THE FOSSIL AARDVARKS (MAMMALIA: TUBULIDENTATA)

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CONTENTS

ABSTRACT. A new tubulidentate, *Leptorycteropus guilielmi* gen. et sp. nov. from Member B of Lothagam–1, Turkana District, Kenya, is described. It is a generalized form for an aardvark, despite its relatively recent age. Review of the known fossils indicates that *Leptorycteropus, Orycteropus* and *Myorycteropus* are representatives of three phyletic lineages. The aberrant Malagasy *Plesiorycteropus* is so distinct from the rest as to suggest that its ancestors reached the island at some time during the Eocene. A division of the family Orycteropodinae into Orycteropodinae and Plesiorycteropodinae nov. is proposed. The biology of *O. afer* and the nature of the myrmecophagous adaptation are reviewed, and the possible adaptations of the extinct genera discussed. The surviving species, as a fully committed myrmecophage, is anomalous in retaining functional posterior cheek teeth, a retention that may be related to the curious symbiosis between this animal and the cucurbitaceous plant *Cucumis humifructus*. Available evidence is consistent with the hypotheses of condylarth-tubulidentate relationships and of Africa as the place of origin of the aardvarks.

INTRODUCTION

Among the fossil vertebrate remains collected in the Pliocene deposits at Lothagam Hill, Turkana, Kenya, during the field season of 1967 was a partial skeleton of an extinct aardvark that had evidently served as a meal for some carnivore. Several of the bones show tooth punctures, and the parts preserved are such as would remain after predator action. I am obliged to this otherwise unknown animal. Study of the surviving portions of its repast revealed the existence of the most generalized member of a peculiar and interesting order so far found and led to this review.

Our field work in East Africa was supported by National Science Foundation Grants GP–1188 and GA–425. For the privilege of examining material in the British Museum (Natural History) and the Muséum Nationale d'Histoire Naturelle I am indebted to Mrs. Shirley Coryndon Savage, Dr. A. J. Sutcliff, Dr. J.-P. Lehman and Dr. R. Hoffstetter. Figures 14 and 15 have been drawn by Mr. Laszlo L. Mészöly from sketches by me; the remainder are by Mr. Arnold Clapman.

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TUBULIDENTATA

ORYCTEROPODIDAE

Orycteropodinae (see p. 216)

Leptorycteropus[1] gen. nov.

Type species. — *L. guilielmi*[1] sp. nov.

Diagnosis. $1\frac{?}{?}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$. Canines oval in section, larger than premolars; canines and premolars with peripheral ring of cement; known molars comparable in size and structure to those of *Orycteropus*, large relative to size of animal. Maxillaries not extending forward to form elongate snout, not notched anteriorly, ventral surface of palatal portion flat, not grooved medially; anterior portion of jugal wider, relatively shallower than in *Orycteropus*, forming, with maxillary, a short, blunt descending process; dorsal portion of frontoparietal suture more oblique than in *Orycteropus*; symphysis of mandible extending back to level of anterior end of $P_{\overline{2}}$. Centra of presacral vertebrae generally wider relative to depth than in *Orycteropus*, sacrals five. Limb bones in general more slenderly constructed than in *Orycteropus*, especially in shafts; much narrower across distal extremities than in *Myorycteropus*. Humerus with deltoid crest merging into shaft distally, not forming distinct terminal projection, no large V-shaped deltopectoral area, entepicondyle extending as far distally as trochlea; anteroposterior diameter of distal end of radius short relative to transverse. Pectineal process of ilium much less projecting than in *Orycteropus*; medial surface of ischium very concave dorsal to obturator foramen. Hind leg bones more slenderly constructed than in *Orycteropus*.

Distribution. Pliocene, East Africa.

Leptorycteropus guilielmi sp. nov. (Figures 1–9)

Type. In Kenya National Museum, M.C.Z. Field No. 94–67K, various fragments of the skeleton of a single, adult individual: anterior portion of right maxilla with broken C and P^{1-2}; posterior portion of right maxilla with broken M^{2-3} and posterior extremity of alveolus of M^1; anterior root of left zygomatic arch with part of orbital rim; part of cranial roof including right postorbital process; part of left horizontal ramus with broken C– $P_{\overline{4}}$ and antero-internal part of alveolus of $M_{\overline{1}}$; several vertebrae in varying states of incompleteness: C 3–4, 6–7, an intermediate dorsal (D. 6?), D. 11–13, L. 3–8, sacrum, Cd. 1 and three other anterior caudals; a rib fragment; most of proximal and distal halves of left humerus, greater tuberosity and part of head missing; two fragments of proximal part of right humerus; distal portion of right radius, fragment of center of shaft of right ulna; distal portion of right Mc. II; pelvis lacking posterior portions of ischia and pubes, iliac crests incomplete; right femur incomplete in shaft and with head, great trochanter and external condyle missing; distal portion of left femur lacking internal condyle; proximal two-thirds and distal extremity of left tibia, proximal and distal portion of right tibia, distal portion of right fibula.

Hypodigm. Type only.

Horizon and locality. Lothagam –1, low in Member B (Patterson, Behrensmeyer and Sill, 1969), Pliocene; Lothagam Hill, southeastern Turkana, Republic of Kenya.

Diagnosis. As for the genus; approximately half the size of *Orycteropus afer.*

Dentition. The maxillary and mandibular fragments combine to reveal that a canine and the normal eutherian complement of cheek teeth were present; the specimen provides no information as to the presence or absence of incisors. $P\frac{1}{1}$ are separated from the canines and $P\frac{2}{2}$ by short diastemata, and the rest of the cheek teeth

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[1] λεπτός, slender + *Orycteropus*; in allusion to the comparatively slender limb bones. The species is named for Dr. William D. Sill, finder of the type specimen.

are set off from each other by small gaps comparable to those occurring in *Orycteropus* and *Myorycteropus.* All teeth show tubular[1] structure. The tubes increase in size from the canines backward and also, particularly in the molars, from the centers to the peripheries of the teeth. Canines and premolars have a continuous peripheral ring of cement[2]; in this feature they closely resemble the sections of the last lower milk molar of *O. afer* figured by Thomas (1890). The ring is thin in $P_{\overline{4}}$ and evidently not present in $M^{\underline{2-3}}$.

The upper canine is oval in contour, wider and slightly longer than any of the premolars preserved, either upper or lower. Of the lower canine only the posterior extremity is present. $P\frac{1}{1}$ are the smallest of the cheek teeth and are rather wider relative to length than the narrow, elongate-oval $P\frac{2}{2-3}$. $P_{\overline{4}}$ is wider posteriorly than its predecessors. What remains of the alveoli of $M\frac{1}{1}$ suggests that the size difference between premolars and molars was at least as pronounced as in *Orycteropus* and perhaps more so. $M^{\underline{2-3}}$ are similar to the corresponding teeth of the living species, both in size and structure. The two lobes of $M^{\underline{2}}$ are approximately equal, the labial groove is deeper than the lingual, the anterior face is flat and the posterior rounded. $M^{\underline{3}}$ is broadly oval in outline with only a vestige of the labial groove present.

Skull. The anterior part of the right maxilla includes the palatal portion as far as the median suture. This fragment shows that the bony palate was flat transversely and very slightly concave anteroposteriorly, did not have a median groove, and was not notched anteriorly for the reception of processes of the premaxillae. The surface of the bone is to a slight and irregular degree undulating, and is perforated by a large number of minute vascular openings. It is probable that a palatal exposure of the vomer was lacking. The facial portion of the bone displays a degree of curvature

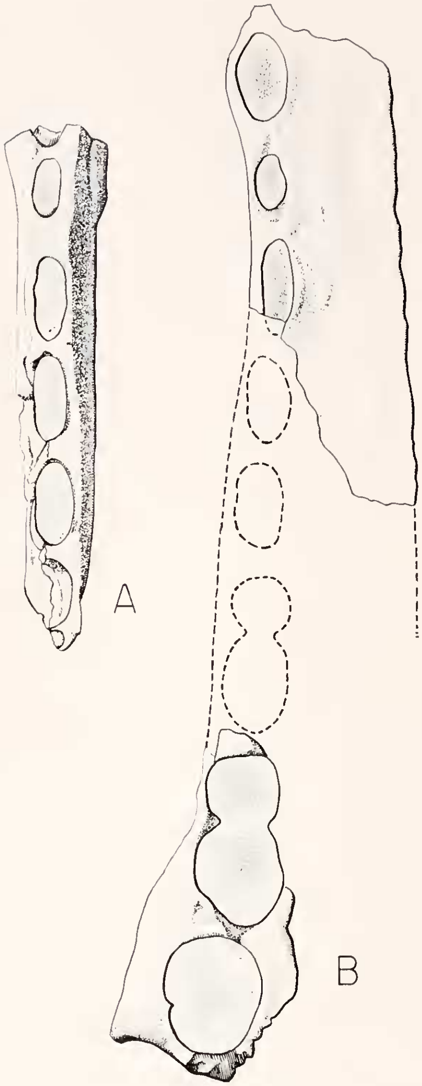

Figure 1. *Leptorycteropus guilielmi* gen. et sp. nov. Dorsal view of portions of left ramus (A) and of right maxilla (B). All teeth are broken and have been restored in the drawings to the alveolar level. × 3/2.

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[1] MacInnes (1956, 9.8), pointing out that tubule, in dental terminology, is universally used for the minute canals that enter the dentine from the pulp cavity, prefers column or pillar as a name for the macroscopically visible structures. However, these are literally tubes of dentine enclosing cores of pulp and it would seem possible, within the context of the Tubulidentata, to use both tube and tubule without confusion, even though the adjectival forms of both are the same.

[2] Confirmed by the preparation of sections.

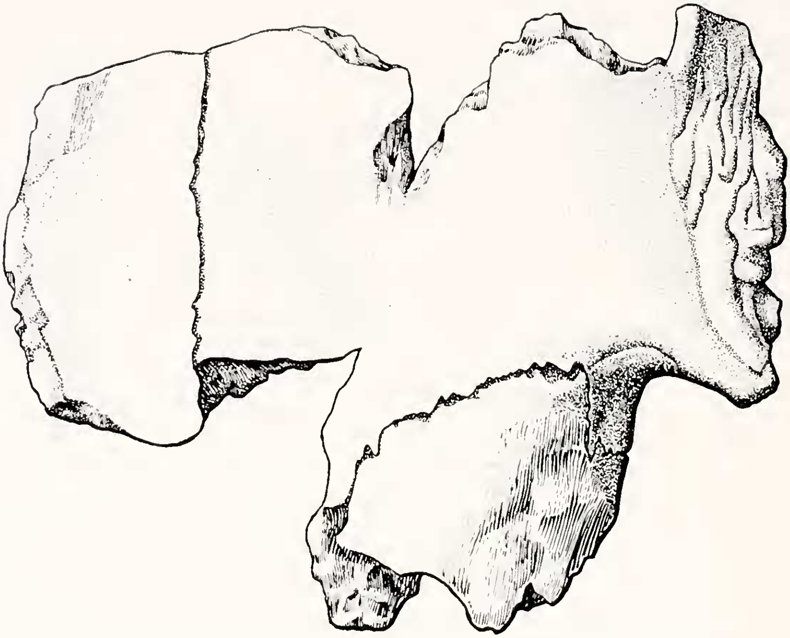

Figure 2. *Leptorycteropus guilielmi* gen. et sp. nov. Dorsal view of portion of cranial roof. × 3.

similar to that of *Orycteropus*. There was no prolongation into a long snout. The posterior portion of the maxilla is large relative to the size of the animal; the anterior root of the zygoma arises as far above $M^{\underline{3}}$ as does that of some specimens of *O. afer*. The root is more massively constructed than in *Orycteropus*, but the jugal is not as deep in this area. With the maxillary, it forms a short, blunt descending process; between this and the sidewall of the maxillary there is a long, wide and shallow groove. The postorbital process is also about as large as specimens of the living species and is similarly rugose above. Part of the frontoparietal suture is preserved; its decidedly oblique course on the cranial roof shows that the frontals extended back between the parietals to a greater extent than in *Orycteropus*. These few pieces show that the proportions of the skull were different from those of the surviving form.

The ramus of the mandible between C and $M_{\overline{1}}$ is laterally compressed, relatively deep, and, in profile, very slightly convex above and concave below. A single mental foramen is present beneath $P_{\overline{2}}$; a well-marked groove runs forward from it. On the lateral face the beginning of a swelling is preserved at the level of the posterior extremity of the canine. The ventral half of the anterior end of the medial surface is thickened, slightly rugose and grooved anteroposteriorly. This can only be a part of the symphysis; it ends posteriorly beneath the anterior extremity of $P_{\overline{2}}$ and is much deeper and more solidly constructed than that of *Orycteropus*.

