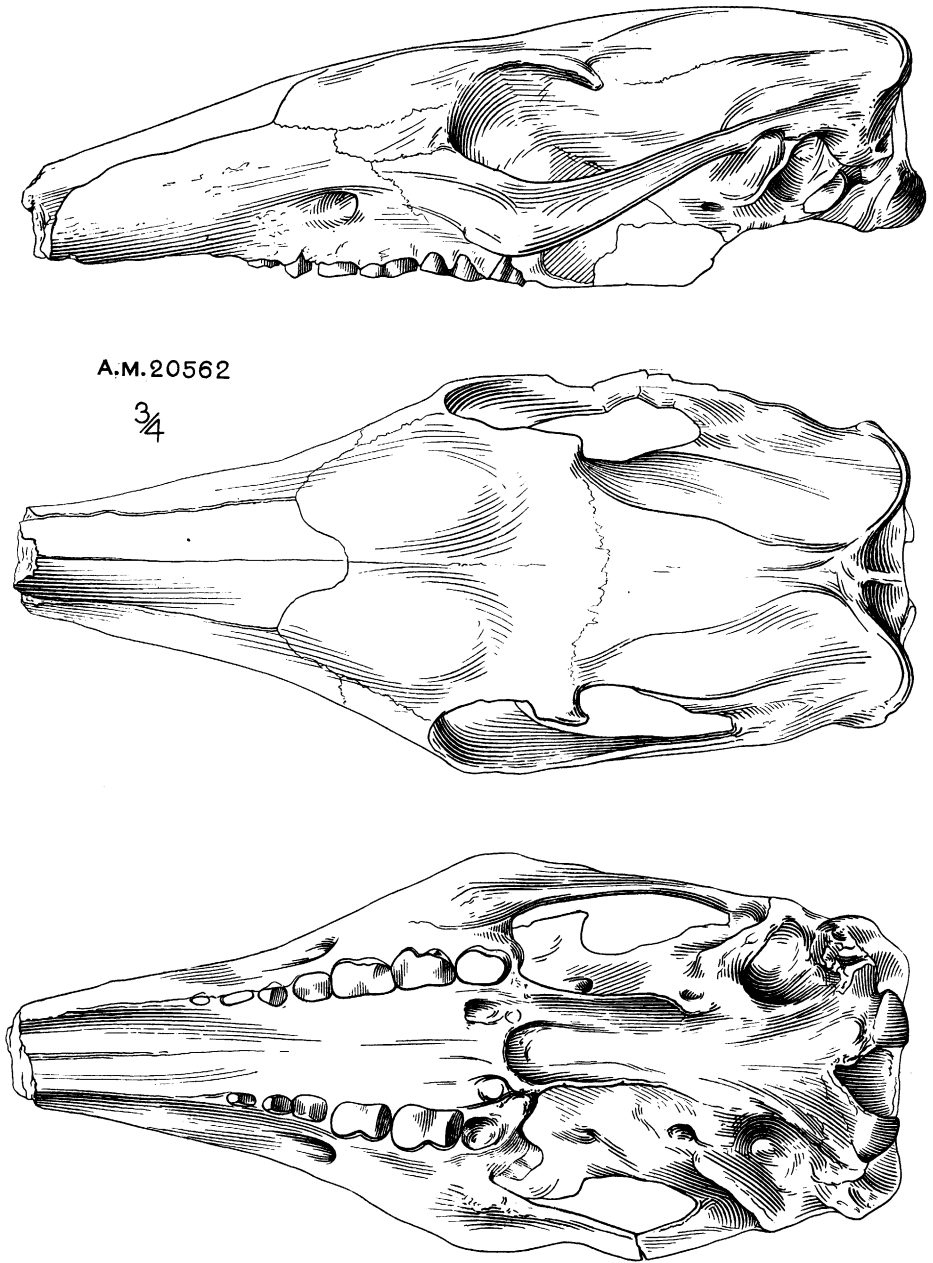


Fig. 4. *Orycteropus gaudryi* Major. Amer. Mus. No. 20562, skull. Lateral view above, dorsal view in middle, ventral view below. Three-fourths natural size.

that no valid distinction seems possible. Finally, Andrews pointed out a difference in the position of the antorbital or infra-orbital foramen in the fossil and recent types, this opening, according to him, being above the first molar in the fossil and for the most part above the second molar in the recent aard-varks. He recognized the fact, however, that the position of the

very apt to push forward during the life of the individual. This fact was recognized by Owen, but has been overlooked or disregarded by many subsequent authors. Consequently, the position of the infra-orbital foramen in relation to the cheek teeth is apt to vary with the age of the animal, occupying a position apparently progressively towards the posterior end

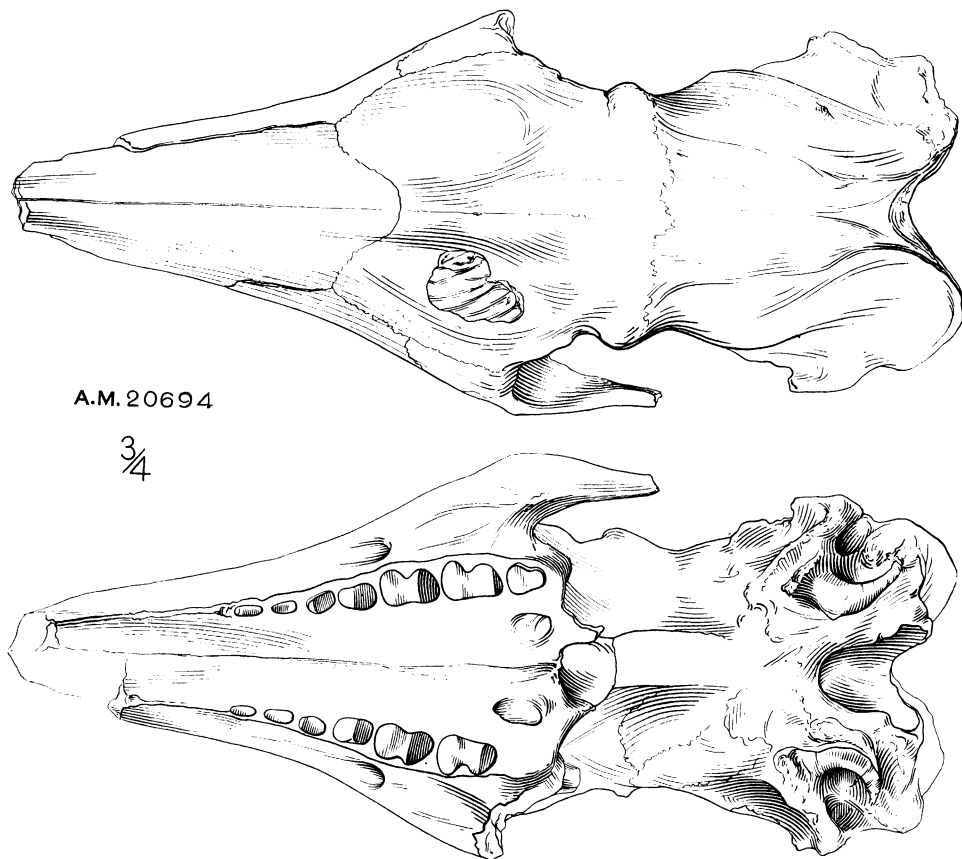


Fig. 5. *Orycteropus gaudryi* Major. Amer. Mus. No. 20694, skull. Dorsal view above, ventral view below. Three-fourths natural size.

foramen might be variable, particularly in the recent species. As a matter of fact, this new material shows that the foramen is variable as to position in both the fossil and recent species.

It has been pointed out to me by Mr. H. C. Raven that in long-faced mammals having a diastema at the front of the cheek teeth, the entire premolar-molar series is

of the dentition due to the actual pushing forward of the cheek teeth with increasing age.

It is quite evident that this factor probably is responsible for the seemingly varying position of the infraorbital foramen in a single species of *Orycteropus*. Actually it is in part the dentition that is variable in relation to the skull.

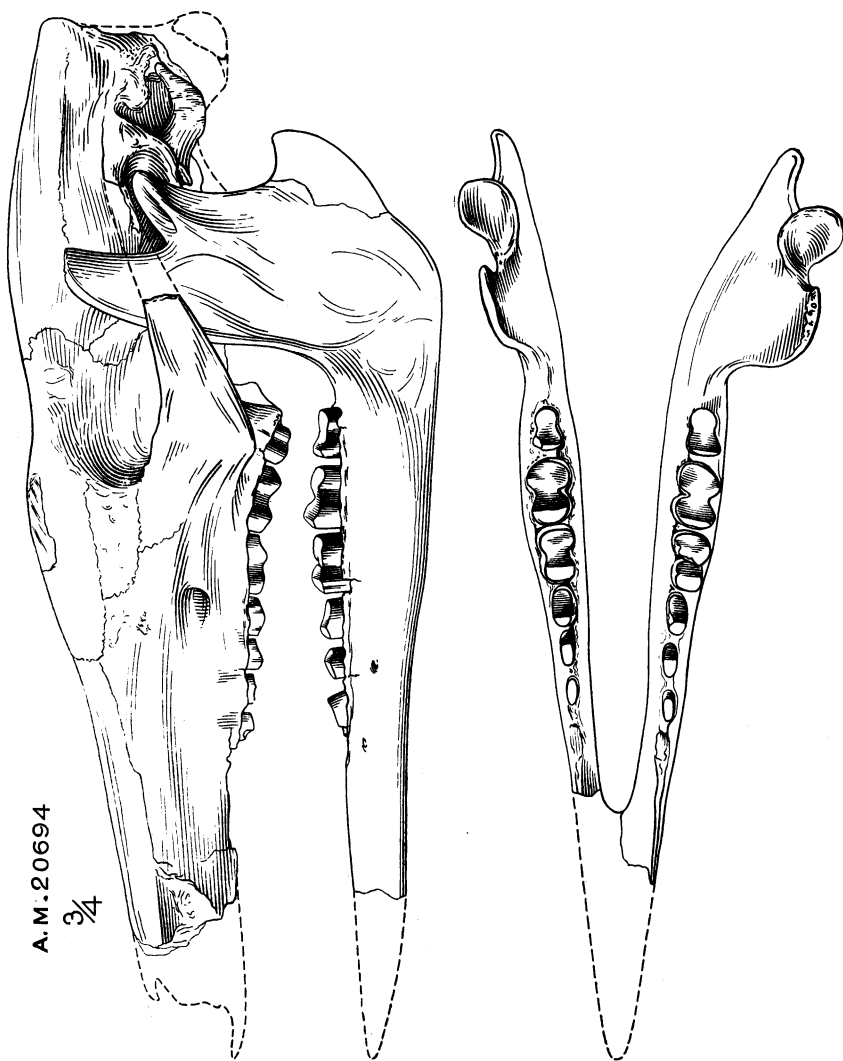


Fig. 6. *Orycteropus gaudryi* Major. Amer. Mus. No. 20694, skull and mandible. Lateral view above, crown view of mandible below. Three-fourths natural size.

On the other hand, there would seem to be a real difference between the fossil and recent forms in the position of the orbit and contiguous structures of the skull with relation to the dentition. Although the position of the infraorbital foramen, variable though it may be, is essentially the same in the fossil and recent species, the orbit in the fossil is constantly above the second molar, while in the recent animal it is constantly above the third molar. Moreover, it is to be noted that the lowest point of the zygomatic arch, approximately at the junction of the maxillary and jugal bones, is above the third molar in the fossil, but considerably behind it in the recent *Orycteropus*. All of this means, of course, that there has been a virtual stretching or lengthening of the preorbital portion of the skull during the interval between Lower Pliocene and recent times. This growth trend is apparent when the tables of measurements and indices are examined, below. It is also visible in a comparison of the figures of fossil and recent forms.

In other characters of the skull *Orycteropus gaudryi* is quite similar to the recent species of the genus. These characters may be reviewed briefly at this point. In *Orycteropus gaudryi*, *O. capensis*, *O. erikssoni*, etc., the frontals become fused with increasing age. There is a tubercle on the alisphenoid bone, perhaps relatively slightly larger in the recent forms than it is in the fossil. The ethmoid foramen is located on the frontal-orbitosphenoid suture. The frontals are separated from the squamosals by a downward projection of the parietals. The lower edge of the postglenoid process articulates with the tympanic ring, and there is a well-developed epitympanic sinus. The paroccipital processes are very small. The occipital condyles are not confluent in the midline of the skull. The arrangement of the basicranial foramina is the same in the fossil and recent forms. In this connection there might be mentioned the presence of a venous foramen within the foramen ovale, leading into a bony canal traversing the basisphenoid—a character whereby the aard-varks may be com-

pared with the insectivores and the rodents. The foramen rotundum is confluent with the sphenoidal fissure. The foramen ovale is complete and there is no carotid canal. Also there is no stylo-mastoid foramen nor is there a postglenoid foramen. The foramen lacerum posterius is long and oval-shaped. The condylar foramen is large. The lacrymal foramen is located outside of the orbital margin. The posterior palatine foramina are large.

The nasal bones are long and narrow and are much broader posteriorly than anteriorly.

The mandible in the fossil and recent *Orycteropus* is distinguished by the long, attenuated horizontal ramus and the large, prominent angular process on the ascending ramus. The only difference of note is to be seen in the form of the horizontal ramus anterior to the molars, which in the fossil is relatively more robust and less attenuated than is the case in the modern species.

Of course, both fossil and recent species are characterized by the unique structure of the cheek teeth, each of which is composed of numerous, closely appressed, sub-hexagonal, vertical tubules. A microscopic examination shows that the tubules are of approximately the same size in both the fossil and the recent forms, so it is quite evident that there is a larger number of tubules composing the individual molar in the recent species than in the fossil, since the former has larger molars than does *Orycteropus gaudryi*.