Vertebrae. The vertebrae preserved closely resemble those of *Orycteropus*. Nothing indicates that the curvature of the column was appreciably different. What remains of the neural spines of D. 6(?) and of the last three dorsals suggests that the spine of the former vertebra was inclined posteriorly to a similar degree and that the anticlinal vertebra was the penultimate dorsal. The last six lumbars are present and the differences between the anterior

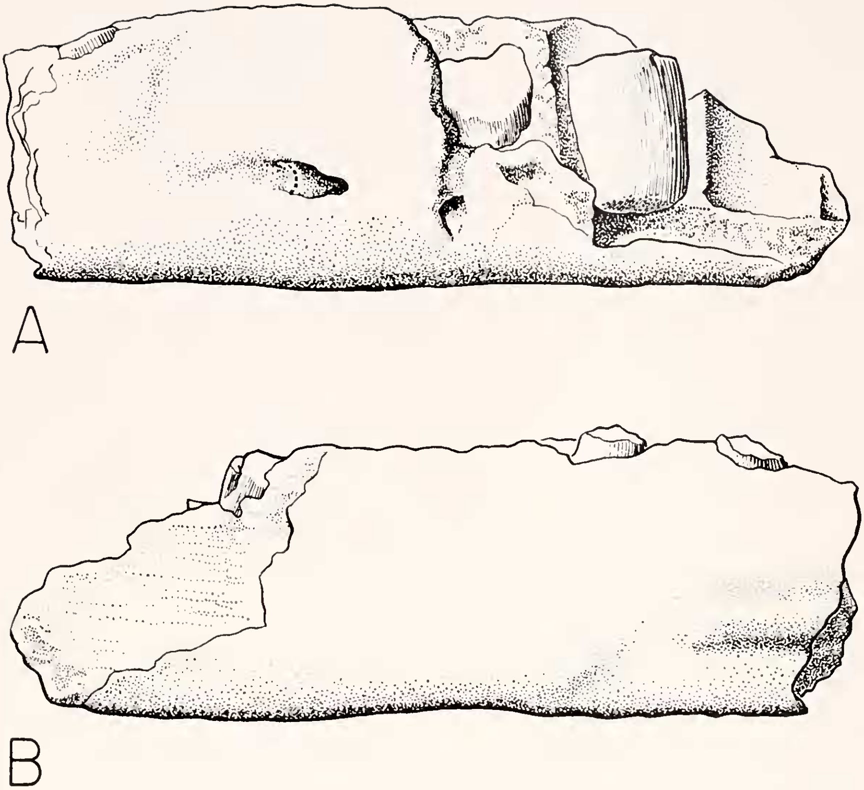

Figure 3. *Leptorycteropus guilielmi* gen. et sp. nov. Lateral, A, and medial, B, views of portion of left ramus. × 3.

of these and the last dorsal would require more than one vertebra to bridge the gap. The trunk formula was therefore probably the same, namely D. 13, L. 8. The caudal vertebrae are proportionally as large.

The presacral vertebrae differ consistently from those of *Orycteropus* in having flatter centra that are shallower dorsoventrally relative to their widths, and in having the pedicles less notched posteriorly. No doubt other minor differences between the two would be apparent were those vertebrae better preserved, but almost all of them have all processes broken off. The left metapophysis of L. 6 is in fact the only nearly complete one present; it differs from the corresponding process of *Orycteropus* in being more vertically directed, relatively higher and less expanded dorsally. Other distinctions detected are: the dorsal portion of the transverse process of C. 6 rises more ventrally[1]; the base of the transverse process of D. 6(?) is narrower anteroposteriorly, oval in section with the long axis dorsoventral; the anapophyses of D. 11–12, to judge from the remains, were longer and more slender; and the hypapophyses of L. 4–5 are relatively deeper. Colbert (1941: 322) pointed out that the zygapophyses of the lumbars of *O. gaudryi* are not as concave and convex—hence less interlocking—as those of the living species. This is like-

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[1] C. 7 has no vertebrarterial canal. Sonntag (1926: 455) and Colbert (1941: 322) state that this is present in the corresponding vertebra of *Orycteropus*. It is a variable character, however, as is shown by two specimens in the museum collections that lack it.

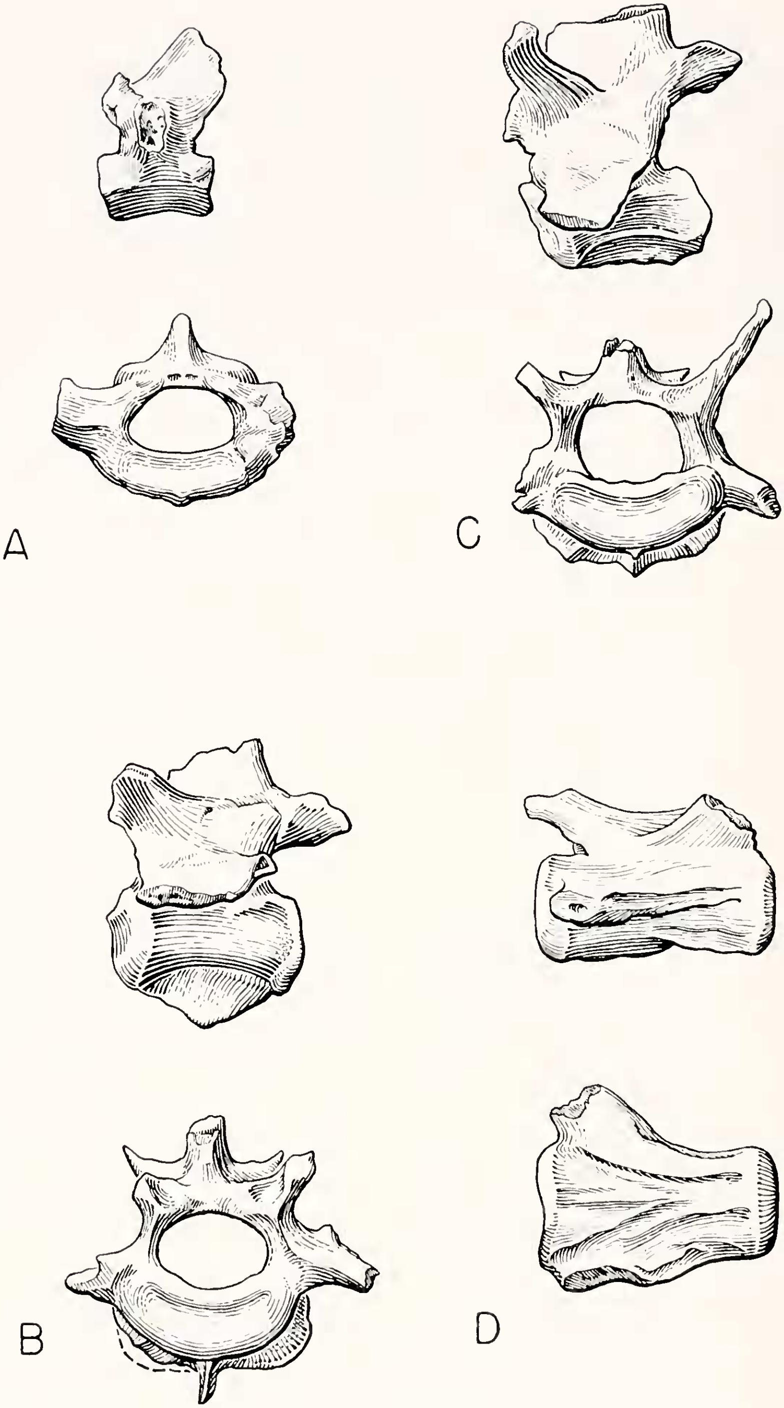

Figure 4. *Leptorycteropus guilielmi* gen. et sp. nov. Vertebrae. Left lateral and anterior views of D6? (A), L5 (B), L6 (C), left lateral and ventral views of Cd. 7 (D), × 3/2.

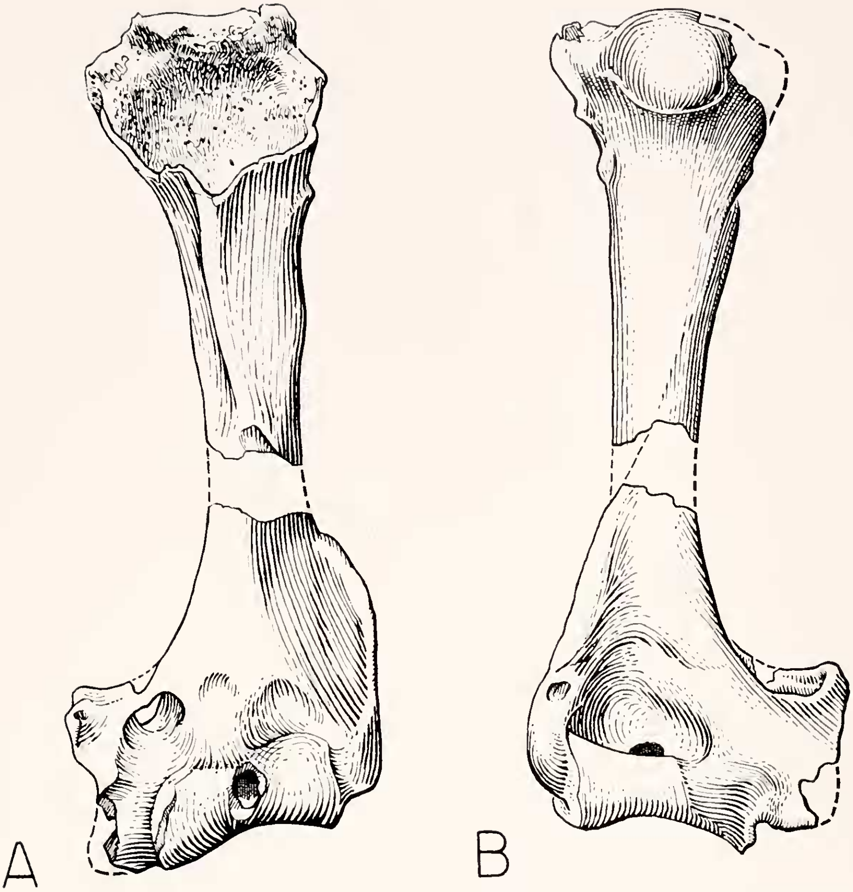

Figure 5. *Leptorycteropus guilielmi* gen. et sp. nov. Anterior (A), and posterior (B), views of left humerus. × 3/2.

wise true of *Leptorycteropus,* in which these articulations in both lumbars and posterior dorsals also do not present medially and laterally to the same degree.

Five vertebrae are incorporated in the sacrum as compared to six in *Orycteropus.* The bone is more deeply notched at the junctions of S. 3 and 4. The spines of S. 3–5 are separate at their bases. The centrum of S. 1 resembles those of the presacrals in its flatness and greater width relative to height; that of the last of the series is closer to *Orycteropus* in proportions. The bone is narrower across S. 3–4, i.e., the transverse processes of these vertebrae are relatively less expanded, and the iliac surface is conspicuously shallower dorsoventrally relative to its length than in the living form.

Insofar as comparison is possible, Cd. 1 is similar to the last pseudosacral (S. 6) of *Orycteropus.* The other three caudals preserved progressively increase posteriorly in the lengths of their centra; although other dimensions progressively decrease in the living form, the lengths of the centra remain nearly constant as far back as Cd. 12, after which a decrease begins. The transverse processes of *Leptorycteropus* arise farther back on the centrum, the neural arches are less notched anteriorly and pos-

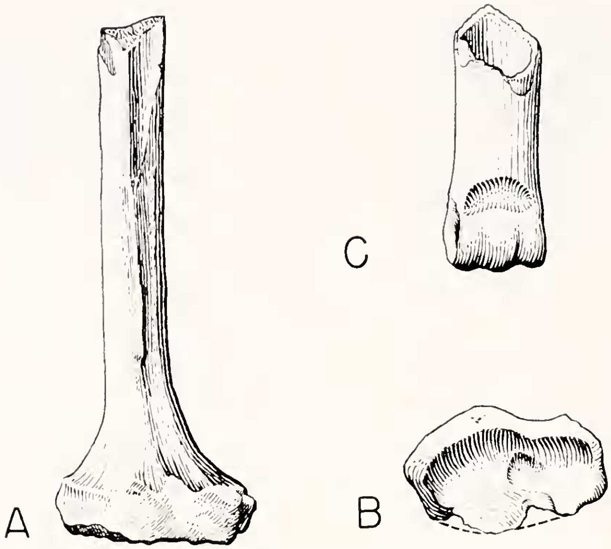

Figure 6. *Leptorycteropus guilielmi* gen. et sp. nov. Anterior (A), and distal (B), views of distal portion of right radius; anterior view (C), of distal portion of right Mc. II. × 3/2.

teriorly, and the zygapophyses are smaller than in the corresponding vertebrae of *Orycteropus.* Raised areas at the posterior ends of the ventral surfaces of the centra mark the positions of the chevron bones.

These three caudals are tentatively determined as 3, 6 and 7. Their relative order is determined by progressive decrease in the size of the bases of their transverse processes. The identification of the last of them as Cd. 7 is based on a general agreement with Cd. 6 of *Orycteropus* (S. 6 of the one being Cd. 1 of the other, and so on), the last of the series in which the neural arch extends posteriorly well beyond the centrum and the spinal nerve passes laterally through a notch. From Cd. 7 to and including Cd. 12 of *Orycteropus,* after which the neural arch disappears, the upper parts of the pedicles enlarge backward and downward to join the centrum, converting the notch into a foramen. This determination is not certain, of course, since characters such as these are subject to intra- and interspecific variation in position within the series; the vertebra of *Leptorycteropus* in question could be Cd. 8 or even perhaps Cd. 9, but not, I think, farther back than that.

Anterior extremity. A section of the shaft of the left humerus is lacking. Calculations based on what is preserved of the radius and the ratio of the radius length to the humerus length in other members of the family suggest that humeral length in *Leptorycteropus* was approximately as restored in Figure 5. The anterior part of the proximal end, including much of the head and greater tuberosity and all of the lesser tuberosity, was lost prior to burial. What remains resembles in general the corresponding part in *Orycteropus;* the depression in the lateral surface of the greater tuberosity is equally well developed in both forms. The comparatively slender shaft appears to have been straighter, less bowed than in the other genera. The deltoid crest is unique in being rather feebly developed, nearly straight and merging imperceptibly at its distal end into the body of the shaft. The pectoral crest, while strong proximally where it forms a small shelf, is weak distally and, like the deltoid, merges into the shaft. It does not curve around onto the anterior face to contribute to a deltoid tuberosity and delimit a definite V-shaped deltoid area. Posteriorly, the shaft shows no indication of the prominent crests described by MacInnes in *Myorycteropus*. The distal end resembles that of *Orycteropus* in most features, as it is less expanded transversely than in *Myorycteropus* and has a more prominent supinator crest than in *Plesiorycteropus*. It differs from all three in the greater distal extent of the entepicondyle.

The distal three-fourths of the radius is preserved. The crest on the anterior surface resembles that of *Orycteropus* but is less salient. The crest in *Myorycteropus* is more salient distally, in *Plesiorycteropus* very greatly expanded. The distal end is shorter relative to width than in *Orycteropus* and *Plesiorycteropus*, and is much less expanded transversely than in *Myorycteropus*.

What appears to be a portion from the center of the shaft of a right ulna is all that is preserved of this bone. It is long and of even length anteroposteriorly, thin transversely, grooved laterally and gently convex medially. If correctly identified—and I can refer the fragment to no other part of the orycteropodid skeleton—*Leptorycteropus* resembled *Myorycteropus* and *Orycteropus* in the anteroposterior dimensions of the ulnar shaft and differed decidedly from *Plesiorycteropus*, in which the shaft tapers distally.

The median keel of the distal articular surface of Mc. II is blunter and less projecting than in *Orycteropus* and *Myorycteropus*; it extends to the dorsal side of the bone.

Posterior extremity. A considerable part of the pelvis is preserved, although the posterior portions of the pubes and ischia and much of the dorsal margins of the ilia are lacking. Pelvic proportions as preserved are much as in *Orycteropus*; the ischium is present as far back as the beginning of the turnout to the lateral process, and this part of the bone bears the same size relation to the ilium as does that of the living form. Unfortunately, neither in *Leptorycteropus* nor in *Myorycteropus* is there any indication as to whether or not the ischium extended as far posteriorly as in *Orycteropus*. It does not do so to any extent in *Plesiorycteropus*, in which the area of the ischial tuberosity is more compact. The marked extension in the living form, whereby the postacetabular portion of the innominate has come to equal the preacetabular in length, may be a specialization within the *Orycteropus* lineage. Ilium and ischium of *Leptorycteropus* together form a straighter line in direct acetabular view than is the case in the living form, in which the two bones slope upward from the articulation. The ilium curves laterally to about the same degree as in *Orycteropus* but is more tapered at the extremity. On the gluteal face the linea glutea inferior is sharp and more prominent, especially anteriorly, than in *Orycteropus*. The portion of the bone below it presents more ventrally. A linea glutea superior is not present on the part of the bone preserved, and was probably situated at or near the missing dorsal rim. The gluteal face is slightly less, the medial face rather more concave than in the living form. The ventral portion of the great sciatic notch is preserved, indicating that there was some posterosuperior expansion of the ilium. As the dorsal rim is broken off, it is impossible to estimate how large this may have been. I suspect that it was considerably less extensive than in *Orycteropus*. In the latter, the deep sacral articulation extends well up on to it, whereas in *Leptorycteropus* the shallower articulation does not extend beyond the part preserved; in the *Myorycteropus* material the critical area is broken off. *Plesiorycteropus* shows no trace of such a structure, the dorsal rim of the ilium flowing rather gently down to the posterior end of the sacral articulation. The large dorsal

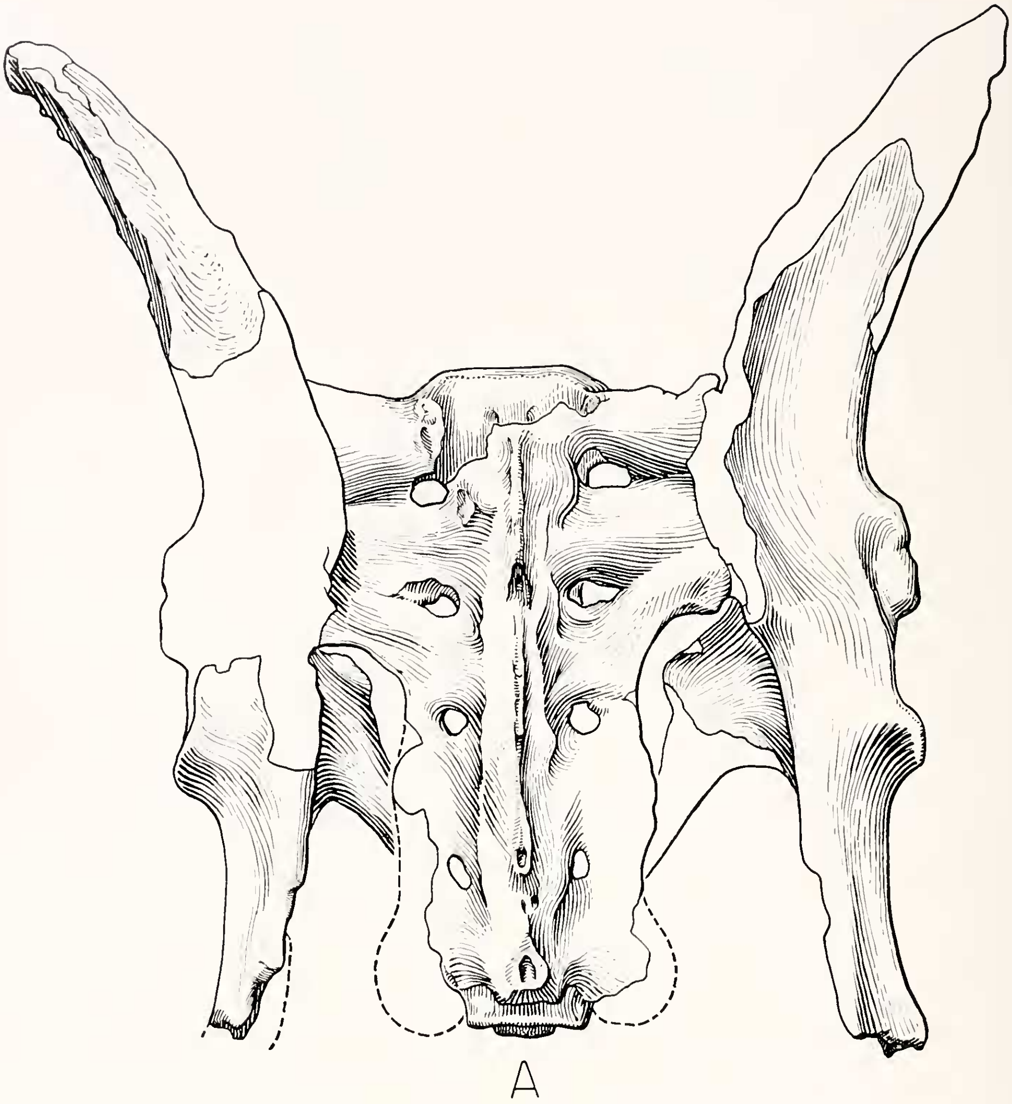

Figure 7. *Leptorycteropus guilielmi* gen. et sp. nov. Dorsal (A), and ventral (B), views of pelvis and sacrum. × 3/5.

area in the living species, all of it dorsal to the linea glutea superior and marked on the gluteal face by prominent muscle scars,[1] may be another specialization within the *Orycteropus* lineage, one perhaps associated

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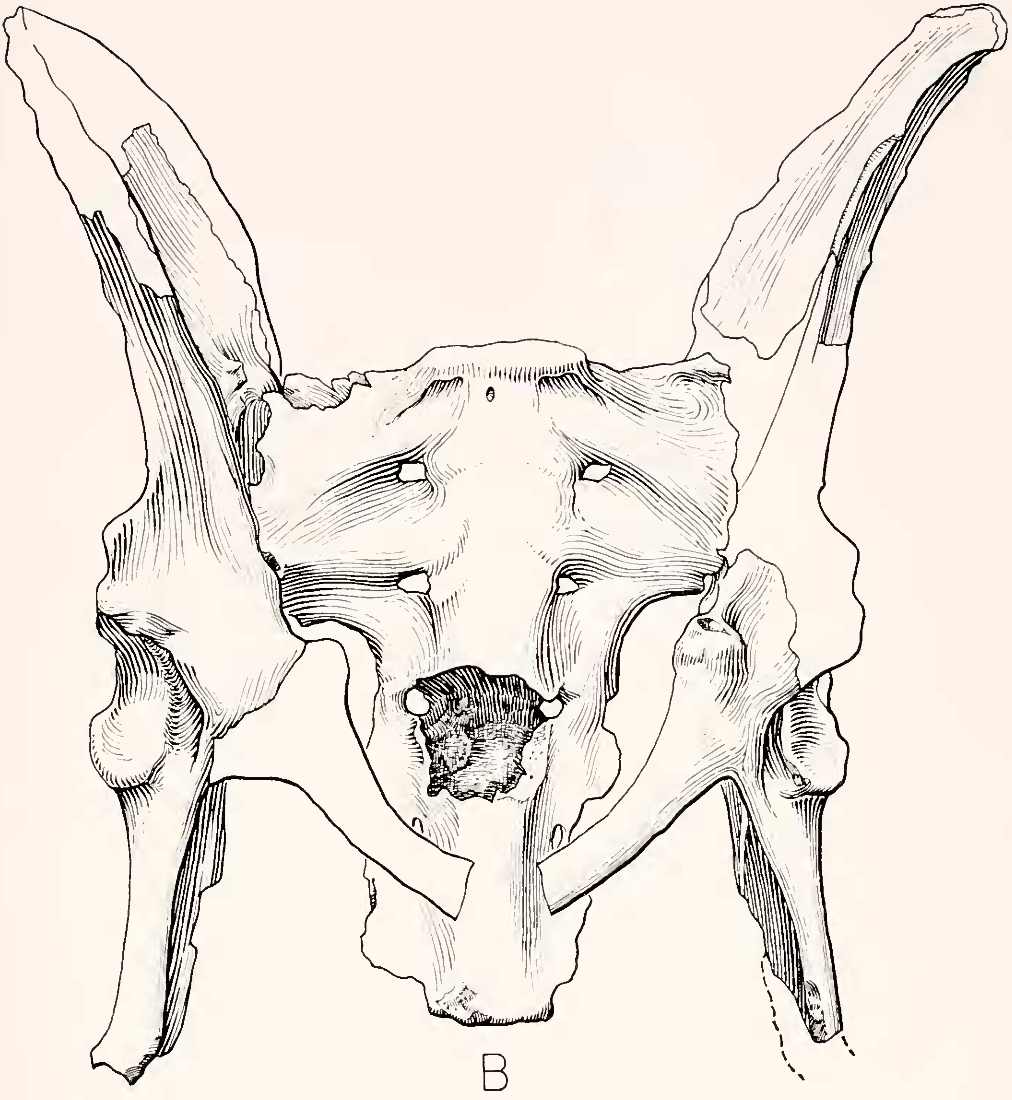
[1] Precisely what muscles is uncertain. The seeker after usable information on bone-muscle relationships in the monograph of *Orycteropus afer* is usually disappointed. Sonntag (1925, 1926) treated the two systems as though they bore virtually no relation to each other, providing the scantiest of data on the exact areas of origin and insertion on the bones. Of two earlier writers, one (Humphrey, 1869) is vague and the other (Galton, 1869) had no skeleton at hand while he was dissecting.