In *Orycteropus gaudryi* the dental formula for the permanent dentition is $\frac{0-0-4-3}{0-0-4-3}$ as compared with a formula of $\frac{0-0-(3-2)-3}{0-0-2-3}$ in the recent forms. The premolars of the modern *Orycteropus* are reduced not only in number, but also in size, so that those teeth remaining in the premolar series are relatively smaller than the homologous teeth in *Orycteropus gaudryi*. The premolar teeth in both fossil and recent forms are single-lobed, while the

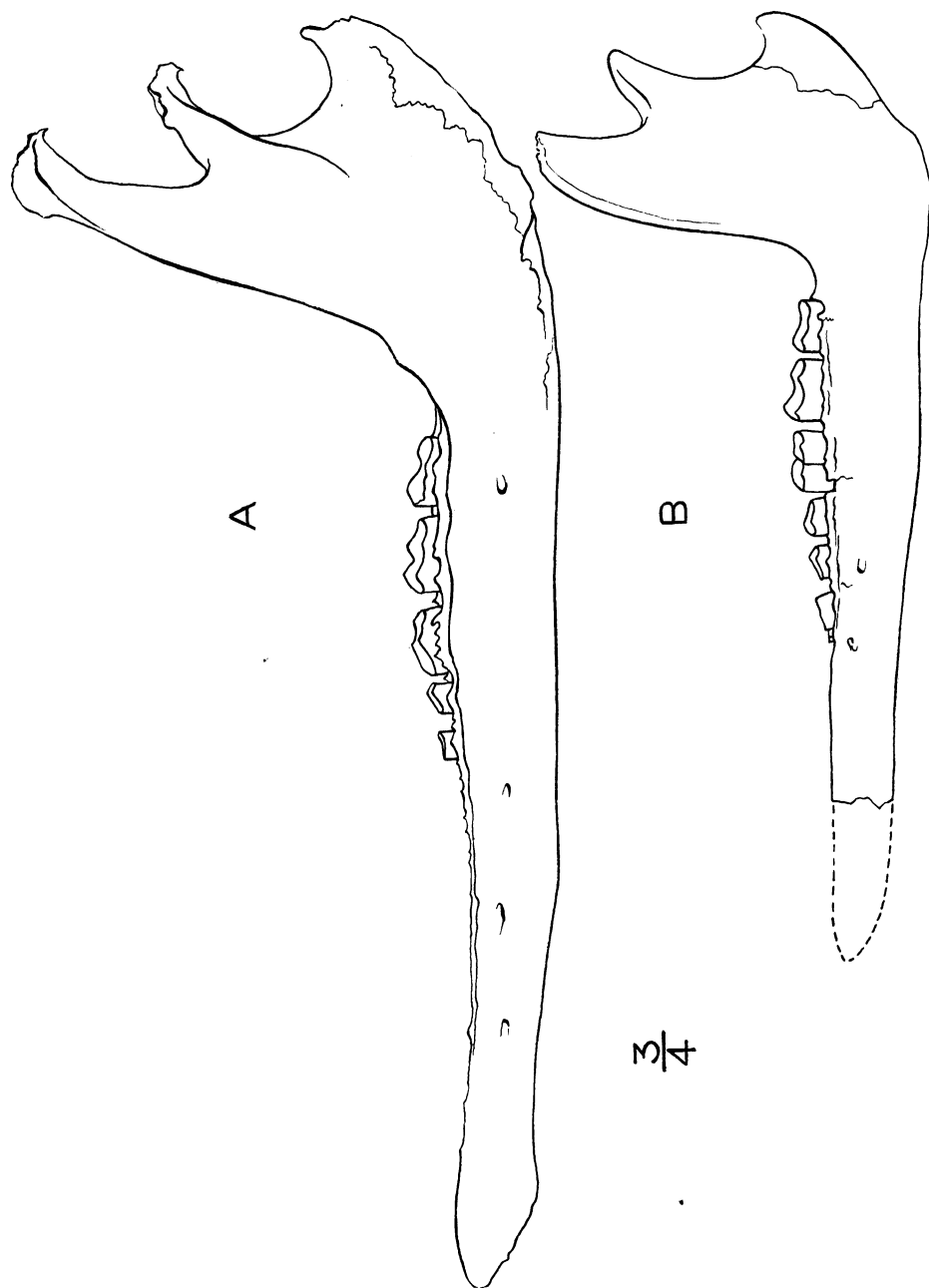


Fig. 7. The mandible of (A) *Orycteropus erikssoni* Eriksson, Hatt. Amer. Mus. No. 51905, as compared with that of (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 20691. Lateral views, three-fourths natural size.

molars are bi-lobed. One difference, correlative with the general trend toward dental reduction in the modern aard-vark, is the reduced posterior lobe of M^3 as compared with a normal-sized lobe in the

M^3 of *Orycteropus gaudryi*. This reduction has progressed so far that in some individuals among the modern aard-varks the M^3 is virtually a secondarily single-lobed tooth.

MEASUREMENTS (IN MM.)

Skull	<i>O. erikssoni</i> : A. M. 51905	<i>O. capensis</i> : A. M. (CA) 2285	<i>O. depereti</i> : A. M. 26961	<i>O. gaudryi</i> : A. M. 20694	A. M. 20560	A. M. 20561	A. M. 20562	A. M. 20563	A. M. 20564	A. M. 20565
Length, cond.-premax.	249	212	195e	180e	185e		180e			
Breadth, postorb. proc.	69	61	58	55e	55e	57	55			
Index	28	29	30	31	30		31			
Antorbital length	147	122	107e	100e	100e		96			
Postorbital length	108	94	88	80	85		84			
Index	74	77	82	80	85		87			
Length, post. nas. ch.-prmx.	158	134	120e	117e	120e		113e			
Breadth, palate at M^3	39	32	27	25	25e		22			
Index	25	24	22	21	21		20			
Breadth, palate at tip of mx.	29	21	18	14			14			
Index { Ant. breadth	74	66	67	56			63			
{ M^3 breadth										
Depth at pmx.-mx. sut.	33	30	25e	21	21	20	20			
Depth ant. border orbit	65	52	45	39	40	40	37			
Index	51	58	56	54	52	50	54			
Breadth, occiput	73	66	58	55			53			
Height, occiput, above for. mag.	36	30	31	30			30			
Index	49	45	53	54			56			
Breadth, nasals ant.	17	13		12			12			
Breadth, nasals post.	53	43		29			25			
Index	32	30		41			48			

Skull crushed—no measurements possible

Skull crushed—no measurements possible

56

22

41

Upper Dentition	<i>O. erikssoni:</i> A. M. 51905	<i>O. capensis:</i> A. M. 2285	<i>O. depereti:</i> A. M. 26961	<i>O. gaudryi:</i> A. M. 20694	A. M. 20560	A. M. 20561
P ¹ length × width				4 ¹ / ₂ × 1 ¹ / ₂	3 ¹ / ₂ × 2	
Index				33	57	
P ² length × width	4 × 2			5 × 2	5 ¹ / ₂ × 2 ¹ / ₂	
Index	50			40	45	
P ³ length × width	4 ¹ / ₂ × 3	5 ¹ / ₂ × 3		5 × 3 ¹ / ₂		5 × 3
Index	67	55		70		60
P ⁴ length × width	7 ¹ / ₂ × 6	7 × 5 ¹ / ₂	7 × 6	7 × 5		7 ¹ / ₂ × 5 ¹ / ₂
Index	80	78	86	72		73
M ¹ length × width	11 ¹ / ₂ × 7 ¹ / ₂	10 × 7	12 × 7 ¹ / ₂	10 × 6 ¹ / ₂	12 × 7 ¹ / ₂	11 ¹ / ₂ × 7 ¹ / ₂
Index	65	63	62	59	62	65
M ² length × width	12 ¹ / ₂ × 9	12 × 8	12 ¹ / ₂ × 7 ¹ / ₂	11 ¹ / ₂ × 7	13 × 8 ¹ / ₂	12 ¹ / ₂ × 8 ¹ / ₂
Index	72	67	60	61	65	68
M ³ length × width	10 × 8 ¹ / ₂	9 ¹ / ₂ × 7	9 ¹ / ₂ × 7	6 ¹ / ₂ × 5 ¹ / ₂	8 ¹ / ₂ × 7	9 × 7
Index	85	74	74	85	82	
Length, M ¹⁻³	36	34	33	29	34 ¹ / ₂	33
Index $\frac{M^{1-3}}{\text{post. na. ch.-pmx.}}$	23	25	27	25	29	

Mandible and Lower Dentition	<i>O. erikssoni:</i> A. M. 51905	<i>O. capensis:</i> A. M. 2285	<i>O. gaudryi:</i> A. M. 20694	A. M. 20560	A. M. 20561
Length, cond.-symph.	216	176	150e		
Depth, ramus at M ₃	22	18	18	18	18 ¹ / ₂
Depth, ramus at P ₃	17	14	12 ¹ / ₂	11	11 ¹ / ₂
Index $\frac{P_3 \text{ depth}}{M_3 \text{ depth}}$	77	78	70	61	62
Height, cond. above vent. bord.	75	72	58		61
Index $\frac{\text{Height}}{\text{Length}}$	35	41	39		
Length M ₁₋₃	40	34	31	34	35
Length ramus (M ₁ -symph.)	105	88	80e		
Index	38	39	39		
P ₁ length × width			5 × 2		
P ₂ length × width			5 ¹ / ₂ × 2	4 × 2	4 × 2
P ₃ length × width	5 × 2	4 ¹ / ₂ × 2	5 ¹ / ₂ × 3	6 ¹ / ₂ × 3 ¹ / ₂	6 × 3
Index	40	45	35	54	50
P ₄ length × width	6 × 4	5 ¹ / ₂ × 3 ¹ / ₂	7 × 3 ¹ / ₂	7 ¹ / ₂ × 5	7 ¹ / ₂ × 4 ¹ / ₂
Index	66	64	50	67	60
M ₁ length × width	11 ¹ / ₂ × 8	10 ¹ / ₂ × 6 ¹ / ₂	9 ¹ / ₂ × 6 ¹ / ₂	11 × 8	11 × 8 ¹ / ₂
Index	70	62	68	73	77
M ₂ length × width	13 × 9	11 ¹ / ₂ × 8	11 × 7	11 ¹ / ₂ × 9	12 × 9
Index	69	70	64	78	75
M ₃ length × width	11 × 8 ¹ / ₂	10 × 7 ¹ / ₂	8 ¹ / ₂ × 6	10 × 7	10 ¹ / ₂ × 7
Index	77	75	70	70	67

A. M. 20562 A. M. 20563 A. M. 20564 A. M. 20565 A. M. 22979 A. M. 22980 A. M. 22978 A. M. 20756

$3\frac{1}{2} \times 1\frac{1}{2}$							
43							
5 \times 2					$5\frac{1}{2} \times 2\frac{1}{2}$		
40					45		
5 \times 3					$5\frac{1}{2} \times 3$		
60					55		
$6\frac{1}{2} \times 5$		$8\frac{1}{2} \times 5\frac{1}{2}$		$7\frac{1}{2} \times 5$	$7\frac{1}{2} \times 5$	$7\frac{1}{2} \times 4\frac{1}{2}$	$7\frac{1}{2} \times 5$
77		65		67	67	60	67
$10\frac{1}{2} \times 6\frac{1}{2}$		$12\frac{1}{2} \times 7\frac{1}{2}$	$11\frac{1}{2} \times 7$	$11\frac{1}{2} \times 7\frac{1}{2}$	12 \times 7	11 \times 7	$10\frac{1}{2} \times 6\frac{1}{2}$
57		60	61	65	58	64	62
$12\frac{1}{2} \times 8$		14 \times $8\frac{1}{2}$	$11\frac{1}{2} \times 7\frac{1}{2}$	13 \times 8	13 \times 8	13 \times $7\frac{1}{2}$	$10\frac{1}{2} \times 7\frac{1}{2}$
64		61	65	61	61	58	71
8 \times 6	$9\frac{1}{2} \times 7$	$8\frac{1}{2} \times 7$	$7\frac{1}{2} \times 6\frac{1}{2}$	$8\frac{1}{2} \times 6\frac{1}{2}$	8 \times $6\frac{1}{2}$	10 \times $6\frac{1}{2}$	$7\frac{1}{2} \times 7$
75	78	82	86	76	81	65	93
30		$34\frac{1}{2}$	30	33	33	38	
27							

A. M. 20652 A. M. 22979 A. M. 22978 A. M. 20756 A. M. 20702 A. M. 20800 A. M. 20979 No data

149e							
17		18	$16\frac{1}{2}$	17	17	$17\frac{1}{2}$	
$11\frac{1}{2}$		12	10	$10\frac{1}{2}$	10		
		67	61	62	59		
68							
59							
40							
32		36	31	$32\frac{1}{2}$	31	37	
79e							
40							
5 \times 2			4 \times $1\frac{1}{2}$				
$5\frac{1}{2} \times 2\frac{1}{2}$		5 \times 2		6 \times 3			
$5\frac{1}{2} \times 3$		$5\frac{1}{2} \times 3$	$5\frac{1}{2} \times 2\frac{1}{2}$	6 \times 3	$5\frac{1}{2} \times 2$		
55		55	45	50	56		
7 \times 4	$7\frac{1}{2} \times 5\frac{1}{2}$	8 \times 5	$7\frac{1}{2} \times 4$	$7\frac{1}{2} \times 4$	$7\frac{1}{2} \times 3\frac{1}{2}$	8 \times $4\frac{1}{2}$	$6\frac{1}{2} \times 4\frac{1}{2}$
57	73	63	53	53	47	56	69
11 \times $6\frac{1}{2}$		12 \times $7\frac{1}{2}$	$10\frac{1}{2} \times 6\frac{1}{2}$	$10\frac{1}{2} \times 6\frac{1}{2}$	11 \times $6\frac{1}{2}$	12 \times $7\frac{1}{2}$	$10\frac{1}{2} \times 6\frac{1}{2}$
59		62	62	62	59	63	62
11 \times $7\frac{1}{2}$		$12\frac{1}{2} \times 8$	11 \times 8	11 \times 7	$11\frac{1}{2} \times 7\frac{1}{2}$	13 \times $8\frac{1}{2}$	$11\frac{1}{2} \times 7$
68		64	73	64	65	65	61
$9\frac{1}{2} \times 6\frac{1}{2}$		$10\frac{1}{2} \times 6\frac{1}{2}$		$9\frac{1}{2} \times 6\frac{1}{2}$	9 \times 6	11 \times 7	$8\frac{1}{2} \times 6$
68		62		68	67	63	70

The Axial Skeleton

THE VERTEBRAL COLUMN

As would be expected, the vertebrae of *Orycteropus gaudryi* are much smaller than those of the recent aard-varks. The differences between the vertebral column of the fossil and recent forms are not confined to those of size, but extend to the expression of proportions as well, and in addition involve the development of individual parts or structures on the vertebrae. That is, the vertebrae of the recent aard-varks are, throughout the series, proportionately wider transversely than are the vertebrae of the fossil. This difference is due, of course, to the general transverse growth of all parts accompanying the increase in size of *Orycteropus* during its evolutionary development from Lower Pliocene to Recent times.