with the extensive use of the hind leg and tail during digging (p. 218); Broom (1905) saw in it a resemblance to *Diademodon*. The tubercle for M. rectus femoris is about as in *Orycteropus*, less extended, less crest-like than in *Plesiorycteropus*. The acetabulum is similar to that of the living form. The articular area is not as expanded posterodorsally and, on the ventral side, does not extend as far posteriorly. The ischium is very concave on its medial surface, the concavity deepening to a fossa at the level of the acetabulum. The bone does not increase in depth in the part preserved. A small spina ischiadica is present. The part of the pubis preserved is similar in structure and proportions to that of *Orycteropus*, differing in the possession of a sharper crest on the ventral surface and in being directed more ventrally. The obturator fora-

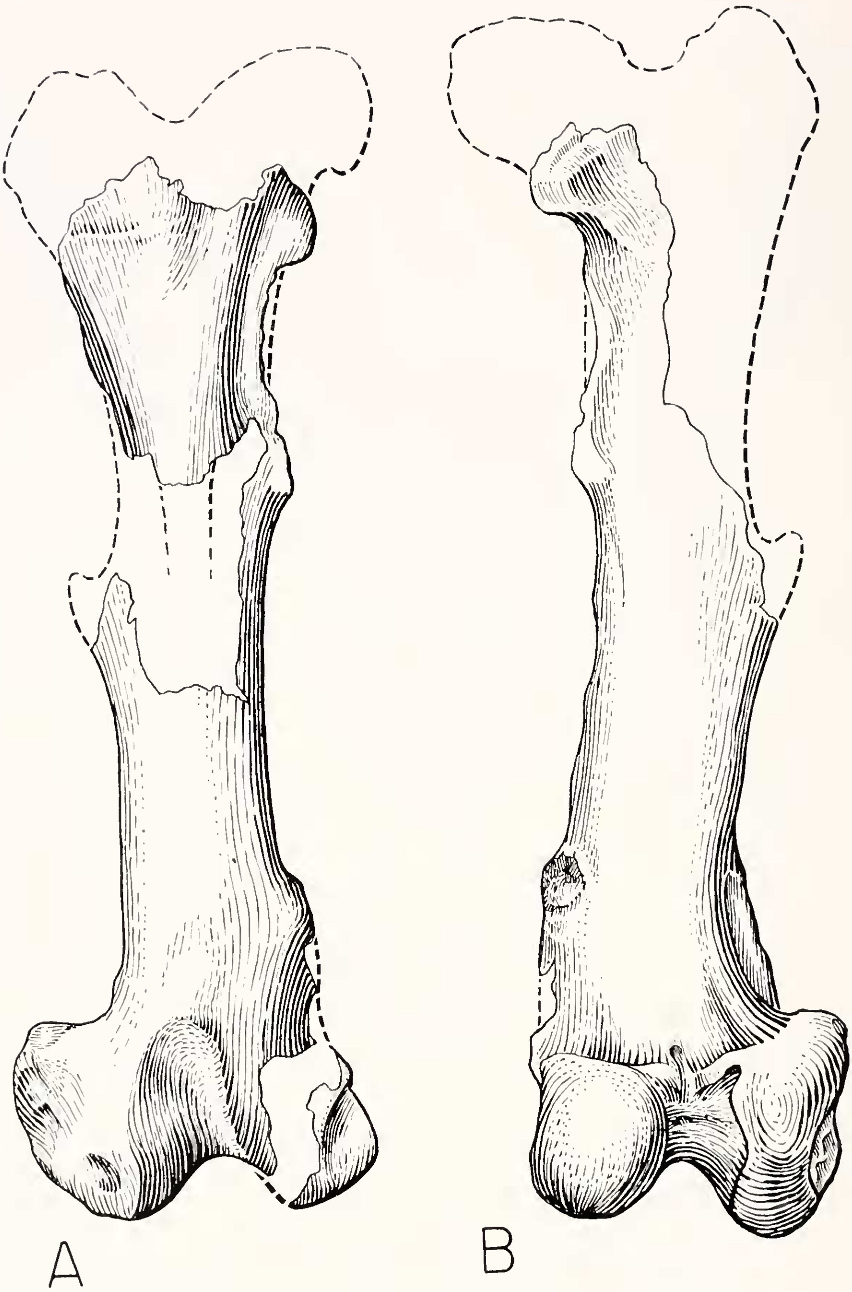


Figure 8. *Leptorycteropus guilielmi* gen. et sp. nov. Anterior (A), and posterior (B), views of right femur. × 3/2.

men, while similar in general outline to that of the living form, is thus relatively larger and deeper, at least anteriorly. The pectineal (iliopectineal) process has the form of a large tubercle and is much less salient than that of *Orycteropus*.

The whole of the proximal end of the femur is missing, together with much of

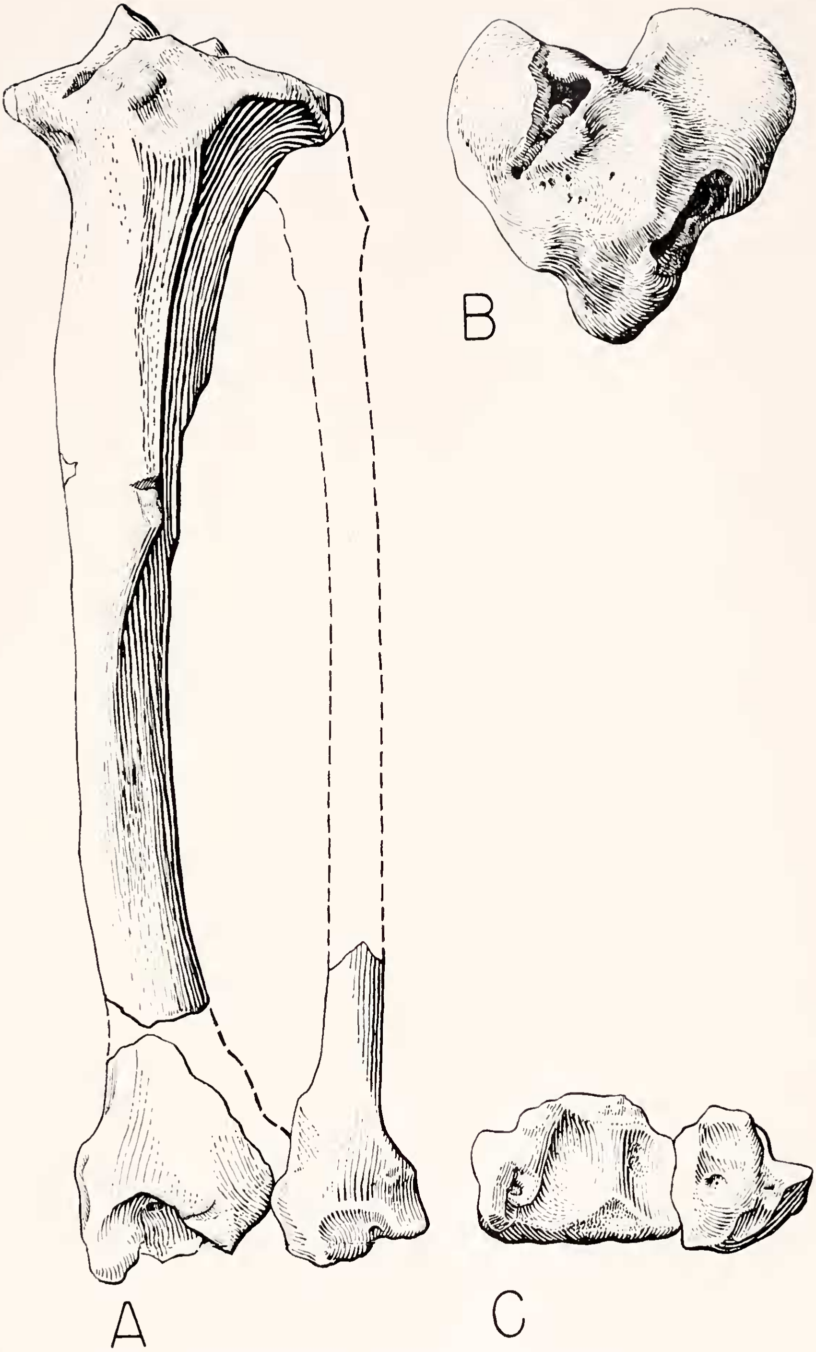


Figure 9. *Leptorycteropus guilielmi* gen. et sp. nov. Anterior (A), proximal (B), and distal (C), views of right tibia and distal end of right fibula. × 3/2.

the anterior face of the shaft. The posterior face is somewhat flattened, as in *Orycteropus*; what is present of the anterior face suggests that it, too, was similar in shape to that of the living form. The lesser trochanter in position, inclination and form is also similar, and is likewise connected by a crest to a pectineal tubercle on the medial side of the bone a little above the level of the third trochanter. Only the base of the latter remains. The distal end is similar in every feature to that of *Orycteropus* except for being relatively more slender in the shaft above the distal articular area. The structure and proportions of the bone as a whole are closer to those of the living form than to *Myorycteropus* and, especially, *Plesiorycteropus*.

The proximal portion of the left tibia and the distal portion of the right fortunately overlap, permitting a good estimate of the length of the bone. Allowing for the missing proximal end of the femur (Fig. 8), the two bones seem about equal in length, with the tibia perhaps slightly longer. The bone is more slenderly constructed than is that of *Orycteropus*, both in the shaft and in the relative width of the proximal end, and is by no means as bowed medially as it is in *O. afer*. The proximal articular areas are essentially similar in the two genera. Tibia and fibula are also fused at their upper ends, although the area of fusion is less massive in *Leptorycteropus*. In agreement with *O. gaudryi*, there is an uninterrupted rim of bone running from the patellar tuberosity to the junction with the fibula, a contrast to the living species in which a deep notch is present in this area. The tuberosity and the cnemial crest are relatively less salient than in *Orycteropus*, the crest terminating slightly higher on the shaft. Distally, the interosseous crest is much less prominent than in *Orycteropus*, otherwise agreement between the two forms is close. The distal end of the fibula differs again in the lesser development of the interosseous crest, and also in the relatively smaller lateral malleolus. As in the case of the femur, the tibia and fibula of *Leptorycteropus* are closer to those of the living form than to those of *Myorycteropus* and *Plesiorycteropus*.

Measurements in mm.

Dentition

	C	P^1	M^2	M^3	P_1	P_2	P_3	P_4
Length	5.9	3.5	11.1	7.4	3.6	5.1	4.8	4.9
Width	3.1	1.6	7.0	6.9	1.6	1.8	1.8	2.7

Skull

Width across canines	20.8
Width of cranial roof across postorbital processes	49.6
Depth of ramus beneath P_2, medial side	10.4

Vertebrae

C. 3, length of centrum	7.7
length of zygapophyses	13.1
C. 4, length of zygapophyses	12.4
C. 6, length of centrum	8.2
width of anterior face of centrum	12.5
height of anterior face of centrum at center	4.7
C. 7, length of centrum	8.3
D. 6(?), length of centrum	9.4
width across postzygapophyses	10.6
Width of anterior face of centrum[1]	11.9
height of anterior face of centrum at center	5.0
width of posterior face of centrum[1]	12.8
height of posterior face of centrum at center	5.5
D. 11, length of centrum	10.7
length at zygapophyses	15.1
width across postzygapophyses	12.4
width of anterior face of centrum[1]	13.6
height of anterior face of centrum at center	5.1
width of posterior face of centrum[1]	15.3
height of posterior face of centrum at center	5.8
D. 12, length of centrum	11.3

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[1] Excluding the rib facets.

length at zygapophyses	17.3
width across prezygapophyses	12.5
width across postzygapophyses	10.3
width of anterior face of centrum[1]	14.0
height of anterior face of centrum at center	5.4
width of posterior face of centrum[1]	15.4
height of posterior face of centrum at center	6.5
D. 13, length of centrum	12.3
length at zygapophyses	17.7
width across prezygapophyses	11.8
width across postzygapophyses	10.2
width of anterior face of centrum[1]	15.5
height of anterior face of centrum at center	6.1
width of posterior face of centrum[1]	16.8
height of posterior face of centrum at center	6.7
L. 3, length of centrum	13.8
width across prezygapophyses	13.5
width of anterior face of centrum	14.9
height of anterior face of centrum at center	6.6
width of posterior face of centrum	16.1
height of posterior face of centrum at center	7.4
L. 4, length of centrum	14.0
width of anterior face of centrum	14.4
height of anterior face of centrum at center	7.1
width of posterior face of centrum	16.3
height of posterior face of centrum at center	7.8
L. 5, length of centrum	14.0
length at zygapophyses	20.2
width across prezygapophyses	14.2
width across postzygapophyses	13.0
width of anterior face of centrum	14.6
height of anterior face of centrum at center	7.0
width of posterior face of centrum	15.7
height of posterior face of centrum at center	7.5
L. 6, length of centrum	13.4
length at zygapophyses	19.9
width across prezygapophyses	14.0
width across postzygapophyses	13.3
width of anterior face of centrum	14.1
height of anterior face of centrum at center	6.8
width of posterior face of centrum	16.4
height of posterior face of centrum at center	7.4
L. 7, length of centrum	14.7
length at zygapophyses	21.7
width across postzygapophyses	16.5
width of anterior face of centrum	15.3
height of anterior face of centrum at center	6.8
width of posterior face of centrum	18.1
L. 8, length of centrum	13.8
length at zygapophyses	22.0
width across prezygapophyses	17.2
width across postzygapophyses	18.4
width of anterior face of centrum	18.6
width of posterior face of centrum	19.7
height of posterior face of centrum at center	7.0
Sacrum, length of centra	71.1
width across iliac articulations	53.5
length of iliac articulation	26.8
height of iliac articulation	13.8
width at junction of S. 3 and 4	26.4
width of centrum of S. 1	18.5
height of centrum of S. 1 at center	6.9
width of centrum of S. 5	13.7
height of centrum of S. 5 at center	6.8
Cd. 1, length of centrum	15.5
length at zygapophyses	21.9
width across prezygapophyses	10.8
width across postzygapophyses	9.0
width of anterior face of centrum	13.5
height of anterior face of centrum at center	6.6
width of posterior face of centrum	13.2
height of posterior face of centrum at center	7.1
Cd. 3, length of centrum	17.1
width of anterior face of centrum	12.7
height of anterior face of centrum	8.3
width of posterior face of centrum	13.7
height of posterior face of centrum	8.3
Cd. 6, length of centrum	19.2
width of anterior face of centrum	12.0
height of anterior face of centrum	9.1

width of posterior face of centrum	12.4
height of posterior face of centrum	9.3
Cd. 7, length of centrum	20.2
width of anterior face of centrum	11.2
height of anterior face of centrum	9.2
width of posterior face of centrum	11.9
height of posterior face of centrum	9.5

Ratios of height to width [100h/w] in the centra of presacral vertebrae

	Leptorycteropus	*Orycteropus*
C.6 ant.	37.6	41.4
D.6(?)		
ant.	42.0	51.2
post.	43.0	50.9
D.11		
ant.	37.5	50.8
post.	37.9	41.2
D.12		
ant.	38.6	47.2
post.	42.2	35.5[2]
D.13		
ant.	39.4	37.8[2]
post.	40.0	38.7
L.3		
ant.	44.3	50.0
post.	44.6	49.3
L.4		
ant.	49.3	51.0
post.	47.9	48.3
L.5		
ant.	47.9	50.5
post.	47.8	48.9
L.6		
ant.	48.2	51.4
post.	45.1	48.0
L.7 ant.	44.4	47.2
L.8 post.	36.1	39.0

Anterior extremity

Humerus, anteroposterior diameter near center of shaft	10.0
transverse diameter near center of shaft	8.9
transverse diameter of distal end	27.5
anteroposterior diameter of distal end	11.7
anteroposterior diameter of trochlea	10.6
transverse diameter of trochlea	16.3
proximodistal diameter near entepicondyle	15.4
Radius, anteroposterior diameter near center of shaft	8.3
transverse diameter near center of shaft	5.6
transverse diameter of distal end	16.5
anteroposterior diameter of distal end	10.9
Ulna, anteroposterior diameter near center of shaft	11.1
transverse diameter near center of shaft	5.5
Mc. II, transverse diameter of distal end	7.9
anteroposterior diameter of distal end	7.0

Posterior extremity

Pelvis, preacetabular length of ilium (est.)	65.0
width of ilium at center	12.3
anteroposterior diameter of acetabulum	17.8
dorsoventral diameter of acetabulum	15.9
width at M. rectus femoris tubercle	16.4
width of ischium anterior to spina ischiadica	7.0
depth of ischium anterior to spina ischiadica	13.2
depth of descending portion of pubis	5.6
width of descending portion of pubis	6.8
Femur, transverse diameter of shaft below third trochanter	15.4
transverse diameter of distal end	28.3
anteroposterior diameter of distal end	27.4
Tibia, length (est.)	111.0

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[2] The medial parts of the rib facets in posterior dorsals have become incorporated into the articular surfaces of the centra, thus increasing their widths.

anteroposterior diameter of proximal end	29.5
transverse diameter of proximal end	30.3
anteroposterior diameter at center of shaft	14.8
transverse diameter at center of shaft	8.8
anteroposterior diameter of distal end	13.3
transverse diameter of distal end	19.5
Fibula, anteroposterior diameter of distal end	12.2
transverse diameter of distal end	12.7

CONSPECTUS OF THE FOSSIL ORYCTEROPODIDAE

Leptorycteropus

As evident from the description, *L. guilielmi* is the most generalized member of the family so far known. Although definitely orycteropodid—and orycteropodine—in structure it is, despite its comparatively recent age, primitive in various features, such as a short facial region, a relatively large canine (and perhaps a complete dentition), a mandibular symphysis extending back to a point beneath the anterior cheek teeth, relatively slender limb bones (Figs. 10, 12–13), humerus without a well defined deltopectoral area, tibia with a relatively weak cnemial crest, and so on.

Until now the Tubulidentata have perforce had to be considered in the light of *Orycteropus*, a rather specialized form. *Leptorycteropus* provides a better vantage point from which to assess phylogeny, relationships and adaptations within the order.

Orycteropus.
(Figures 10–13)

I follow those (e.g., Allen, 1939: 270–272) who include all living forms in *O. afer*. Confined today to subsaharan Africa the species evidently enjoyed a more northerly distribution within the continent in relatively recent times, to judge from a partial skull found in the Tanezrouft region, central Sahara, in deposits of very late Pleistocene or early Recent age (Romer, 1938: 177).

A number of extinct forms have been referred to the genus. Those so identified only on the basis of isolated teeth or of maxillary and mandibular fragments must be regarded with reserve. *Leptorycteropus*, for the molars, and *Myorycteropus*, for the cheek teeth as a whole, show that orycteropodines differing decidedly from *Orycteropus* in cranial and postcranial characters may have teeth so similar to those of *Orycteropus* as to make generic discrimination on such evidence impossible.

The following, arranged in geochronologic order, may on available data be included in the genus:

O. mauritanicus Arambourg (1954: 295; 296, as *O. gaudryi*; 1959: 42–53) from the "Vindobonian" of Algeria is known from much of a badly crushed skull, mandibular fragments, tibia and elements of the fore and hind feet. Larger than *O. gaudryi*, it is, next to that form, the best known extinct member of the genus. Five antemolar teeth are present, the maxillaries extending beyond them anteriorly for an unknown distance; the tooth rows are more arched and more convergent anteriorly than in the other species, the premolars are somewhat larger, and M^1 is longer than M^2. The facial region would appear to have been longer relative to the cranial than in *O. gaudryi*. The tibia resembles that of *O. gaudryi* in slenderness and lesser degree of bowing; that of *O. afer* in the structure of the proximal end. The rather narrow astragalus has a relatively longer neck than that of any other orycteropodid in which this bone is known. Mt. V, as in *O. gaudryi*, is relatively longer than in *O. afer*.

O. gaudryi Major (Colbert, 1941) is by far the best known of any of the extinct orycteropodids; nearly all parts of the postcranial skeleton except the clavicle and pelvis are present in an individual from Samos. This and other specimens from that locality have been admirably described and compared with *O. afer* by Colbert, and de

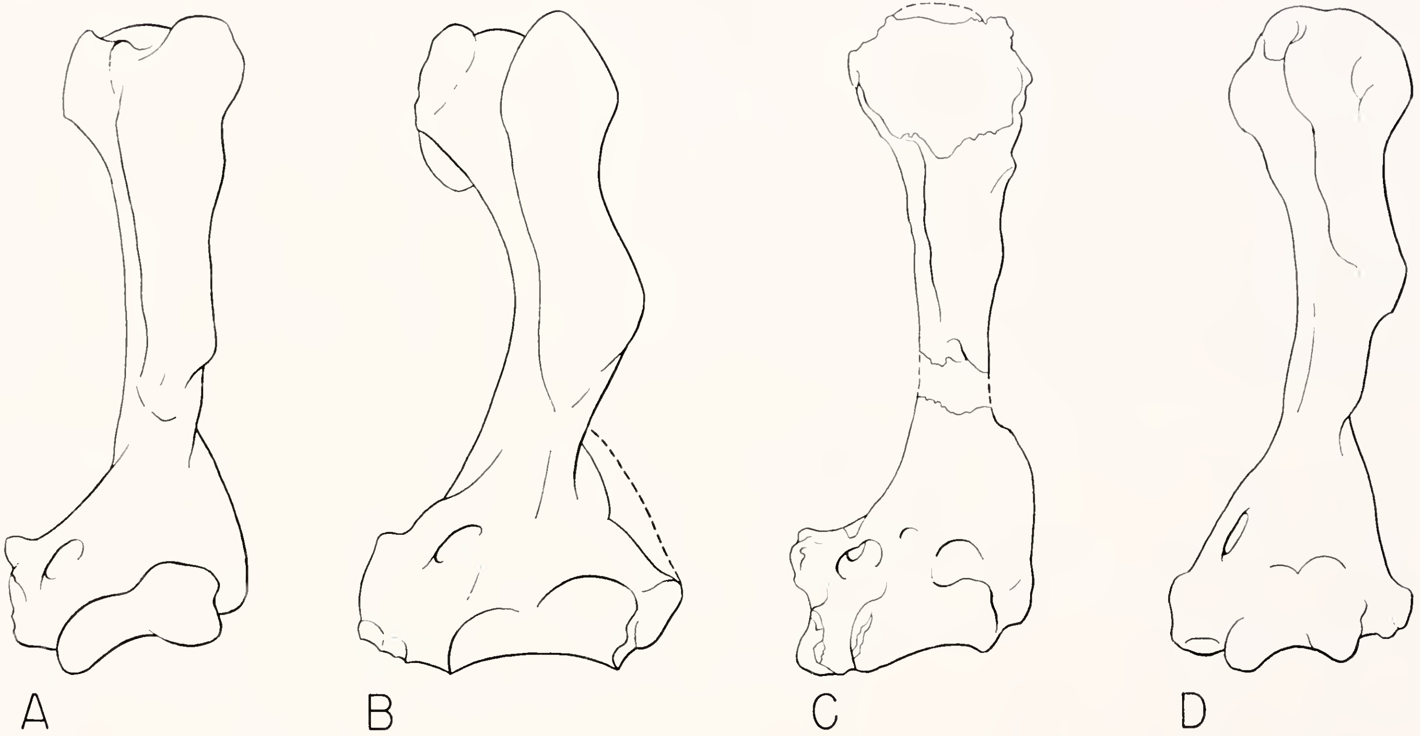

Figure 10. Anterior views of left humeri of *Orycteropus* (A), *Myorycteropus* (B), *Leptorycteropus* (C), and *Plesiorycteropus* (D). This and the three following figures are not to scale; *O. afer* is approximately twice the size of the others. *Orycteropus* and *Myorycteropus* are after MacInnes (13B modified); *Plesiorycteropus* is from Lamberton (10D, 12D and 13D reversed).

Beaumont (1970) has contributed supplementary observations. In addition to the Samos quarries, the species has long been known to occur at Maragha in Iran and has also been recorded from the Ukraine. *O. gaudryi* is the smallest of the several species so far described that can be referred with assurance to the genus. The molars are larger relative to the size of the skull than in the living species. A complete set of premolars is usually present, but no tooth anterior to them is known. The rostrum extends well beyond P^1, but is more tapering and the palate narrower than in *O. afer*. The nasals are more deeply inset between the frontals, the occiput is more nearly vertical and narrower relative to height, the facial region is shorter, the olfactory area is less expanded, the anterior border of the orbit lies over the anterior part of M^2, and the ascending ramus is more vertically inclined. The skull is longer relative to the leg bones than in *O. afer*. The postcranial skeleton is in general more slenderly constructed as the bones, both axial and appendicular, are relatively narrower. The manus, but not the pes, is relatively smaller than in the living species. Mc. V and the fifth digit of the pes are relatively longer, and the great trochanter of the femur is lower relative to the head than in *O. afer*. A further difference, not mentioned by Colbert but evident from his figures and measurements, lies in the proportions of the hind leg bones—the tibia of *O. gaudryi* is definitely longer than the femur, whereas the reverse is the case in other orycteropodids with the possible exception of *Leptorycteropus*.