The general transverse growth of the vertebrae during evolution is particularly well exemplified by the atlas, which is larger and heavier in the recent than in the fossil species, but in which the growth increments have been proportionately equal, so that there has been little change in the proportion of the separate parts of vertebrae to the structure as a whole. The same is generally true of the axis, except that in this vertebra there has been a slight forward growth of the odontoid and the anterior part of the centrum, with the result that in the largest of the recent forms the facets for articulation with the axis are not quite so transversely placed as they are in the fossil. Again, the same is generally true of the following cervical vertebrae, except that here there has been a differential growth of parts, causing the transverse processes in the recent aard-varks to be expanded laterally, in relation to the centrum, so that they show a greater relative increase in size than does the vertebra as a whole in a comparison between the fossil and the recent forms.

In the dorsal or thoracic vertebrae there is a general increase in size and a relative increase in transverse dimensions in the recent *Orycteropus* as compared with the Pliocene species. As in the case of the cervicals, the dorsals show a differential

lateral growth of the transverse processes, so that these structures are relatively more expanded in the recent than in the fossil form. None of the lumbar vertebrae of the fossil has the transverse processes completely preserved, but it would seem probable that much the same differential increment was present in this section of the vertebral column as characterized the more anterior region. In addition it would appear as if the zygapophyses in the recent forms are somewhat more strongly convex than is the case in the fossil, thereby affording a strengthened series of articulations in this portion of the back, subjected in increasingly larger animals to increasingly more severe stresses. Moreover, it would appear as if the anterior oblique processes are proportionately larger in the recent form than they are in the fossil.

The sacral vertebrae are not preserved in the fossil. In the caudal region it would seem that there has been a simple increase in size in the modern *Orycteropus* over the fossil with very little differential growth.

These are the differences to be seen between *Orycteropus gaudryi*, *Orycteropus capensis* and *Orycteropus erikssoni faradjius* in the vertebral column. Except for these size differences, both general and differential, the vertebral series in the forms being compared are similar. The characters distinguishing the vertebral column of *Orycteropus* as a genus from that of other mammals are as follows.

In the first place, the back is strongly arched, the retention of a primitive character inherited from an Eocene ancestor. In the modern form there are seven cervicals, thirteen dorsals, eight lumbar, six sacrals and about twenty-five caudals. This same vertebral formula, so far as can be determined, is characteristic of *Orycteropus gaudryi*. The large number of sacrals is, of course, distinctive. In the axis there is a backwardly-extending spine. A vertebro-arterial canal is present in the seventh cervical. There are no accessory articular surfaces on the lumbar vertebrae as are characteristic of the edentates.

There are no essential differences except those of size to be seen between the fossil

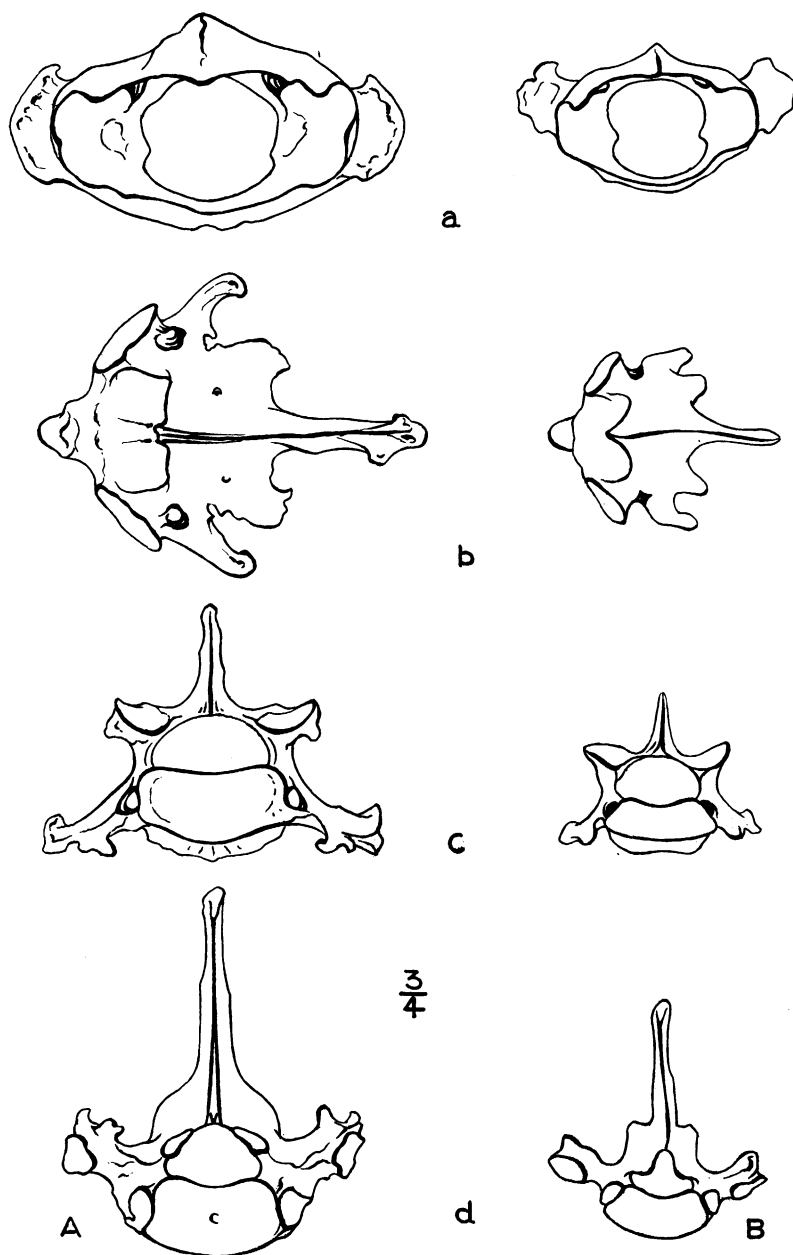


Fig. 8. Vertebrae of (A) *Orycteropus erikssoni faradjius* Hatt, Amer. Mus. No. 51905, as compared with those of (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 22762. (a) atlas; (b) axis; (c) fourth cervical; (d) sixth dorsal. Dorsal views of axis vertebra, anterior views of all others. Three-fourths natural size.

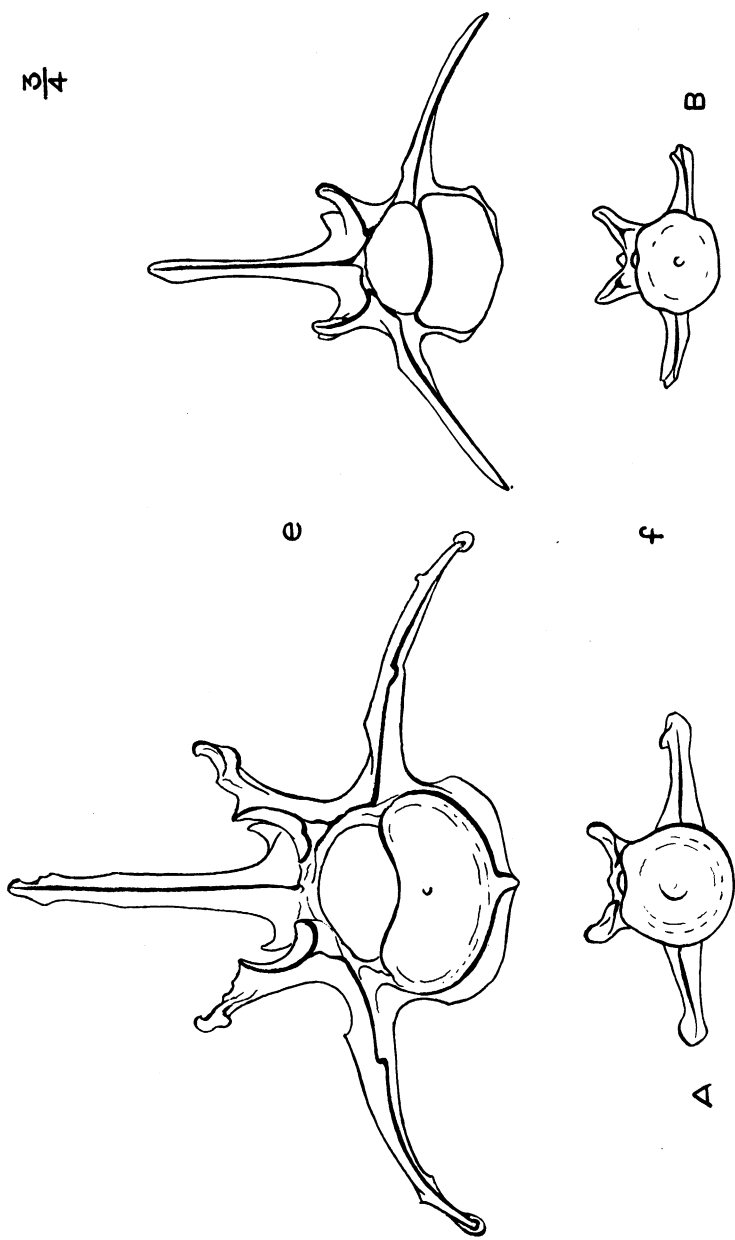


Fig. 9. Vertebrae of (A) *Orycteropus eriksoni* Jaradjius Hatt, Amer. Mus. No. 51905, as compared with those of (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 22762. (e) seventh lumbar; (f) tenth caudal. Anterior views, three-fourths natural size.



Fig. 10. The right scapula of (A) *Orycteropus erikssoni faradjius* Hatt, Amer. Mus. No. 51905, as compared with that of (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 22762. External lateral views, three-fourths natural size.

and recent species as regards the ribs and sternum.

The Appendicular Skeleton

THE FORE-LIMB

The scapula in both the fossil and the recent *Orycteropus* is a rather broad, quadrate bone, due to the expansion of the infraspinal portion of the bone so that the inferior border is more or less parallel to the superior border. This character in the scapula is, however, more pronounced in the fossil than in the recent species because the inferior border of the bone is proportionately longer in the extinct than in the recent form. And this in turn is due to the fact that in the recent *Orycteropus* there has been a lengthening or pulling out of the distal portion of the scapula so that the "neck" of the bone is proportionately longer and the scapular notch is broader than is the case with the fossil. The differential growth of the lower part of the scapula is more pronounced in *Orycteropus erikssoni faradjius* than it is in the smaller *Orycteropus capensis*, so that this latter species is generally intermediate as regards this character between the large recent species and the fossil. In both fossil and recent species there is a large, posteriorly-directed process on the acromion, and in both the scapular spine is high and strong. In the recent *Orycteropus erikssoni faradjius* the coracoid process terminates in a heavy tubercle, whereas in *Orycteropus capensis* and in the fossil this tubercle is quite small. Moreover, the coracoid of *Orycteropus erikssoni faradjius* is not expanded upwardly, as it is in the Cape aard-vark and the fossil.

The humeri of the fossil and recent forms are on the whole much alike, the principal differences being those of size and of proportion, due to the transverse expansion that has taken place in the recent species. There has been some differential growth in the development of the humerus of the recent *Orycteropus* in that the inner condyle has grown laterally and downwardly or distally with relation to the rest of the bone. Also, the epicondylar crest is somewhat more expanded in the recent aard-varks than it is in the fossil. In

both, the greater and lesser tuberosities are well developed, the bicapital groove is deep, there are strong deltoid and epicondylar ridges and a large entepicondylar foramen, while the trochlea and capitellum are well marked, the latter being globular in form. The principal qualitative difference is that in the fossil the olecranon fossa is not bounded proximally by a rim as it is in the recent species.

The development of the radius and ulna during the interval between lower Pliocene and recent times has been a simple process of size increase, with very little differential growth to change the relative proportions of the bones. Of course, there has been the usual transverse expansion in the recent forms as compared with the fossil. But otherwise the similarities are close, the ulna being marked by its compressed shaft and massive, inwardly-bent olecranon—the radius by its expanded distal articular surface and the keeled anterior border. One difference is apparent—in the modern *Orycteropus* the olecranon is expanded so that it is relatively somewhat heavier than is the same process in the fossil. As in the case of the other bones, the radius and ulna of *Orycteropus capensis* is intermediate in size and form between that of *Orycteropus gaudryi* and *Orycteropus erikssoni faradjius*.

Differences between the fossil and recent species in the manus are mainly those of proportion, there being an increment in the transverse relative dimensions in the recent forms. As applied to the carpal elements, this means that the individual carpal bones of the fossil are slightly less robust than they are in the modern aard-varks. Also, in the modern forms, the proximal articulations of the metacarpals are somewhat expanded, as compared with these articular surfaces in the fossil. Perhaps the most significant change in proportion is the relatively larger size of the manus in the recent aard-vark as compared with that of the fossil, a change in proportion that is most noticeable in the length of the digits. Thus the third digit in the manus of *Orycteropus gaudryi* is considerably shorter than the third digit of the pes of that same animal, whereas in *Orycteropus*

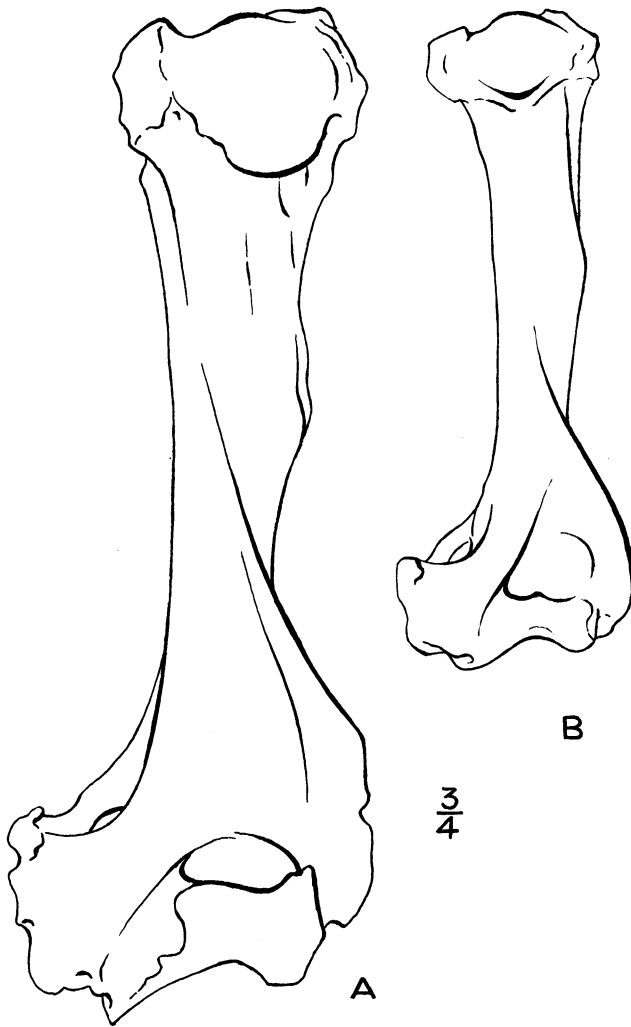


Fig. 11. The right humerus of (A) *Orycteropus erikssoni faradjius* Hatt, Amer. Mus. No. 51905, as compared with that of (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 22762. Posterior views, three-fourths natural size.

erikssoni faradjius the length of the third digit of the manus is approximately equal to that of the same digit in the pes. *Orycteropus capensis*, as might be expected, is about midway between the fossil and the Congo form with regard to this character. Evidently there has been an increase in the relative size of the fore-foot during the evolution of *Orycteropus* as a result of

the accentuation of its fossorial habits—a change that is reflected in other parts of the body.