O. depereti Helbing (1933), known from a nearly complete skull from the Pliocene of Perpignan, southern France, is comparable in size to *O. mauritanicus* and, as in that species, has five antemolar teeth, with the maxillary extending beyond them anteriorly for an unknown distance. While agreeing with *O. gaudryi* in rostral width and in the possession of a nearly vertical occiput, the species approaches *O. afer* in the width of the palate relative to the total width of the facial region, the rather more inflated olfactory area, the lesser degree of convergence of the tooth rows anteriorly, the position of the anterior border of the orbit above the posterior border of M^2, and the greater width relative to height of the occiput.

O. pottieri Ozansoy (1965: 45–46) from the late Pliocene, Astian, of Turkey is based on a mandibular ramus that lacks the symphysis.[1] Five antemolar teeth are present, as in *O. mauritanicus* and *O. depereti*. The condyle is not as high relative to the alveolar level as in *O. gaudryi* and *O. afer*; the inclination of the ascending ramus is comparable to that in the living species. Ozansoy gave no measurements. To judge from his figures, the length of the lower tooth row of *O. pottieri* may have been greater than that of the upper tooth row of *O. depereti*: ca. 76.0 mm as against 64.0 mm. Differences of this magnitude, however, occur in *O. afer*, and in individuals of that species, e.g., M.C.Z. 2097, the lower tooth row may be longer than the upper. The possibility, even probability, exists that *O. pottieri* is based on a jaw of the essentially contemporaneous *O. depereti*. It is unfortunate that no information on the limb bones is available as it would be interesting to learn if these were advanced in the direction of *O. afer* over those of *O. gaudryi* and *O. mauritanicus*.

O. sp. (*O.* sp. cf. *O. aethiopicus* Sundevall, Dietrich, 1942: 54). Three specimens, a ramus fragment with M_3 and two Mc. V, all isolated finds, have been collected in the Laetolil area, Tanzania. Whether they were found in the Pliocene or the

---

[1] A maxillary and some isolated teeth and limb bones were mentioned but not described. Ozansoy did not designate a type, nor give numbers to his specimens, nor state the institutions in which they are preserved. The mandible, as the only bone described, is obviously the type. Presumably, most if not all, of his specimens are in the collections of the Institut d'études et de recherches minières de Turquie (M.T.A.), Ankara.

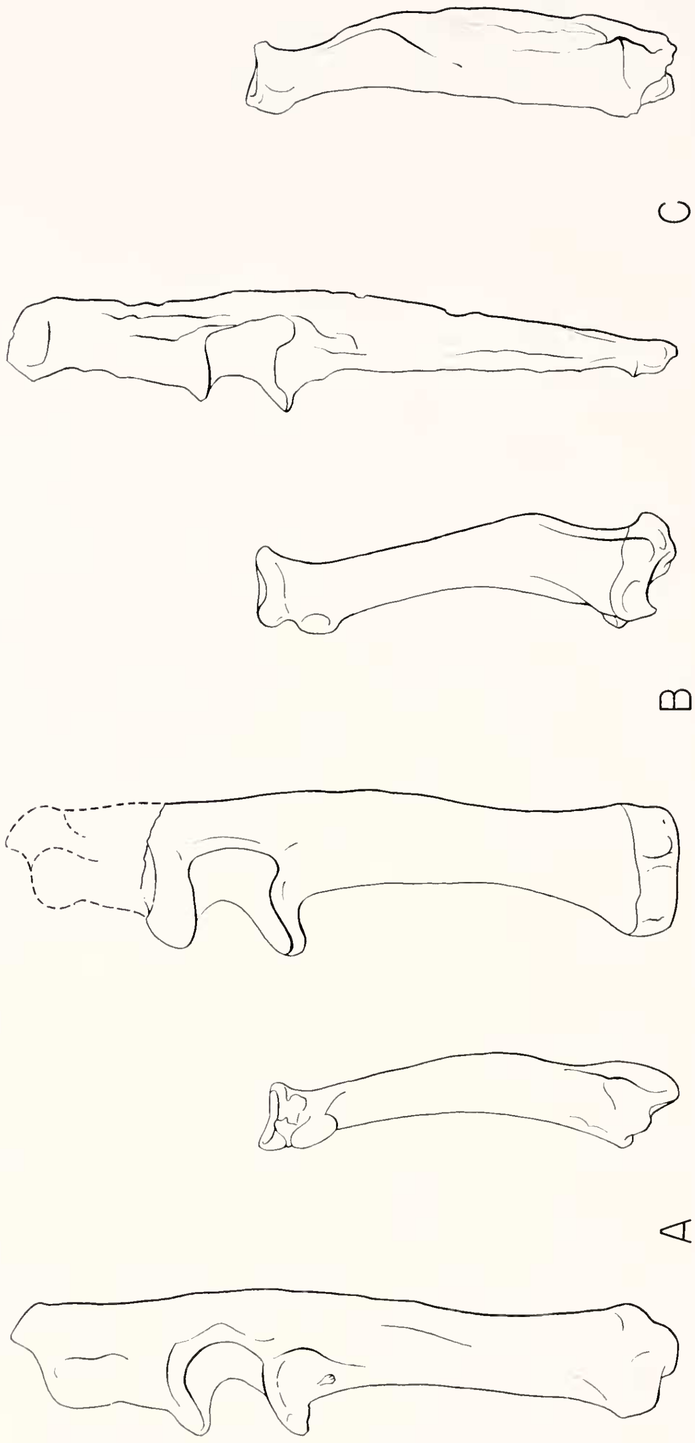

Figure 11. Lateral views of left ulnae and medial views of left radii of *Orycteropus* (A), *Myorycteropus* (B), and *Plesiorycteropus* (C).

early Pleistocene deposits there (Maglio, 1969: 12), or in both, is not known. The metacarpals are essentially identical with those of *O. afer*, but, as Leakey (1967: 19) has pointed out, this form could pertain to *O. crassidens* or, it may be added, to some species as yet unknown.

O. crassidens MacInnes (1956: 28–37) from the later Pleistocene of Kenya, type from Rusinga Island (found in deposits of uncertain age but suspected by MacInnes to be not earlier than late middle Pleistocene and possibly younger), referred specimen from Kanjera, is known from a partial skull, a nearly complete mandible and elements of the axial and appendicular skeleton. Not surprisingly, this form is very close to the living species, differing in only a few characters, such as relatively larger teeth and more vertically implanted $M^{\underline{3}}$. It may prove to be no more than subspecifically distinct. MacInnes (p. 35) tentatively assigned to it an isolated ungual from Rusinga. This bone differs from the unguals of *O. afer* and of the Kanjera specimen of *O. crassidens* in characters that suggest less proficiency in digging. It may not be referable to the genus, and is indeed the sort of ungual one would expect in *Leptorycteropus.*

The following should, I believe, be queried until better known:

O.? sp. (MacInnes, 1956: 27–28), represented by a single molar, identified as $M^{\underline{1}}$, from the early Miocene of Koru, Kenya. The tooth is comparable in size and structure to M^1 of *O. afer*, but this does not necessarily reveal much about the animal that bore it. The upper molars of *Leptorycteropus* (p. 187) are also similar in both respects to those of the living species.

O.? sp. (Gabuniya, 1956). This earliest record to date of a tubulidentate in Eurasia consists of part of a left mandibular ramus from the middle Miocene of the Kuban region, North Caucasus. Alveoli of six antemolar teeth and of M_1 are preserved, and also part of the alveolus of M_2. From the high number of antemolars Gabuniya believed the specimen to be a young individual; the marked posterior increase in the depth of the ramus also suggests this. The animal seems to have resembled *Orycteropus* and *Myorycteropus* in the elongation of the muzzle beyond the cheek teeth. It is hoped that additional material sufficient to determine its affinities with greater precision will soon be found.

O.? *browni* Colbert (1933: 2–6) was founded on a maxillary fragment with M^{2-3} from the Nagri of Pakistan. Colbert believed the type to represent an adult individual with molars three-fifths as large as those of *O. gaudryi*. Accepting this, all that can at present be said is that in *O.*? *browni* we have an orycteropodine with M^{2-3} smaller than those known in any described member of the family except *Myorycteropus africanus.*

O.? *pilgrimi* Colbert (1933: 6–7) was described on the basis of an isolated tooth, identified as $M_{\overline{2}}$[1], comparable in size that of *O. gaudryi* from "the lower part of the Middle Siwaliks," which suggests Nagri age. Lewis (1938) referred a specimen from the Dhok Pathan to the species; this consists of an incomplete cranium, including the posterior portion of the palate with molars, and part of the ascending ramus. The cranium, as restored by him, and the molars agree in general with *Orycteropus* but nothing is known of the facial region.

O.? sp. (*O.* sp. cf. *O. afer* Pallas, Kitching, 1963). Two specimens, an isolated M^1 and a ramus fragment with M_3 and broken M_2, have been recovered from the Makapan breccias. Kitching's measurements indicate a form with lower molars that are slightly longer but notably narrower proportionaly than those of the type of *O. crassidens.*

Myorycteropus
Figures 10–13

M. africanus MacInnes (1956) from the early Miocene of Rusinga and Mfwanganu

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[1] Lewis (1938: 403) regarded it, incorrectly I think, as M^2. Colbert in the caption to his figure 5, states "... anterior edge of tooth facing the left": "left" appears to be a *lapsus* for "right".

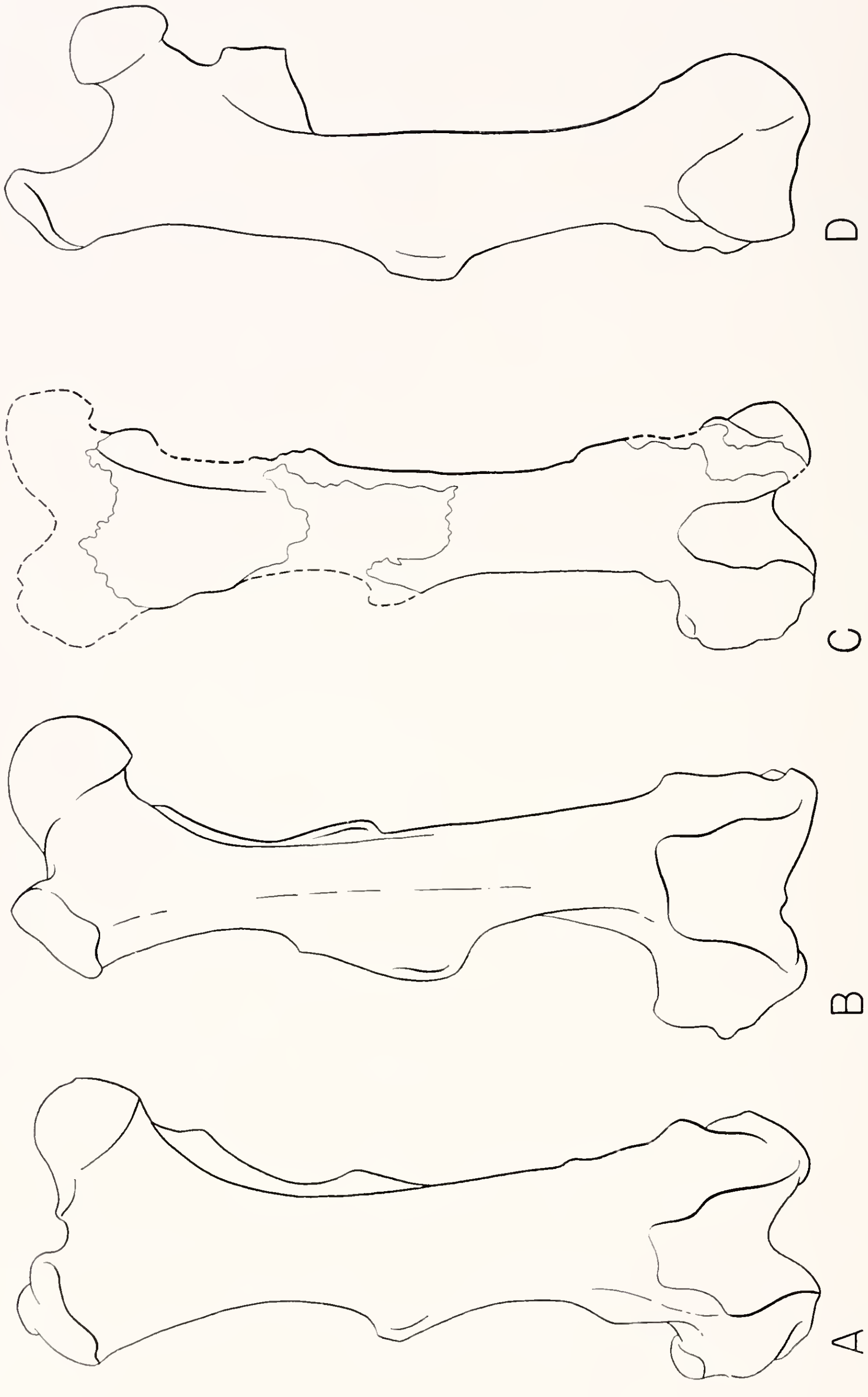

Figure 12. Anterior views of right femora of *Orycteropus* (A), *Myorycteropus* (B), *Leptorycteropus* (C), and *Plesiorycteropus* (D).