Generally speaking, the manus of the fossil and recent aard-varks is marked by the decided asymmetry of the foot, due to the elongation of the inner digits and the shortening of the outer ones. The first digit is virtually suppressed, while the re-

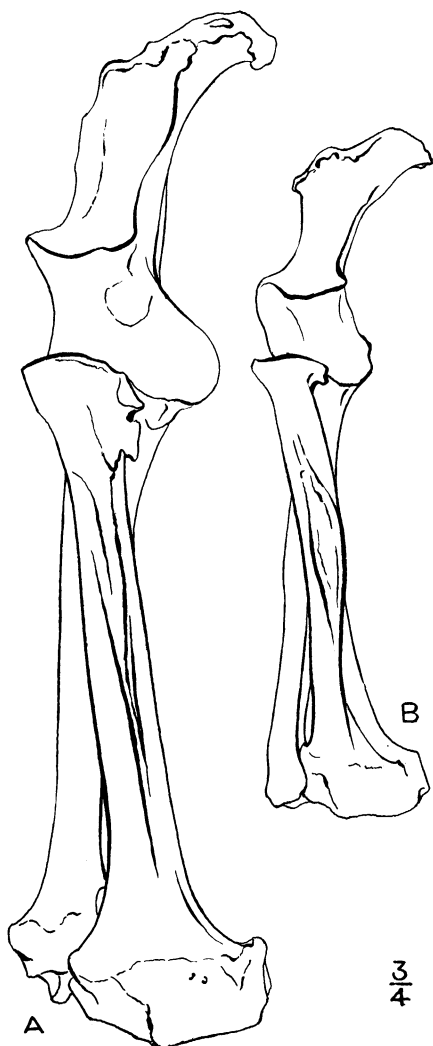


Fig. 12. The right radius and ulna of (A) *Orycteropus erikssoni faradjius* Hatt, Amer. Mus. No. 51905, as compared with those of (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 22762. Anterior views, three-fourths natural size.

maining ones are increasingly shorter, from the second to the fifth. There is a large scapho-centrale in *Orycteropus*.

Parenthetically, it might be said that Gregory's statement (1910) that the lunar and unciform are separated while the scapho-centrale is fused with the lunar, is in error.

There is a broad articulation between the lunar and the unciform in *Orycteropus*, while the scapho-centrale is quite separate from the lunar. (See Fig. 14.)

THE HIND-LIMB

The femur is proportionately broader and heavier in the modern *Orycteropus* than it is in the fossil. In fossil and recent forms there is a large greater trochanter, extending up as high as the head of the femur, a well-developed lesser trochanter and a prominent third trochanter. There are well-marked supra-condyloid fossae above both internal and external condyles (epicondyles), these being much deeper in the recent forms than in the fossil. In fact, *Orycteropus erikssoni faradjius* is characterized by the very prominent fossa above the internal condyle, its borders being marked by a raised rim. In all of the species there is a prominent pit for the ligamentum teres. In *Orycteropus erikssoni faradjius* the notch between the greater trochanter and the head of the femur is broader and shallower than in the fossil form—the result of transverse growth, while the third trochanter is considerably enlarged in relation to the rest of the bone. The femur of *Orycteropus capensis* is more or less intermediate between the fossil and the recent large species, in these respects.

As in the recent forms, the tibia and fibula of *Orycteropus gaudryi* are fused proximally. In the fossil and recent species these bones are characterized by the heaviness of the tibia, and the height and strength of its supinator crest, and by the well-developed fibula having an articular surface for contact with the calcaneum. In the course of the transverse growth of these bones, consequent upon the increase in size, there has been a certain amount of "bowing out" of the mid-shaft of the fibula, so that in the recent species this bone is more curved laterally than it is in the fossil. Thus there is a relatively greater space between the tibia and the fibula in the recent forms than there is in the Pliocene species.

The principal difference between the pes

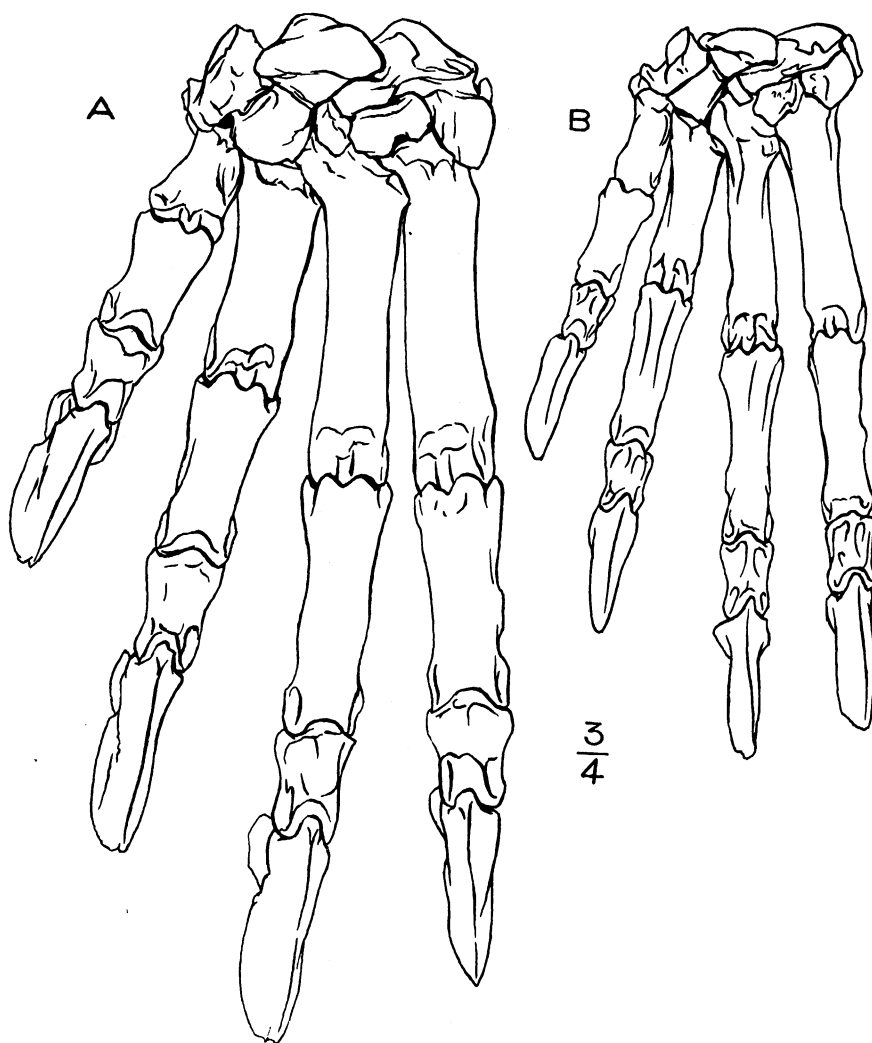


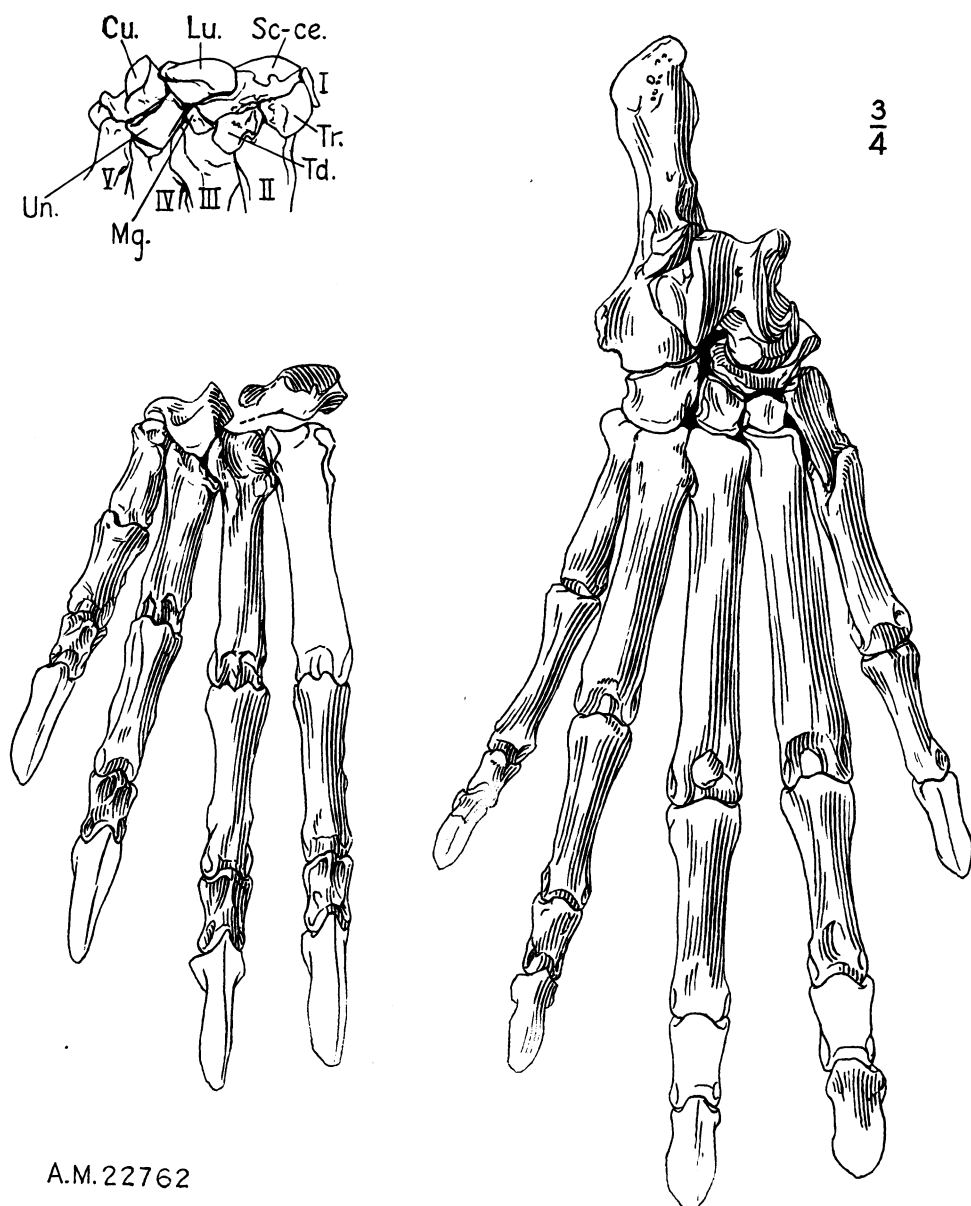
Fig. 13. The right manus of (A) *Orycteropus erikssoni faradjius* Hatt, Amer. Mus. No. 51905, as compared with that of (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 22762. Dorsal views, three-fourths natural size.

of the recent *Orycteropus* and that of the fossil form is the greater relative breadth of all of the component bones in the recent forms. This is particularly evident in a comparison of the tarsus, and especially as concerns the astragalus. Also the fifth digit in the recent aard-vark is relatively shorter than it is in the Pliocene form.

Otherwise the hind feet in the fossil and

recent *Orycteropus* are quite similar, showing those characters typical of the genus, such as the astragalar foramen, the ball-like navicular articulation on the astragalus and the five well-developed digits.

In contrast to the development of the manus, there has been no relative increase in the size of the pes in *Orycteropus* between Lower Pliocene and Recent times.



A.M. 22762

Fig. 14. *Orycteropus audryi* Major. Amer. Mus. No. 22762, right manus and pes. Dorsal views, three-fourths natural size.

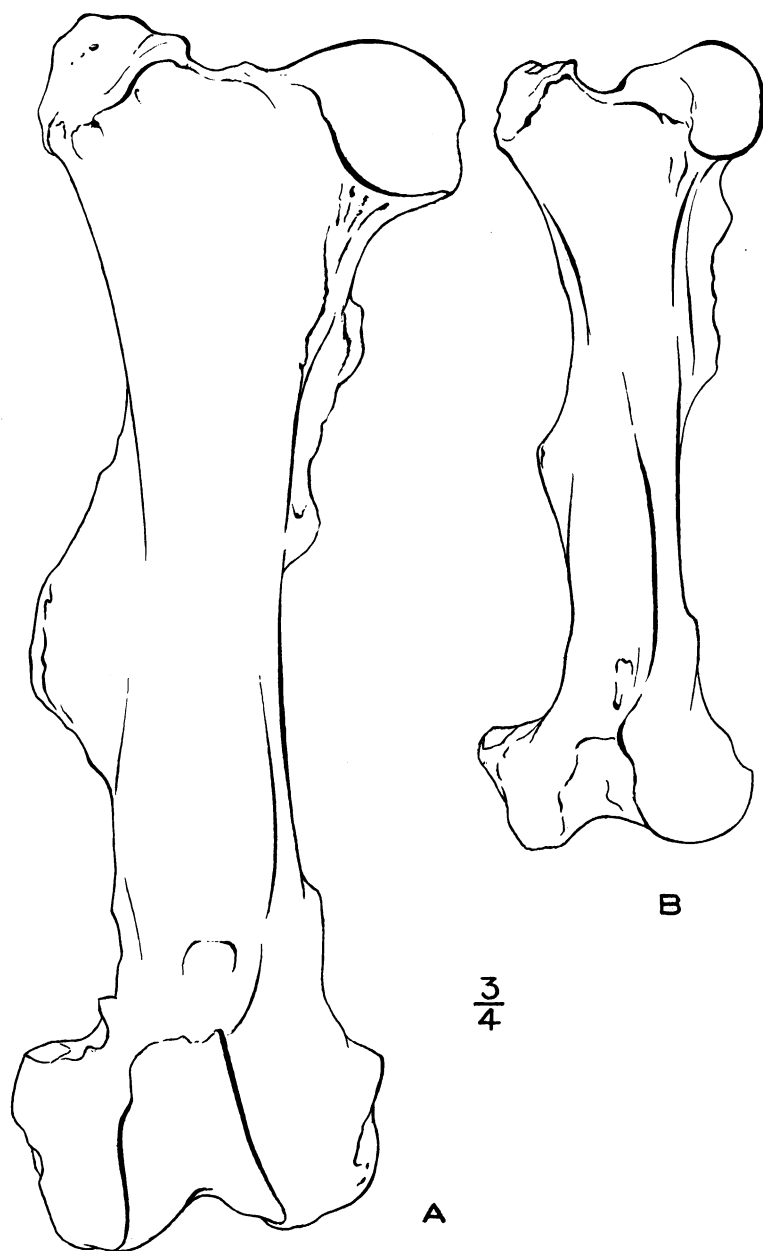


Fig. 15. The right femur of (A) *Orycteropus erikssoni faradjius* Hatt, Amer. Mus. No. 51905, as compared with that of (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 22762. Anterior views, three-fourths natural size.

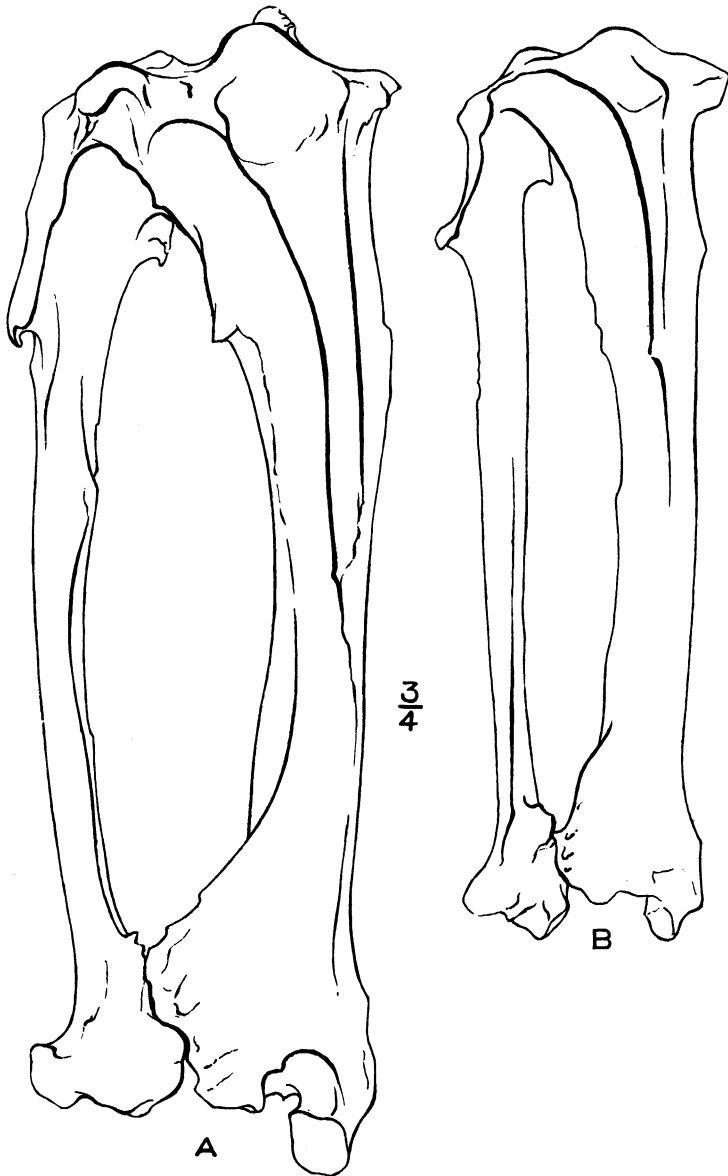


Fig. 16. The right tibia and fibula of (A) *Orycteropus erikssoni faradjius* Hatt, Amer. Mus. No. 51905, as compared with those of (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 22762. Anterior views, three-fourths natural size.



Fig. 17. The right pes of (A) *Orycteropus erikssoni faradjius* Hatt, Amer. Mus. No. 51905, to be compared with that of *Orycteropus gaudryi* Major (Fig. 18). Dorsal view, three-fourths natural size.

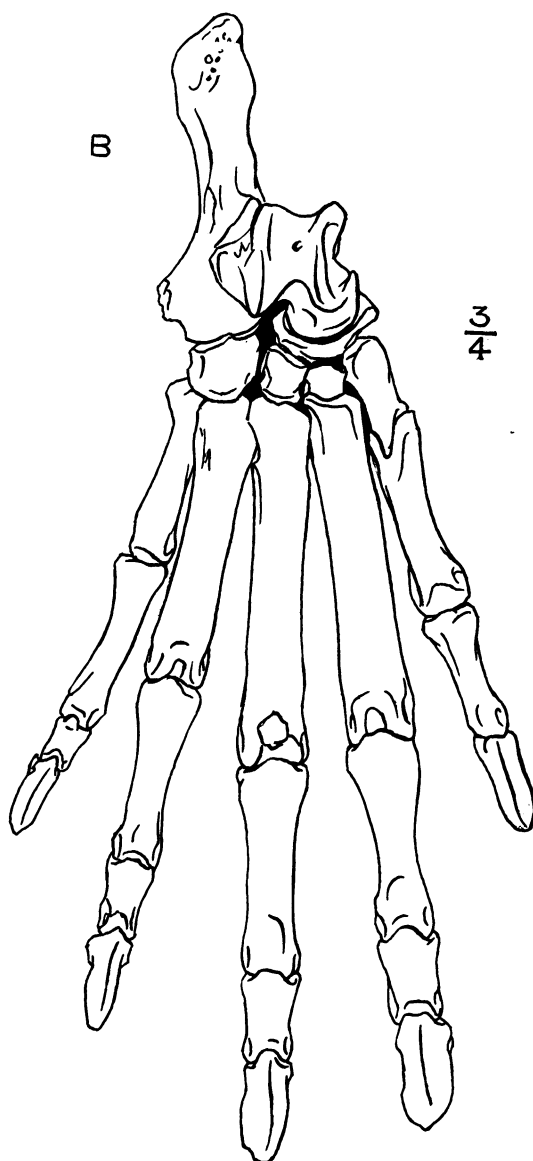


Fig. 18. The right pes of (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 22762, to be compared with that of *Orycteropus erikssoni faradjius* Hatt (Fig. 17). Dorsal view, three-fourths natural size.

MEASUREMENTS

	<i>Orycteropus erikssoni faradjius</i> A. M. 51905	<i>Orycteropus capensis</i> A. M. (CA) 2285	<i>Orycteropus gaudryi</i> A. M. 22762
Atlas—greatest breadth	67 mm.	53 mm.	47 mm.
breadth, condylar articulation	52	42	34
height	38	33 $\frac{1}{2}$	26 $\frac{1}{2}$
Axis—greatest breadth	53	45	32e
breadth of centrum	24	20	17
height “ “	11 $\frac{1}{2}$	9 $\frac{1}{2}$	8
length “ “	27	23	18
Cervical—greatest breadth	61	53	35e
(5) breadth of centrum	26	21	18
height “ “	13	10	7 $\frac{1}{2}$
length “ “	17 $\frac{1}{2}$	14	11
Dorsal—greatest breadth	53	44	35e
(5) breadth of centrum	30	21	19
height “ “	13	10	9
length “ “	19	15	12
Lumbar—greatest breadth	119	101	85e
(6) breadth of centrum	36 $\frac{1}{2}$	31	26 $\frac{1}{2}$
height “ “	19	14	12
length “ “	27 $\frac{1}{2}$	23	21
Caudal—breadth of centrum	25	19	19
height “ “	21	16 $\frac{1}{2}$	14
length “ “	30	26	24
greatest breadth	84	53	46
Scapula—articular height	154	128	100
greatest ant.-post. dia.	106	82	71
Humerus—length	174	142	113
tr. dia. (distal)	62	52	41e
Radius—length	118 $\frac{1}{2}$	99	82
tr. dia. (distal)	35	30	20
Ulna—length (greatest)	173	147	120e
tr. dia. (prox.)	28 $\frac{1}{2}$	23	16
Manus—breadth of carpus	53	44	38
length of McIII	65	55	47 $\frac{1}{2}$
“ “ (III) phal. prox.	39	35	32
“ “ “ “ med.	20	17	14
“ “ “ “ ung.	35	30	26
“ “ extended manus	175	149	125
Femur—length	206	179	137
breadth (prox.)	75	66	45
“ (dist.)	60	54	41
Tibia-fibula—length	190	163	154
breadth (prox.)	59	52	41
“ (dist.)	61 $\frac{1}{2}$	53	38
Pes—breadth of tarsus	55	51	40
“ “ astragalus	40	34	23
height of astragalus	45	35	32
length of MtIII	85	75	69
“ “ (III) phal. prox.	41	38	39e
“ “ “ “ med.	18 $\frac{1}{2}$	17 $\frac{1}{2}$	16e
“ “ “ “ ung.	25 $\frac{1}{2}$	24	19e
“ “ extended pes	210	193	170

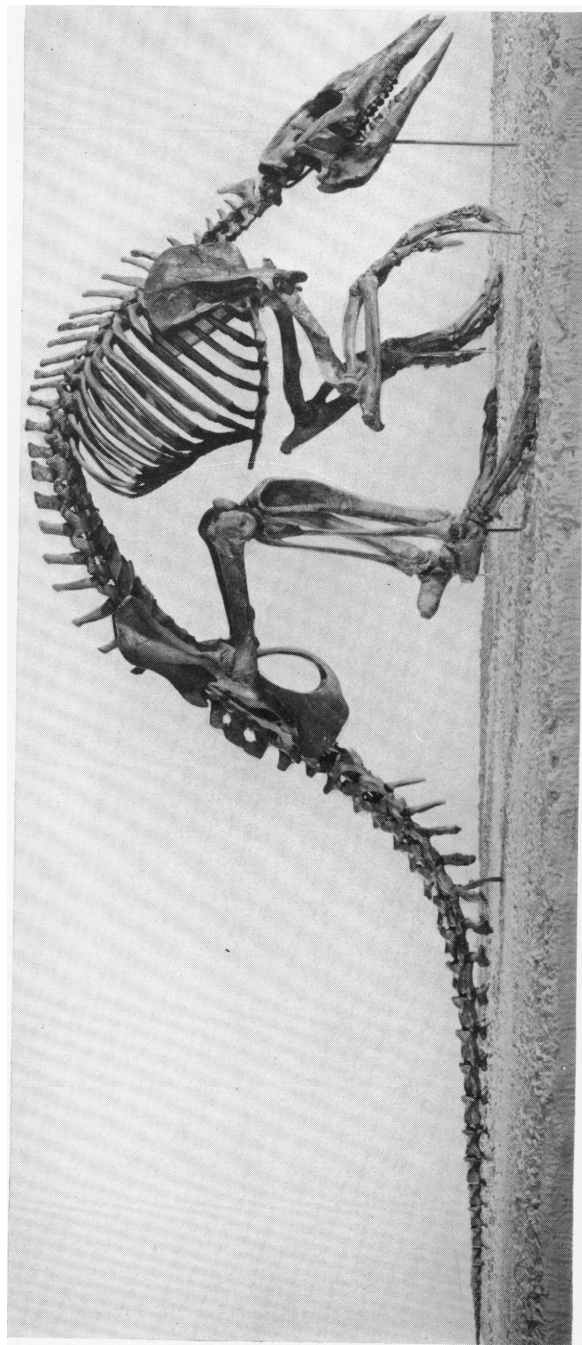


Fig. 19. *Orycteropus gaudryi* Major. Skeleton, as mounted by Charles Lang in The American Museum of Natural History. Skull and mandible, Amer. Mus. No. 20694; post-cranial skeleton, Amer. Mus. No. 22762. Lateral view of right side, one-sixth natural size.