Islands, Kenya, the only species, is the earliest adequately known member of the order and also the most specialized of described orycteropodines. The type consists of an incomplete maxilla with $P^{\underline{3}}$–$M^{\underline{3}}$, some isolated teeth, a ramus with $P_{\overline{1}}$–$M_{\overline{3}}$ but lacking the symphysis, coronoid process and part of the angle, elements of the vertebral column and a rather good representation of the appendicular skeleton. A complete series of premolars was present and a very small tooth found in the matrix surrounding the type is perhaps a fifth upper antemolar. As in *O. mauritanicus*, $M^{\underline{1}}$ is longer than $M^{\underline{2}}$. By itself the dentition would not suffice to exclude the species from *Orycteropus*, but it is quite otherwise with respect to the skeleton. As MacInnes noted, the skull appears to have been relatively lower than that of *Orycteropus*, the ascending ramus of the mandible meets the horizontal at a much shallower angle, and the condyle evidently extended posterad of the angular process. The symphysis is lacking. Since there is no indication of it on the part preserved, which extends forward to $P_{\overline{1}}$,[1] it would appear that the muzzle was prolonged anteriorly beyond the teeth, in contrast to *Leptorycteropus* and in general agreement with *Orycteropus*. Mandible and molars are somewhat larger relative to leg bone lengths than in *O. afer*. The distal portion of the scapular spine has an expansion on the prespinous side opposite the metacromion. The clavicle is larger, relatively, than in *Orycteropus*. The humerus is laterally more bowed, the deltoid area relatively larger, and the distal end relatively much wider than in *Orycteropus*. Radius and ulna of *Myorycteropus* are also relatively wider distally. The radius is somewhat shorter relative to the humerus than in the other forms, and differs from that of *Orycteropus* in the humeral and proximal ulnar articulations. The metacarpals and phalanges of the forefoot are relatively larger than in *O. afer*; Mc. V in both is equally short relative to Mc. II, but in *O. gaudryi* Mc. V is relatively longer. The trapezium covers a much larger part of Mc. II than is the case in *Orycteropus*. The unguals are relatively narrower than in *Orycteropus* and have longer plantar protuberances. The pelvis is more slenderly constructed. The femur, in contrast to those of *Orycteropus* and—so far as known—*Leptorycteropus*, has a more slender shaft, especially proximally, a more globular head set on a more distinct neck and separated from the great trochanter by a deeper notch, and a much larger third trochanter. The shaft of the tibia is more compressed transversely and the cnemial crest terminates in a blunt tubercle. MacInnes restored the proximal end of the bone as having the articular area for the femur decidedly oblique to the long axis, with the lateral condyle facing more outward than upward (1956, fig. 9, (b) 1, p. 20). Attempts at a paper fit of the tibia, thus restored, to the femur result in an outward inclination of the former bone at an angle of about 45° to the long axis of the latter, surely an impossible position. MacInnes stated that the tibia was somewhat crushed and preserved no point of contact with the fibula, which lacked the proximal epiphysis. As his restoration made no allowance for this missing portion I present (Fig. 13B) an alternative one that does and in so doing provides a better fit with the femur. There are various differences between the tarsi of the Miocene and living forms, the most conspicuous of which lie in the astragalus: in *Myorycteropus* the medial flange of the trochlea does not extend distally on the neck, and both neck and head are wider transversely and flatter dorsoventrally. The pes, like the manus, was relatively larger than in *Orycteropus*.

Lavocat (1958: 142) has commented regarding the distinctive characters of *Myorycteropus*: "On voudrait être assuré

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[1] The lighting of MacInnes' figure 4, plate 1 is such as to suggest that the symphysis began beneath P_{1-2}. Examination of the specimen, however, reveals no trace of it.

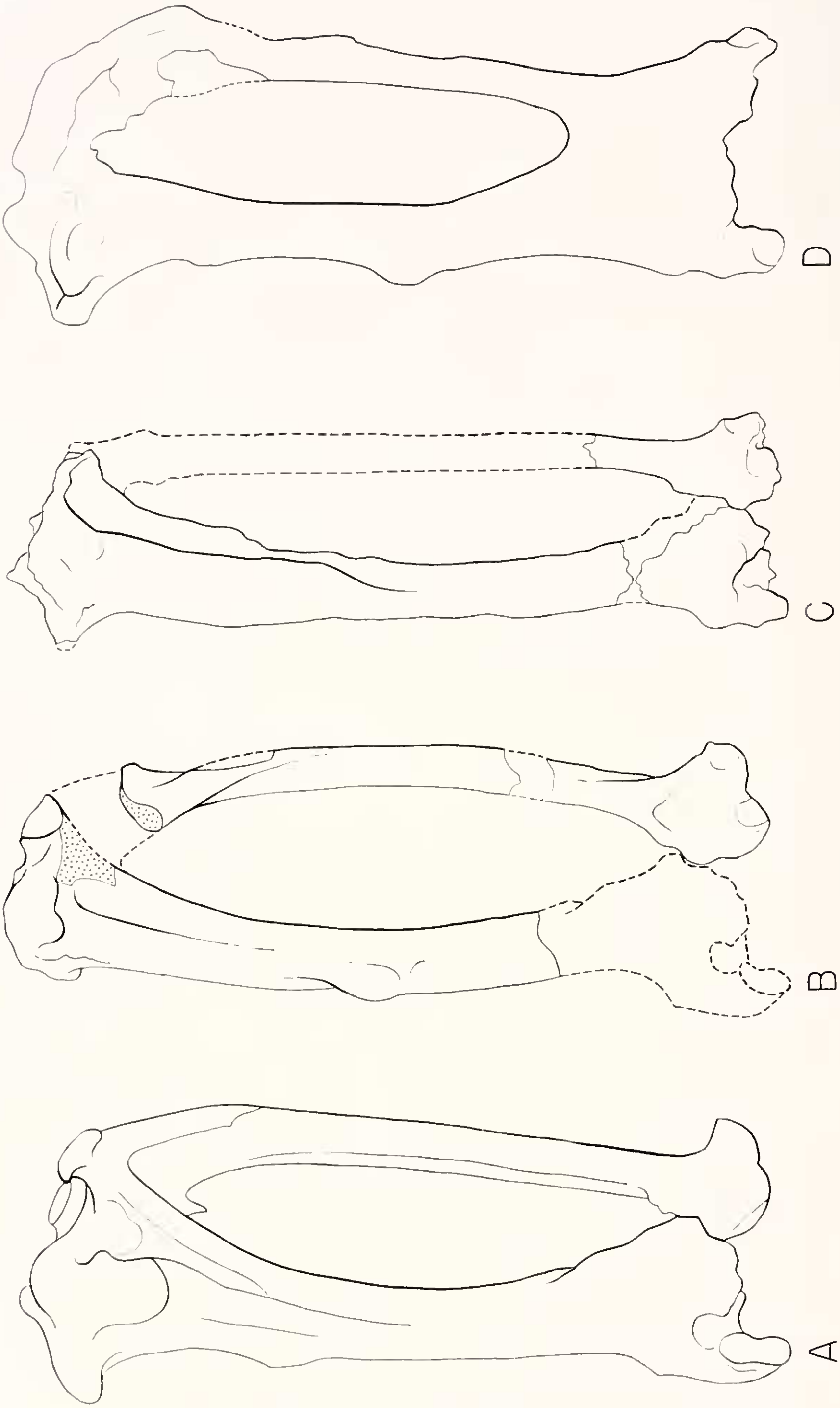

Figure 13. Anterior views of left tibiae-fibulae of *Orycteropus* (A), *Myorycteropus* (B), *Leptorycteropus* (C), and *Plesiorycteropus* (D).

qu'elles nécessitent réellement l'admission d'un nouveau genre." I believe, on the contrary, that one could hardly ask for better generic characterization than is afforded by the postcranial skeleton.

Plesiorycteropus
Figures 10–15

The most isolated tubulidentate, morphologically as well as geographically, is *P. madagascariensis* Filhol 1895. This is an extinct Recent species known from several of the superficial deposits of the island—Ampasambazimba, Ambolisatra, Antsirabe, Belo-sur-Mer, Beloha, and Tsiravé. For one of these, Ampasambazimba, a C^{14} date of 1035 ± 50 B.P. has been obtained (Tattersall, 1973B).

The type is the cranial portion of a skull. Filhol's description of it was exceedingly brief, expressed some doubt as to affinities and was unaccompanied by figures. *P. madagascariensis* remained virtually a *nomen dubium* for half a century.[1] Real knowledge of it dates from Lamberton (1946), who redescribed the type (which he did not specifically identify, but which is obviously M.N.H.N. no. 1906–717, the specimen shown in his plate 1, figs. b′ and b″) and referred a number of additional specimens to the species. These were: two crania, one with the nasals attached, a sacrum, more than sixteen other vertebrae, all of them incomplete, two humeri, a radius, an ulna, several metacarpals and phalanges, much of a pelvis, eight femora (from his text it would seem that Lamberton had at his disposal pelves and femora other than those he described or listed, but he did not state how many), three tibiae-fibulae, and three astragali. I have been able to study a cranium evidently not seen by him and some postcranial elements that he may or may not have seen, a point which cannot be determined from his paper. Some of these bones are strikingly different from the corresponding elements of the other orycteropodids, which resemble each other in most of their known parts much more than any one of them does *Plesiorycteropus*. Lamberton noted resemblances in the Malagasy form not only to *Orycteropus* but also to dasypodids, myrmecophagids and manids. *Plesiorycteropus* merits extended discussion.

Two questions at once present themselves—How good is the evidence that the various skeletal elements referred to *P. madagascariensis* really pertain to one form?, and What weight should be given to the resemblances to this group or to that?

As regards the first question, Lamberton himself seems to have had lingering doubts (1946: 47, 49) since he expressed concern that some of the bones might, after all, represent manids and dasypodids. Lavocat (1958: 139) echoed his uncertainty. I do not believe that there is any real justification for such hesitation. None of the bones in question, with the very dubious exception of the femur (see below), could be referred to any of the other groups known to inhabit or to have inhabited the island. They therefore pertain to one or to several animals that represent an additional group or groups. If they represent several then it is indeed remarkable that only one kind of peculiar humerus, one kind of peculiar femur, one kind of peculiar tibia-fibula and so on—all of appropriate size to belong together—is known. The

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[1] It was not listed by Simpson in his classification (1945)—and for good reason. He plainly stated (p. 34), "An effort has been made to include all genera that are well defined . . . . Nevertheless, a great number . . . . surely or probably invalid . . . . . or . . . so poorly known as now to have little real meaning are deliberately omitted." Late in 1942, when the manuscript of the classification was closed (p. 1x), *Plesiorycteropus* amply fulfilled the last of these criteria for exclusion. I call attention to all this only because statements occur in the literature, sometimes with apparent surprise, sometimes with overtones of chortling, that this or that obscure genus "is not in Simpson" or that some revision made before publication but after the closing of the manuscript, when he was on active service in the army, was "overlooked" by him.

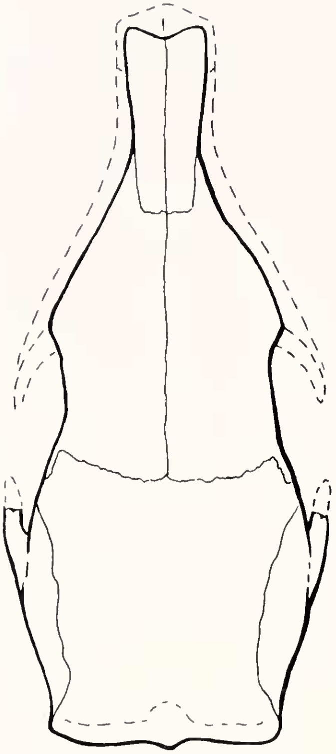

Figure 14. *Plesiorycteropus madagascariensis.* Tentative reconstruction of the skull in dorsal view. Based on the type and an unnumbered specimen in the Muséum Nationale d'Histoire Naturelle, and on Lamberton, 1946: pl. 1, fig. c. × 1/1 approx.

bones have been found in various combinations at several localities. For example, at Ambolisatra the sacrum was found in articulation with the pelvis, and nine other vertebrae and a cranium were in close proximity; at Tsiravé metacarpals and unguals, five femora, a tibia-fibula and two astragali were collected. The peculiar femur articulates well with the pelvis, the peculiar tibia-fibula with the femur, the peculiar astragalus with the tibia-fibula, etc. It seems evident that we are dealing with the remains of one form only.