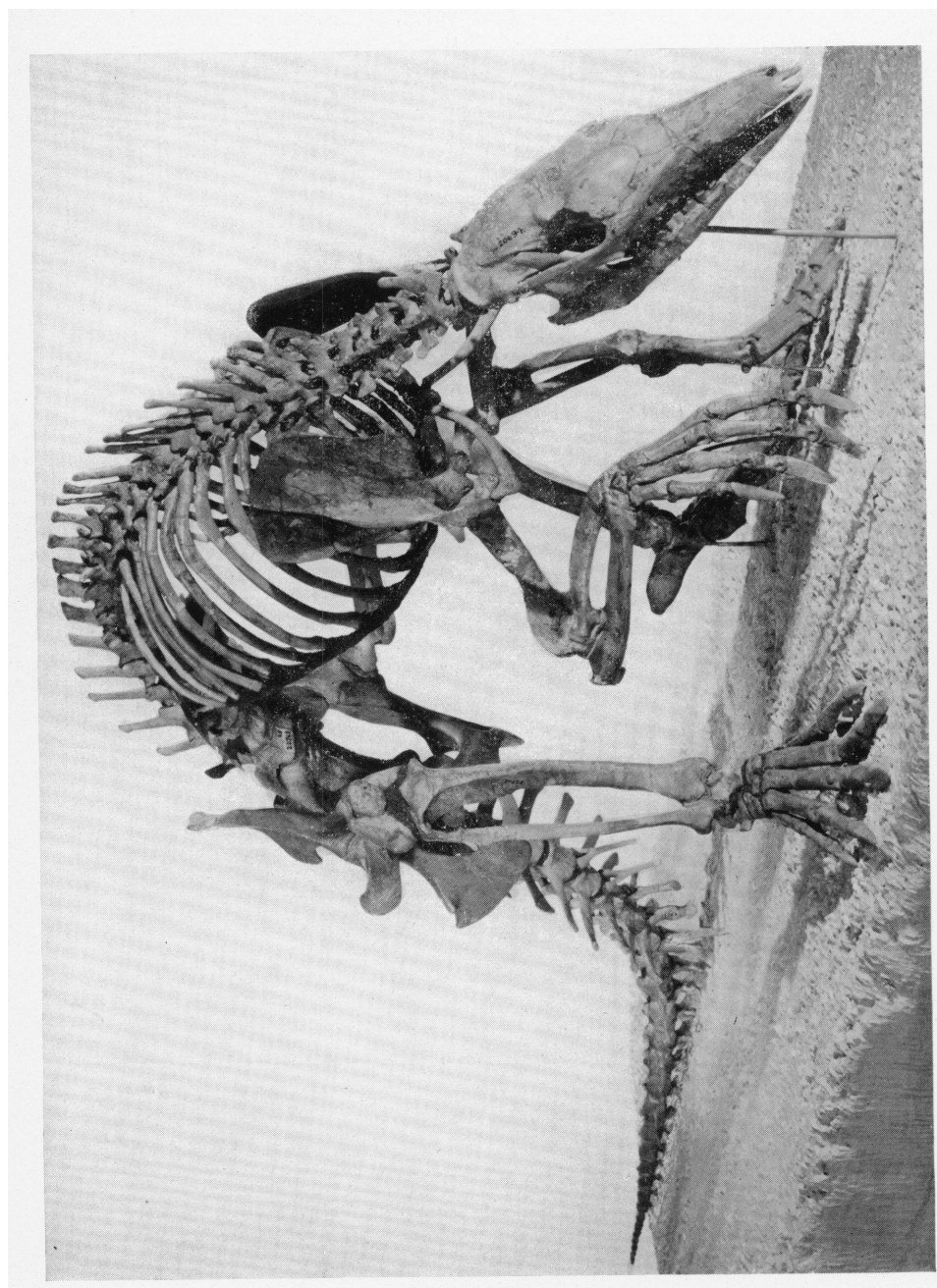


Fig. 20. *Orycteropus gaudryi* Major. The same specimen as shown in figure 19. Oblique view, approximately one-fourth natural size.

A COMPARISON OF *Orycteropus gaudryi*
AND *Orycteropus erikssoni faradjius* BY
THE USE OF DEFORMED COÖRDINATES

The use of deformed coördinates to illustrate changes of proportion in related animals was devised by D'Arcy Thompson in 1917. As applied by Thompson, the method is essentially as follows:

"On a drawing of all or any part of an animal a regular system of rectangular coördinates is superposed. The same parts of an allied animal are then drawn, and on it are superposed lines, some or all of which usually must be curved, such that each line passes as nearly as is practical through points homologous with those touched by a corresponding line on the first drawing and each space between the lines covers approximately the same anatomical features as a corresponding square (or rectangle) on the first drawing. There is no way of making all the points and areas correspond absolutely if the animals differ markedly, but a close approximation is usually possible for forms that are visibly related. An effort is made to make the second system, the deformed coördinates, as simple as possible, with its lines smooth curves and not strongly irregular."¹

It occurred to the author some years ago that this system might be modified by making the points and lines of the second or deformed system correspond as nearly as possible in their homologous positions to the points and lines of the first or undeformed system. In this way, the small changes within a structure, as well as the general trend of proportional change might be shown. This modification of Thompson's method is applied as follows:

"The method is most usefully applied by taking an ancestral or a presumably primitive animal as a standard of comparison, laying the rectangular coördinates on it, and then developing from it systems of deformed coördinates for more specialized descendants or relatives. The deformed coördinates then provide a vivid visualization of the differential expansion,

contraction, and skewing that have taken place in the course of evolution."²

In the accompanying figures, the changes involved in the presumed transformation of *Orycteropus gaudryi* into a modern species of *Orycteropus* are shown by the deformed coördinate method. A system of rectangular coördinates is laid down over the drawings of the various skeletal parts of the Pliocene species. These coördinates are then fitted to the skeletal parts of the recent form, *Orycteropus erikssoni faradjius* (the largest and most specialized species of the genus), making all points and lines as nearly homologous in position as possible to their location on the more primitive type, without regard for regularity of the consequent grid.³ In this way, the various expansions, contractions and skewing resulting during the transformation of a lower Pliocene type into a larger, more advanced modern type are shown. Naturally this procedure does not necessarily prove anything—but it does show in a very graphic way the changes described and figured on preceding pages of this work.

² Simpson, G. G., and Roe, Anne. 1939. *Op. cit.*, p. 335.

³ In establishing the rectangular coördinates upon the skeletal elements of the primitive form (*Orycteropus gaudryi*) certain procedures were followed, which it might be well to explain briefly at this place, in order that the reader may have an understanding as to how this method of graphic illustration was actually carried out. The original rectangular grid, drawn over the elements of the primitive type, was arbitrarily chosen as to arrangement and size. Certain anatomical characters were utilized, however, as a guide in the establishment of the grid. Thus in the side view of the skull, the front of the orbit was used as the reference point for the vertical lines, and the alveolar line of the maxilla for the horizontal lines. The squares were laid out regularly from these two "base-lines" at such an interval that there would be a sufficient number of them to make the changes undergone in the transition from the primitive to the advanced type readily apparent. On the top view of the skull, the midline and the front of the orbit were used for the base-lines. On the side view of the mandible, the alveolar line and the anterior border of the first molar. On the vertebrae the midline was used as the base-line for the vertical lines, while the top of the neural arch was utilized for the horizontal lines. In the axis, shown in top view, the anterior borders of the atlantal articulations were used for one set of coördinates. On the bones of the limbs and feet, a general median line was chosen as a base-line for the vertical coördinates, while the proximal end of the bone was used for the horizontal system of lines. It will be noticed that on the spines of the vertebrae and on the limb elements the coördinates are not laid down in squares, but in rectangles, with their long dimensions parallel to the long axis of the bone in each case. This was done merely as a matter of convenience, since it was felt that rectangles were just as useful as squares for showing changes in proportion, while their use involved the plotting of fewer points—thereby making for increased clarity in the resultant figures.

¹ Simpson, G. G., and Roe, Anne. 1939. *Quantitative Zoology*, pp. 333-335.

The Skull and Mandible

In a lateral aspect, the most important changes shown by the deformed coördinates are those whereby the frontal sinuses are enlarged in the recent form and the tooth row is shifted forwardly in relation to the orbit and the infraorbital foramen. All of this latter change is not due, however, to the forward shift of the teeth, for the coördinates show that there has been a certain degree of shortening in the brain case, caused to some extent by a limited backward shift of the orbit. The compression in the otic region is particularly marked. Also, it is to be noticed that there has been a backward growth of the occipital condyles.

In the backward shifting of the orbit there has been a certain amount of depression of its lower border, as can be seen.

In its dorsal aspect the skull shows the effect of differential growth of parts during the course of evolution between Lower Pliocene and Recent times. Accompanying the enlargement of the frontal sinuses there has been a lengthening in that portion of the skull-roof immediately over the orbits. The other large change apparent is the broadening of the muzzle, from the naso-frontal suture to its tip.

The mandible in lateral aspect shows a certain amount of lengthening, but more particularly a backward compression of the coronoid and that portion of the ascending ramus below it towards the condyle.

The Vertebrae

The main change shown by the deformed coördinates is the transverse increment of growth in the recent species as compared with the fossil. The differential lateral

growth of the transverse processes is also made apparent by this method of graphic representation—particularly as it affects the cervical vertebrae.

The Fore-Limb

SCAPULA

The elongation of the distal portion, or neck, of the scapula as compared with the blade is quite apparent. In addition, this distal section of the bone has tended to push anteriorly somewhat, in comparison to the upper part of the bone.

HUMERUS

In this bone there has been some elongation of the distal part as compared with the more proximal region, and in addition differential inward and downward growth of the internal condyle.

RADIUS-ULNA

As the deformed coördinates show, the evolutionary growth of the radius and ulna has been fairly uniform. In the modern species there is a differential growth in length of the proximal part of these bones, as compared with their shafts—also a certain degree of broadening of the distal articular region.

MANUS

The change here has been one mainly of uniformly correlated size increase of the individual elements.

The Hind-Limb

FEMUR

The most noticeable changes in this bone are the relative increase of the greater and the third trochanters in the modern form, as compared with the fossil.

TIBIA-FIBULA

As the deformed coördinates show, there has been a noticeable outbowing of the fibula during the transformation of the Pliocene into the recent species. Also the general increase in the relative transverse dimensions of these bones is apparent from the comparatively broader coördinate rectangles developed upon the drawing of the recent bones.

In locating the points on the derived type (*Orycteropus erikssoni faradjius*) corresponding to the intersections of the coördinate lines on the primitive type (*Orycteropus gaudryi*) it was found helpful to locate first of all certain "key points," such as those near the orbit, the infraorbital foramen, sutures, articular surfaces, etc. Working out from these, the other points were established with greater ease and more accuracy than might otherwise have been possible. Thus the trends of the deformed coördinate lines were established.

It is very important, of course, that the drawings on which the coördinates are plotted should be very accurate. The drawings used in this present contribution were made with a pantograph and were carefully checked.

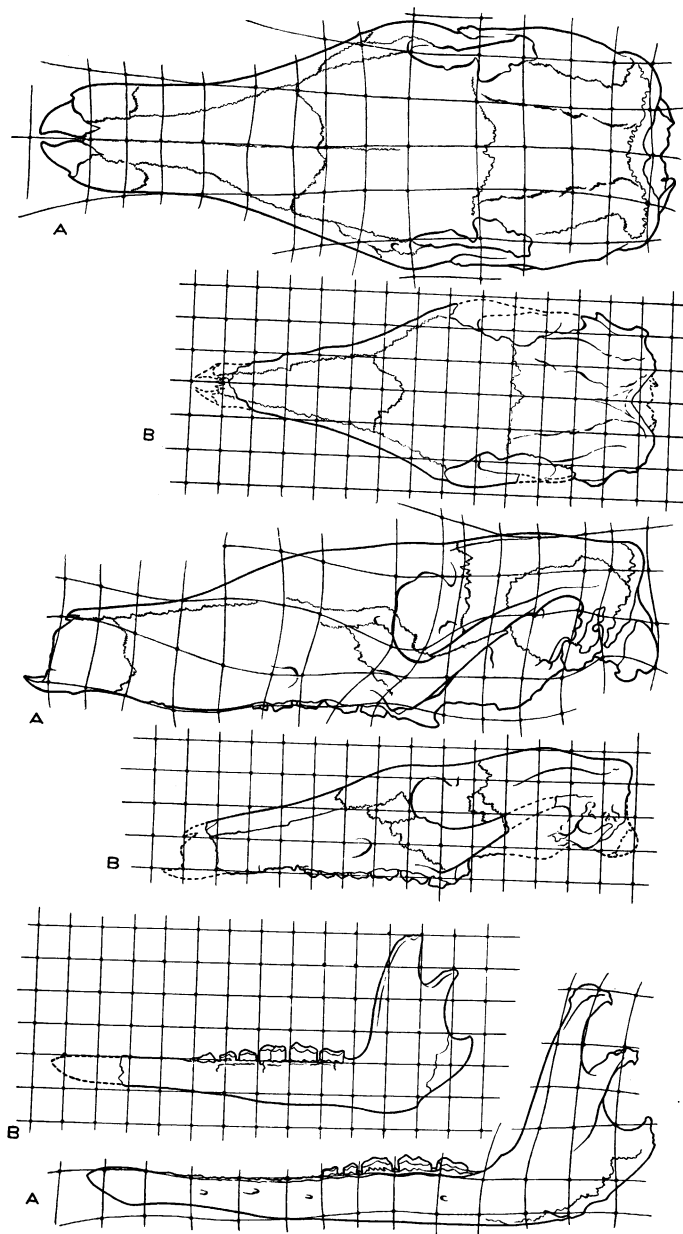


Fig. 21. Comparison of the skull and mandible of the modern aard-vark, (A) *Orycteropus erikssoni faradjius* Hatt, Amer. Mus. No. 51905, with those of the Pliocene form, (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 20694, by the use of deformed coordinates. (B) is used as the standard of comparison; the deformed coordinates in (A) show the differential growth that has taken place during evolution. Dorsal and lateral views of skull at top and in middle, lateral view of mandible at bottom. One-third natural size.

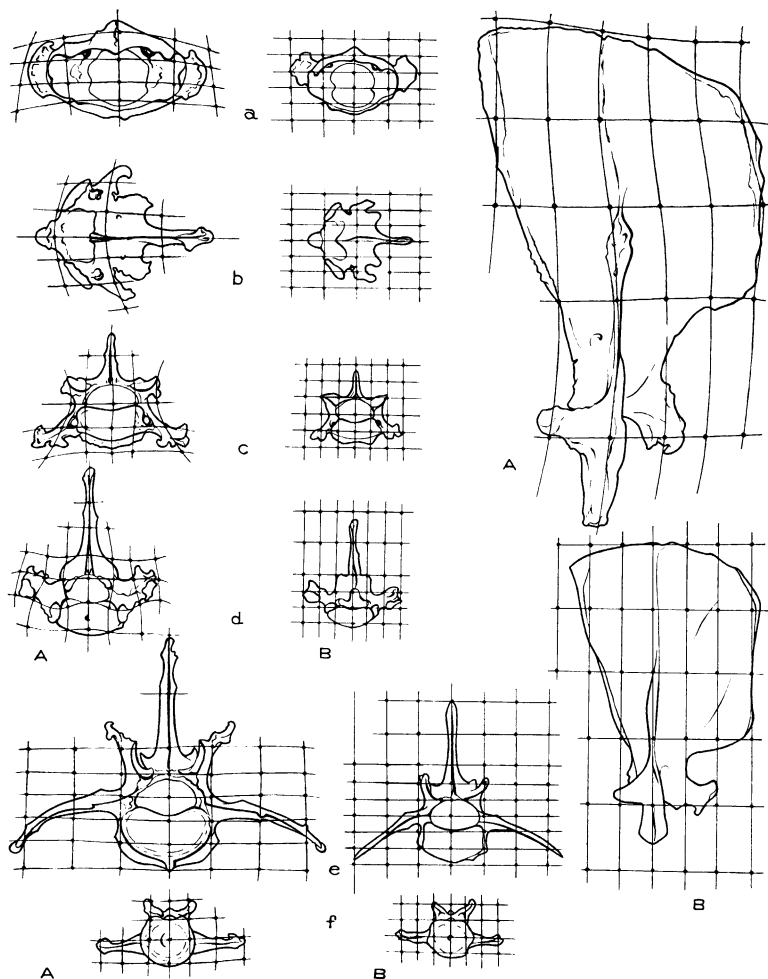


Fig. 22. Comparison of the vertebrae and scapula of the modern aard-vark, (A) *Orycteropus erikssoni faradjius* Hatt, Amer. Mus. No. 51905, with those of the Pliocene form, (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 22762, by the use of deformed coördinates. (B) is used as the standard of comparison; the deformed coördinates in (A) show the differential growth that has taken place during evolution. (a) atlas; (b) axis; (c) fourth cervical; (d) sixth dorsal; (e) seventh lumbar; (f) tenth caudal. Anterior views of vertebrae, except axis, of which dorsal views are shown; external lateral views of scapula. One-third natural size.

PES

The change here is mainly due to the broadening of the individual elements constituting the foot (as shown particularly by the comparative diagrams of the astraga-

lus). In the foot as a whole there has been the slightly increased disparity in size between the fifth digit and the three median digits in the recent form, as compared with the fossil—a change already discussed on a preceding page.

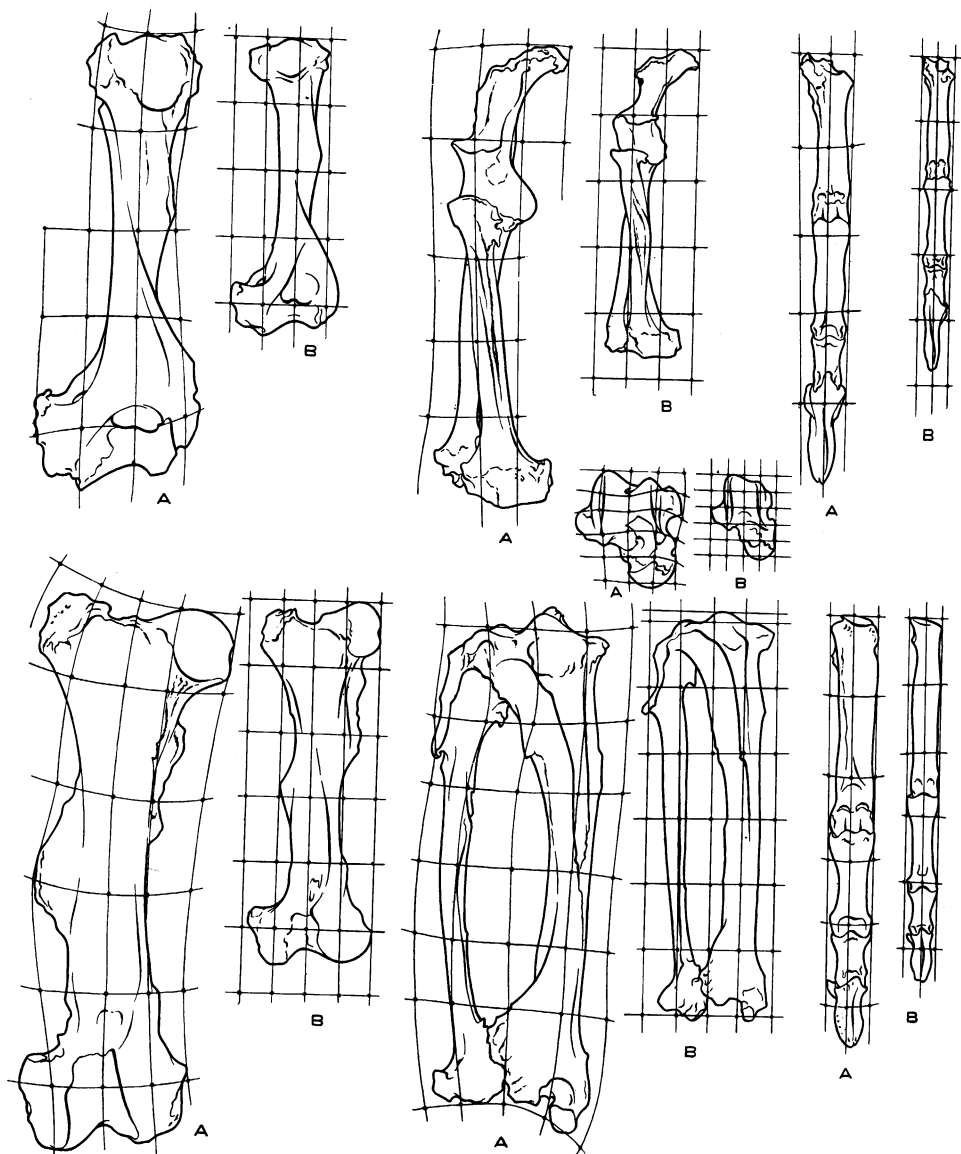


Fig. 23. Comparison of the limb and foot bones of the modern aard-vark, (A) *Orycteropus erikssoni faradjius* Hatt, Amer. Mus. No. 51905, with those of the Pliocene form, (B) *Orycteropus gaudryi* Major, Amer. Mus. No. 22762, by the use of deformed coordinates. (B) is used as the standard of comparison; the deformed coordinates in (A) show the differential growth that has taken place in evolution. Top, left to right: right humerus, right radius and ulna, right astragalus, right third metacarpal and phalanges. Bottom, left to right: right femur, right tibia and fibula, right third metatarsal and phalanges. Posterior views of humerus; anterior views of all other bones. One-third natural size.

THE ORIGIN OF THE TUBULIDENTATA

GENERAL CONSIDERATIONS

The position of *Orycteropus* as an isolated type, set apart from all of the other orders of modern mammals, has long been recognized by many students of mammalian taxonomy and phylogeny. Among the earlier authors it was customary to regard *Orycteropus* as being related in some way to the Edentata, so that its position in or near this order characterizes the earlier works on systematic zoology. In recent years, however, there has come to be a feeling that this animal is to be differentiated from the true edentates, its resemblances to the order being due to convergent evolution correlated with similarities in habits and diet.

Consequently, the recognition that the true position of the Tubulidentata is as a very distinct order of mammals having a heritage running far back into the history of mammalian evolution is now pretty well established. Many authors having an intimate acquaintance with fossil and recent mammals have advocated for some time that the origin of the Tubulidentata is to be found in or near certain of the "proto-ungulates," particularly the extinct order of Condylarthra. As opposed to this idea is the opinion of Jepsen, who studied the jaw and lower teeth of an Eocene mammal from North America, named by him *Tubulodon taylori*, and decided that this early type was more or less an approximate ancestor to the tubulidentates. Jepsen concluded that:

"The preserved fragments of *Tubulodon* do not support the proto-ungulate hypothesis. There is not a single character of the highly specialized jaws or teeth which can be considered as derived from or related to any described Paleocene form such as *Euprotogonia* or *Tetraclaenodon* or *Phenacodus* or any other known early Tertiary group. By late Lower Eocene time the jaw and tooth structures of the tubulidentates had already specialized so far along their unique evolutionary trend as to mask any obvious relationship to other Tertiary mammals. This fact adds a further degree of plausibility to the opinions of Broom

and Sonntag that the connection of the tubulidentates with other orders must be sought in the Mesozoic."¹

It is interesting to compare this opinion with that of Matthew expressed in his posthumously published report on the Paleocene mammals of New Mexico, in which he calls attention to the general resemblances of the primitive proto-ungulate genus *Ectoconus*—a genus of condylarth, or amblypod, or taligrade relationships, depending upon the system of classification followed—to the modern aard-vark.

His statement is as follows:

"The skeleton of *Ectoconus* compares in size and in most of its general proportions with that of *Orycteropus*. The tail is not so heavy and the feet are shorter, wider, less specialized and diversely adapted, but the proportions of neck, back, ribs, girdles and limbs are not very different. The skull is shorter and different in proportions, and the teeth are wholly diverse, but aside from the shape of the head the general appearance and proportions of the animal must have been more like those of *Orycteropus* than any other modern animal, only with much smaller tail and small, flattened, cony-like hoofs. This general resemblance does not involve any near relationship but indicates merely that the modern *Orycteropus* has retained with little alteration much of the proportions and structure that were common among primitive placentals of similar size. It is convenient, therefore, in describing the skeleton of *Ectoconus*, to make comparisons with that of *Orycteropus*."²

Matthew then proceeded to describe the skeleton of *Ectoconus* in a detailed fashion, making numerous comparisons throughout the extent of his description, between the individual skeletal elements of the Paleocene genus and the modern aard-vark. Yet this description, detailed as it is, may not fully convey the reality of the close resemblances throughout the skeleton be-

¹ Jepsen, G. L. 1932. Proc. Amer. Philos. Soc., LXXI, No. 5, p. 274.

² Matthew, W. D. 1937. Trans. Amer. Philos. Soc. (N. S.), XXX, p. 134.

tween the genera under consideration. Therefore it may be helpful to compare the postcranial skeletons of *Orycteropus* and *Ectoconus* in a graphic manner, using the method of deformed coördinates in a way similar to that whereby the skeletons of the fossil and recent *Orycteropus* were compared on preceding pages of this work. In the comparison of *Orycteropus* with *Ectoconus*, this latter genus, being a much earlier and an admittedly more primitive type of animal even than the earliest species of *Orycteropus*, is used as the standard of comparison, plotted against rectilinear coördinates. The amount of deformation then shown by the coördinates as plotted against the elements in *Orycteropus* will give some idea as to the degree of divergence that may have occurred during tubulidentate evolution.

A COMPARISON OF *Orycteropus* AND THE PALEOCENE CONDYLARTH, *Ectoconus*, BY THE USE OF DEFORMED COÖRDINATES

The Vertebrae

ATLAS

The main difference to be seen between the atlas of *Ectoconus* and that of *Orycteropus* is the relative broadening of the articulations in the modern genus. This indicates a larger and heavier neck in the aard-vark than in the condylarth.

AXIS

In keeping with the increase in the size of the neck during the long period of time during which the aard-varks have been developing, the axis shows a very great increase in actual and relative size, as compared with the same element in *Ectoconus*. Also there have been local growth increments in the modern genus, particularly noticeable in the backward extension of the spine.

CERVICALS

The size increase is less noticeable in the posterior cervicals of *Orycteropus*, as compared with those of *Ectoconus*. The striking difference here is the transverse expansion of the lower portion of the vertebra in the modern genus.

DORSALS

In contrast to the increase in the size of the neck, there has been a reduction in the size of the vertebrae of the dorsal region in the modern form, as is readily apparent from the figures. Also, as in the posterior cervical region, there is a certain amount of lateral expansion in the lower portion of the dorsal vertebrae in *Orycteropus*, as compared with *Ectoconus*.

LUMBARS

Orycteropus is very strong in the lumbar region, and this is shown by the heavy robust lumbar vertebrae, even when compared with the heavy lumbar of *Ectoconus*. In their general form, however, the lumbar vertebrae of these two genera are much alike, as is the case in other parts of the vertebral column. *Orycteropus* is distinguished by the downward bending of the transverse processes.

CAUDALS

A comparison of these vertebrae is not practicable.

The Fore-Limb

SCAPULA

As to the broad features, there is a striking similarity between the scapulae in *Ectoconus* and *Orycteropus*. In both the blade is flattened and roughly quadrangular. The scapula of *Orycteropus* has become specialized to a certain extent in the elongation and narrowing of the "neck," while the acromion process is extended ventrally. The acromion in all of the available *Ectoconus* material is broken, but from a comparison with *Pantolambda* it would seem that there was probably an extension and an enlargement of the process, even in the Paleocene types.

HUMERUS

The humerus of *Orycteropus* is specialized over that of *Ectoconus* mainly by virtue of its somewhat more slender form, with a resultant decrease in size of the deltoid crest, the expansion of the distal articulation, and the outward and upward twisting of the proximal articular surface.

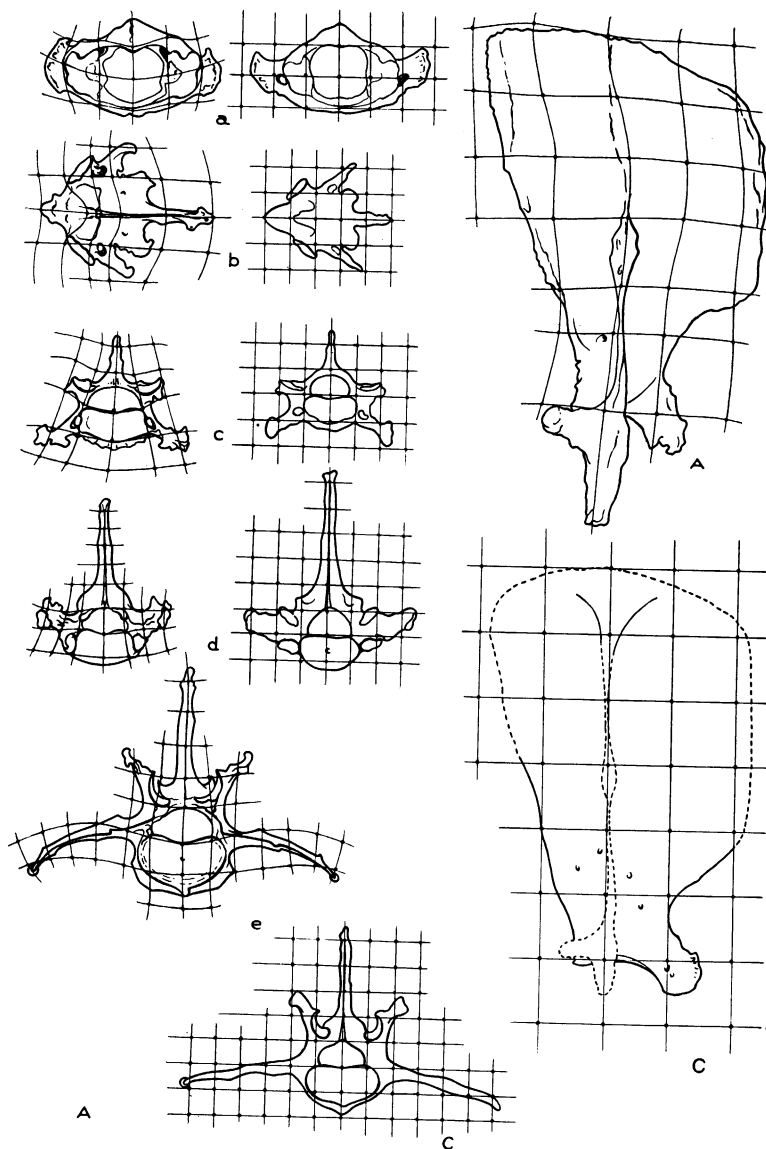


Fig. 24. Comparison of the vertebrae and scapula of the modern aard-vark, (A) *Orycteropus erikssoni faradjius* Hatt, Amer. Mus. No. 51905, with those of the Paleocene condylarth, (C) *Ectaconus majusculus* Matthew, Amer. Mus. No. 16500, by the use of deformed coördinates. (C) is used as the standard of comparison; the deformed coördinates in (A) show the amount of change and distortion required to derive A from C. (a) atlas; (b) axis; (c) fourth cervical; (d) sixth dorsal; (e) seventh lumbar. Anterior views of vertebrae, except axis, of which dorsal views are shown; external lateral views of scapula. One-third natural size.

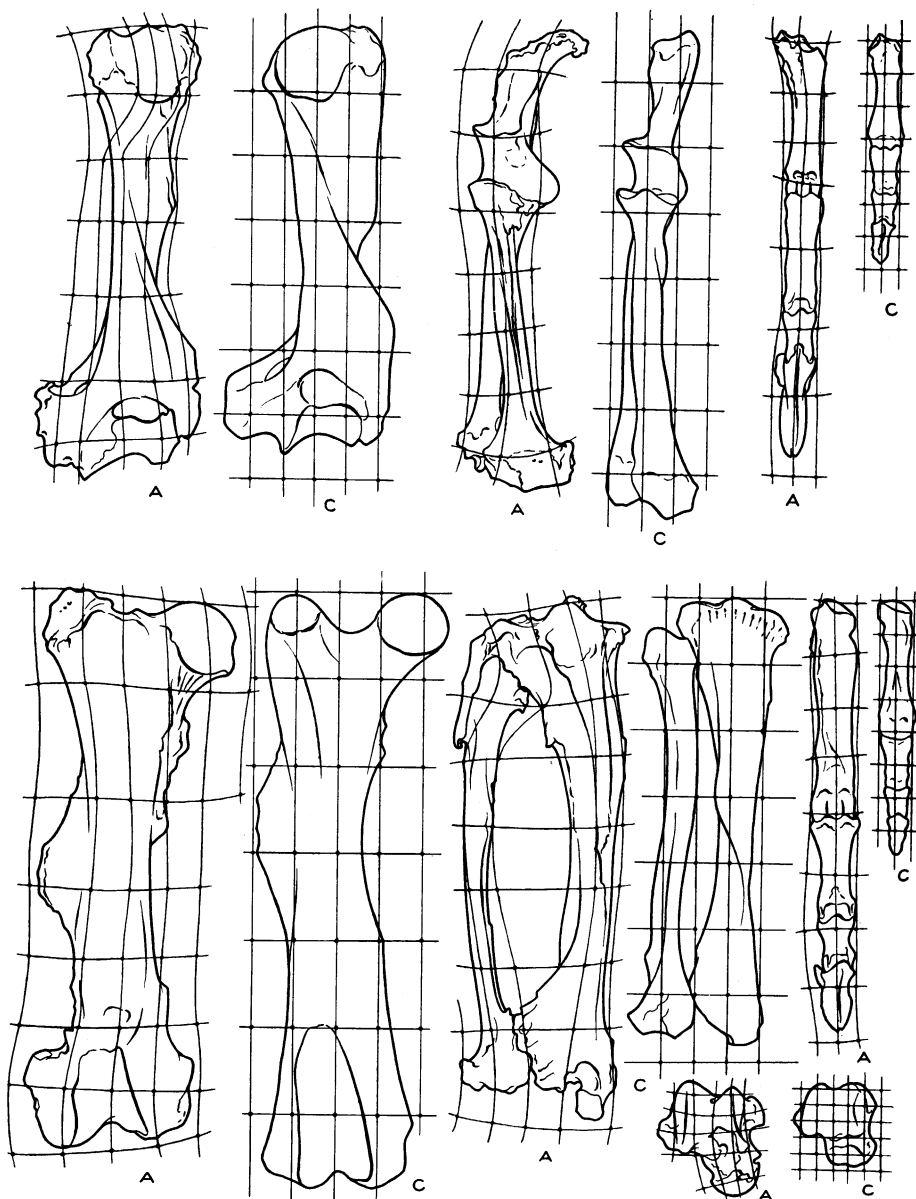


Fig. 25. Comparison of the limb and foot bones of the modern aard-vark, (A) *Orycteropus erikssoni* faradjius Hatt, Amer. Mus. No. 51905, with those of the Paleocene condylarth, (C) *Ectoconus majusculus* Matthew, Amer. Mus. No. 16500, by the use of deformed coordinates. (C) is used as the standard of comparison; the deformed coordinates in (A) show the amount of change and distortion required to derive A from C. Top, left to right: right humerus, right radius and ulna, right third metacarpal and phalanges. Bottom, left to right: right femur, right tibia and fibula, right third metatarsal and phalanges, right astragalus. Posterior views of humerus; anterior views of all other bones. One-third natural size.

RADIUS-ULNA

In *Orycteropus* these bones have advanced over the condition typical of a Paleocene condylarth by the broadening of the articular surfaces and the inward curving of the olecranon.

MANUS

Orycteropus is distinguished from the Paleocene condylarth because of the general increase in size of the feet—obviously correlated with the development of fossorial habits in the aard-vark. This is particularly apparent in the phalanges of the manus, which are relatively and actually very long as compared with the same elements in *Ectoconus*.

The Hind-Limb

FEMUR

Orycteropus shows specializations in this bone over the condition typical of *Ectoconus*, mainly in the slight expansions of the proximal and distal ends of the bone, and particularly the considerable increase in size of the third trochanter. There has been a local increment in length in the portion of the shaft between the third trochanter and the head of the bone, and a certain amount of longitudinal compression in the shaft between the trochanter and the distal condyles.

TIBIA-FIBULA

The great change that has occurred in the development of these bones in the aard-vark is their lateral "bowing" in opposite directions, so that the shafts become widely separated from each other in their middle regions. This transformation takes place mainly in the proximal portion of the fibula, as may be seen from the deformed coördinates. Such development results in a stronger hind-limb.

PES

As in the manus, the pes of *Orycteropus* is distinguished from the pes of *Ectoconus* by the actual and relative increase in size. The increase, as in the hand, has been particularly marked in the phalanges. The *astragalus* of *Orycteropus* is specialized over the condition found in a Paleocene condylarth mainly by the development of a long

"neck," carrying the navicular articulation ventrad as in its relation to the trochlea.

CONCLUSIONS

From the foregoing comparisons of the post-cranial skeleton of *Orycteropus* and *Ectoconus* by the deformed coördinate method, it is readily apparent that these two genera show numerous close resemblances to each other, which by their nature are probably of greater significance than is to be attributed to a general convergence in the habitus of the two animals. Therefore, this comparison justifies Matthew's contention that "The modern *Orycteropus* has retained with little alteration much of the proportions and structure that were common among primitive placentals of similar size."

This general resemblance between the two forms would indicate to the present author that although there may not be any very close relationship between the modern aard-varks and the early Tertiary condylarths, nevertheless these groups must have had a common ancestry in basal Tertiary or late Cretaceous times. Moreover, it seems to me that this primitive ancestor probably was a condylarth.

Looking at the Tubulidentates as we know them it might be reasonable to describe them as "persistent condylarths" in which the dentition has become completely transformed, the skull has been greatly modified and the feet have been moderately changed as adaptations to a myrmecophagous diet and a fossorial habitat. Yet these changes, distinct as they may be, do not mask the essential condylarth heritage as shown in the post-cranial skeleton of *Orycteropus*.

There is now to be considered the phylogenetic position of *Tubulodon*, accepted by various authors including the present writer as a form approximating an ancestral tubulidentate. Jepsen postulated this general relationship for the Eocene genus upon the basis of:

- 1.—The general shape of the lower jaw, and especially the structure in the symphyseal region.
- 2.—The loss of the anterior teeth.
- 3.—The somewhat columnar form of the tooth

crowns, coupled with a certain amount of reduction in their roots.

- 4.—The loss of enamel from the occlusal surfaces of the tooth crowns, perhaps a result of the softness of the enamel in this genus.
- 5.—The reduction of the cusps to more or less vestigial elements.
- 6.—The presence of tubules or nutritive canals in the dentine.
- 7.—The supposed insectivorous habits, as shown by the presence of chitin in the coprolites associated with the type jaw.
- 8.—The small size.

As for the first of the above points, it is difficult to know whether in this respect *Tubulodon* resembles the aard-vark because of its phylogenetic relationships or because of convergence resulting from similar myrmecophagous or insectivorous habits. Thus a jaw similar in shape to that of *Tubulodon* may be found in various mammals adapted to an insect diet and showing a partial loss of the lower teeth. *Palaeonodon* and *Metacheiromys* are early Tertiary types that illustrate this. The same considerations hold with regard to the loss of the anterior teeth. Such a line of development has been followed by so many insect-eating mammals that it cannot be utilized with any great degree of confidence in the establishment of relationships.

As for the form of the teeth in *Tubulodon*, it is difficult to see here any real proof either for or against a distant relationship with *Orycteropus*. The same holds true for the loss of enamel on the tooth crowns. In these respects the teeth in *Tubulodon* might be logically as truly antecedent to the teeth in the Dasypodidae as they are to those of the Tubulidentata. On the other hand, the reduction of the cusps in *Tubulodon* represents an adaptation that might very well foreshadow the complete suppression of the crown pattern in the aard-vark, but again such a development might just as well presage the change leading to certain other peg-toothed types such as the armadillos. Incidentally, Jepsen was very cautious about identifying the vestigial cusps on the crowns of the *Tubulodon* molars with the typical mammalian cusps, but it seems to the present author that the arrangement of an antero-

internal cusp, followed by two pairs, each of an external and an internal cusp, suggests very strongly the characteristic paraconid, protoconid-metaconid, hypoconid-entoconid arrangement that one might expect.

It is the presence of tubules in the dentine of *Tubulodon* that constitutes the strongest evidence for linking this genus with the tubulidentates. While the foregoing evidence may not be at all definitive as applied to the phylogenetic relationships of the Wind River fossil, if associated with a histologic structure that could be definitely proven as homologous to that of the aard-varks, form strong support for the tubulidentate theory. The tubules in *Tubulodon* show very little resemblance, at first sight, to those in *Orycteropus*. In the Eocene genus they are small, irregularly spaced and very contorted, especially near the surface of the crown. Jepsen has described them very graphically in the following words.

"As they ascend, roughly parallel to the outside of the tooth, they branch and twist until toward the tooth top they become a contorted mosslike maze."¹

It may be, of course, that these small, irregular tubules are homologous with the central medullary canals in the *Orycteropus* dentine prisms. Jepsen describes in *Tubulodon* minute calcigerous tubes that enter the dentine at right angles from the tubules; these might be homologous with the calcigerous tubes that radiate from the medullary canal to the periphery of each dentine prism in *Orycteropus*. If these homologies are granted, then the tooth structure so characteristic of *Orycteropus* is just becoming established in *Tubulodon*. Yet because of the irregularity in the spacing and form of the tubules in *Tubulodon* and because of the lack of definite boundaries defining dentine prisms, of which each medullary canal is the center in *Orycteropus*, the homologies in dentine structure between *Tubulodon* and *Orycteropus* are indeed questionable.

The supposed insectivorous diet of *Tubulodon* would not in itself relate this genus

Jepsen, G. L. 1932. Proc. Amer. Philos. Soc., LXXI, No. 5, p. 260.

to *Orycteropus* any more than to various other insect-eating forms. In fact, *Orycteropus* lives almost exclusively upon termites, so that an ancestor having food habits similar to those of its descendant would show little if any chitinous remains in the coprolites. On the other hand, it is quite possible that the restricted diet of *Orycteropus* was established at some post-Eocene date, so the evidence is not conclusive either way.

The small size of *Tubulodon* might favor its position as an ancestor to the aardvarks, but here again the evidence is not conclusive in either direction. In this connection it might be said that *Ectoconus*, compared in foregoing pages of the present work with *Orycteropus*, is as large as the largest recent forms of the aardvark, and much larger than the Pliocene type, *O. gaudryi*. Therefore, if the anatomical features of *Ectoconus* suggest a relationship with *Orycteropus* as is here considered possible, the relationship may be one of parallel descent from a common ancestor, rather than of linear derivation from the ancestral type through *Ectoconus* to

Orycteropus. In other words, it would be very unlikely, though not at all improbable, for an ancestor to give rise to small descendants, which in turn would give rise to large descendants approaching the size of the ancestral type.

To sum up, it seems to me that in any attempt at speculation as to the ultimate ancestors of the Tubulidentata, the evidence afforded by the comparative anatomy of the skeletons of *Orycteropus* and the condylarths is much stronger than that shown by a comparison of the jaw and dentition of *Tubulodon* and *Orycteropus*. *Tubulodon*, it seems to me, is a form of uncertain relationships; certainly it is not a tubulidentate. Of course, it may be related to the tubulidentates, representing a separate branch from a common ancestral type, just as the condylarths and the tubulidentates probably represent separate branches from a common ancestral type. But even if this is so, it cannot be regarded as sufficiently diagnostic to invalidate the evidence for an approximate condylarth ancestry for the tubulidentates, as expressed by various authors and as presented in the preceding pages of this work.

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