Concerning the second question, Lamberton himself came to no positive conclusion as to the affinities of *Plesiorycteropus.* It might be, he thought, a "synthetic type," combining characters of edentates, pangolins and aardvarks. His text gives the impression that he favored the concept of an inclusive Edentata, in the 19th century sense of the term, and regarded the fossil as lending some support, as a possible survivor of the ancestral stock, to this now abandoned grouping. But his prose is somewhat elusive on the point. The similarities to dasypodids that he noted are several and striking, but are habitus resemblances (they are discussed below under Adaptation, p. 224), those to myrmecophagids few and minor. It may safely be concluded, with Lavocat (1958: 142), that similarities between *Plesiorycteropus* and edentates are due to convergence. There is no evidence that any member of the Edentata, in the modern taxonomic sense, ever inhabited Madagascar.[1] The similarities to pangolins may be considered together with the more fundamental and more numerous resemblances to orycteropodines.

Skull. Of the facial region only the nasals are known. These are short, suggesting that the face was probably not as long as the cranium. Rather narrow and well inset between the frontals, they widen anteriorly—the reverse of the situation in *Orycteropus*—and their anterior border is concave rather than projecting forward in the midline. The orbital rim is not well defined dorsally and a postorbital process is lacking. The extent of the frontolachrymal suture suggests the presence of a lachrymal that was probably comparable in position and relative size to that of *O.*

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[1] That they may have done so was a minor myth of Paleontology that never achieved much currency. It rested on *Plesiorycteropus* (the distal end of a tibia-fibula was figured by Carleton, 1936, as an "unknown type resembling armadillo"), and on limb bones once thought to indicate the presence of a possible relative of the tree sloths (*Bradytherium madagascariensis* Grandidier 1901) but now regarded as probably pertaining to the extinct lemuroid *Palaeopropithecus* (Lamberton, 1947). The degree of convergence between tree sloths and *Palaeopropithecus* in various characters is rather striking.

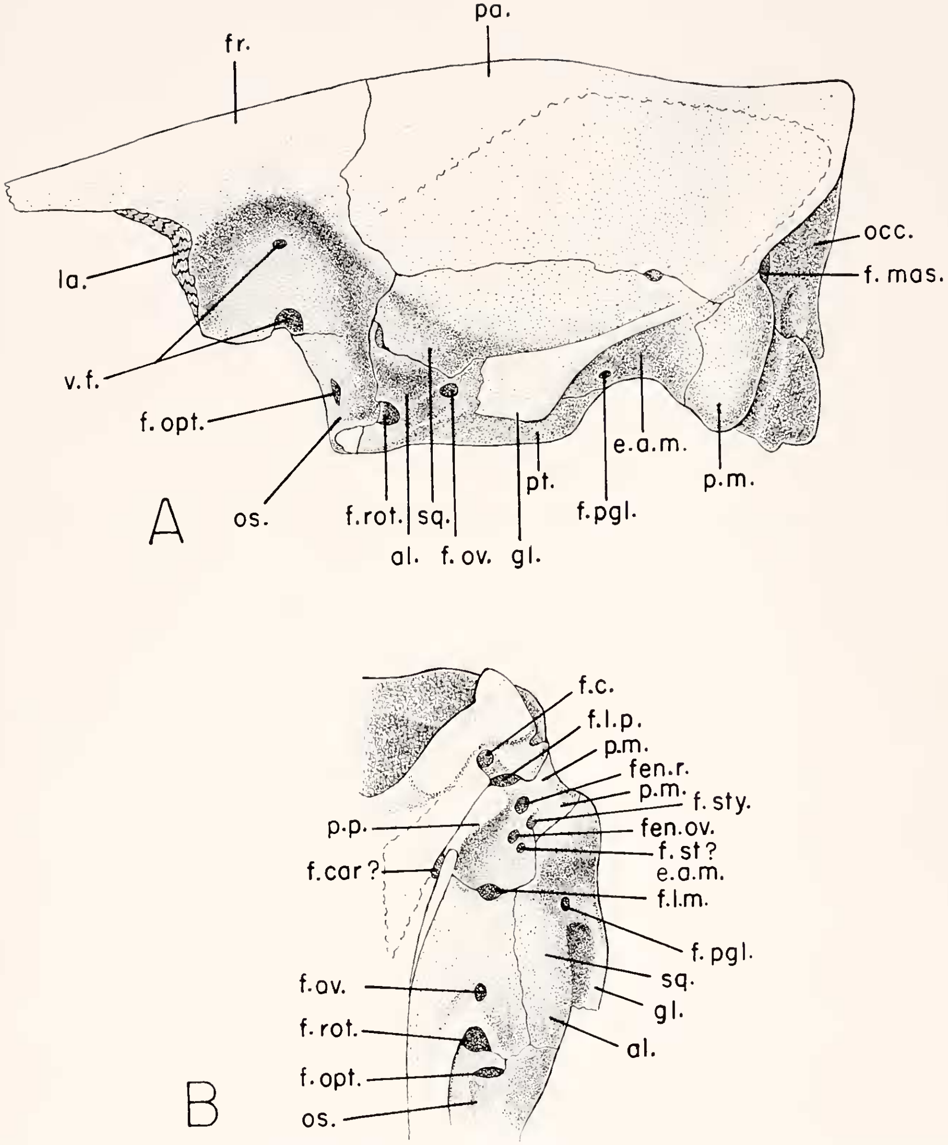

Figure 15. *Plesiorycteropus madagascariensis*. Left lateral, A, and ventral, B, views of cranium. Unnumbered specimen in Muséum Nationale d'Histoire Naturelle. × 3/2.

al., alisphenoid; e.a.m., external auditory meatus; f.c., condylar foramen; f. car?, carotid foramen; f.l.m., foramen lacerum medium; f.l.p., foramen lacerum posterius; f. opt., optic foramen; f. ov., foramen ovale; f. pgl., postglenoid foramen; f. rot., foramen rotundum; f. sty., foramen stylomastoideum primitivum; fen. ov., fenestra ovalis; fen. r., fenestra rotundum; fr. frontal; gl., glenoid process; la., fronto-lachrymal suture; occ., occipital; os., orbitosphenoid; p.m., pars mastoidea; p.p., pars petrosa; pa., parietal; pt., pterygoid; sq., squamosal; v.f., vascular foramina.

gaudryi. This is a contrast to the mandids, in which the lachrymal, when present, is more ventrally situated and has only a small facial portion. The cranial roof is more smoothly rounded across the parietals than in *Orycteropus*, and the area of origin of M. temporalis is poorly developed. The degrees of participation of the frontals, parietals and supraoccipital in the formation of the skull roof are essentially the same as in *Orycteropus*. As in *O. gaudryi*, but not as in *O. afer*, the occiput is essentially vertical. The occipital condyles and foramen magnum are in every respect comparable to those of *Orycteropus*. A lamboidal crest is present, running transversely without the median indentation present in *Orycteropus*. It is confluent laterally with the dorsal margins of the posterior roots of the zygomatic arches. The cranial portion of the squamosal is relatively longer and not as deep as in *Orycteropus*. It meets the frontal and thus excludes the alisphenoid from contact with the parietal. The ascending portion of the orbitosphenoid does not extend as far dorsally as it does in *Orycteropus*.

The position and structure of the glenoid articulation, revealed by the hitherto undescribed specimen in the Muséum Nationale d' Histoire Naturelle, is of great interest. The squamosal sends down a moderately extensive, rather long glenoid projection that is set off below from the side wall of the cranium by a notch. This process bears at its free extremity an elongate, narrow, transversely convex and poorly-defined articular surface for the mandibular condyle.[1] The articulation is thus brought downward to a level corresponding with that of the base of the occipital condyle and below that of the external auditory meatus. This is a point of major contrast to *Orycteropus*, in which the articulation occupies a much higher position—above both condyle and meatus—and of resemblance to manids and other fully myrmecophagous mammals, in which the articulation is on a level with the palate (see p. 220). The glenoid projection differs from that of manids in being relatively smaller, more posteriorly situated and directed more ventrally than anteroventrally. The zygomatic arch was probably reduced, and may perhaps have been incomplete. There is no postglenoid process, as in manids. The postglenoid portion of the skull is longer, relatively, than in *Orycteropus*.

The auditory region is basically orycteropodid, although the auditory meatus is wider and more laterally situated and the epitympanic recess smaller than in *Orycteropus*. There appears to be no epitympanic sinus; one is present in the living form. In both genera the pars mastoidea is large and well exposed on the surface of the skull between squamosal, exoccipital and parietal; it is wider dorsally in *Plesiorycteropus*. In manids there is a large epitympanic sinus and the mastoid exposure is smaller and situated ventrally between squamosal and exoccipital. The foramina of the Malagasy form differ in only a few particulars from those of *Orycteropus*—lachrymal within the orbit rather than on the side of the face, opticum slitlike and aligned dorsoventrally, not round, postglenoid present.

Nothing is known of the mandible or of the dentition. From the lowered position of the glenoid articulation, the loss of the postorbital process, and the evidently weak temporal musculature I would infer that the mandibular rami were reduced to rather straight, slender rods, with little in the way of ascending portions, and that the teeth were greatly reduced if not entirely lost. In other words, the masticatory apparatus of *Plesiorycteropus* resembles that of other fully committed myrmecophagous mammals, which *Orycteropus*, in this respect only, does not (see pp. 226–228).

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[1] The projection was lacking in the material available to Lamberton, who identified as the glenoid cavity a shallow depression on the cranium above the foramen ovale. This depression is variably developed in both *Plesiorycteropus* and *Orycteropus*.

The resemblances between *Plesiorycteropus* and the manids in skull structure are adaptive in nature, and hence convergent; those between it and the orycteropodines are indicative of affinity.

Vertebrae. Lamberton did not point out any specific resemblances to manids, and I am unable to detect any. On the other hand similarities to orycteropodines and differences from manids are evident. The centra of the anterior dorsals are much wider than deep, their articular surfaces slightly convex in front and concave behind. The spines of these vertebrae are rather slender, long and inclined posteriorly, not elongate anteroposteriorly, rather than short and upright as in pangolins. The only known posterior dorsal has a slight hypapophysis. The anterior caudals[1] have high, slender spines, the ventral surfaces of the centra bear conspicuous, forwardly converging vascular grooves, as in *Orycteropus*, and lack the prominent, paired, anterior and posterior tubercles present in manids. Lamberton reported that the faces of centra of the anterior caudals (including his "lumbar") are strongly inclined. The sacrum is decidedly orycteropodid, differing from that of the manids in numerous characters. The number of vertebrae, seven, is high, but only the first two are significantly involved in the pelvic attachment;[2] the width of the bone decreases across the middle vertebrae and increases again posteriorly, decidedly more so than in *Orycteropus*; there is no direct sacroischial connection, and the transverse process of the last pseudosacral does not form a heavy, blunt process projecting laterally beyond the dorsal rim of the ischium. The spines of the anterior sacrals are slight, low, largely fused and strongly inclined posteriorly, those of the posterior are larger, less fused and upstanding. The zygapophyses of sacrals 2 to 6 are not prominent.

Anterior extremity. It is in the structure of the limb bones, both fore and hind, that *Plesiorycteropus* differs most notably from the other members of the family, although differences from the pangolins are even more impressive. In the humerus the deltopectoral area is of orycteropodid, rather than manid, type, and the medial epicondyle is not drawn out into a long, bluntly pointed process. The radius is the most manid-like bone in the *Plesiorycteropus* body, a resemblance brought about by the hypertrophy of the linea obliqua and the transverse (not anteroposterior, as stated by Lamberton) flattening of the shaft. Both can be regarded as exaggerations of features present in other orycteropodids, however. Absence or very slight development of the radial tuberosity is a point of resemblance to manids. The distal articulation is greater in the transverse than in the anteroposterior diameter and is divided by a shallow groove; in both respects the resemblance is to the Orycteropodidae and not to the Manidae.[1] The ulna differs radically from that of other orycteropodids and of manids in the distal diminution of the shaft, which terminates in a small, styloid process bearing a facet for the cuneiform only. The large olecranon is straight, whereas in *Orycteropus* it is moderately and in manids more deflected medially. The groove in the lateral face does not terminate proximally in a fossa as it does in manids. Among the materials available to Lamberton were three kinds of metapodials, which he identified, with some hesitation, as Mc. II, IV and V. If he was correct, and I believe he was, then IV is longer relative to II and V longer

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[1] The vertebra described and figured (pl. 4, figs. 13, 13[1], 13a) by Lamberton as a lumbar is an anterior caudal.

[2] Lumberton stated that *Orycteropus* has seven sacrals. This is possibly a lapsus, but he may have had an exceptional specimen. He also mentioned an ankylosis with the ilia in *Plesiorycteropus*; his figures do not support this, and the Paris fragment proves the contrary.

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[1] Lamberton was not explicit as to whether or not the groove traverses the articular surfaces; in other orycteropodids the division is partial, not reaching the anterior border.

relative to IV than in *Orycteropus*. Other differences are to be seen in the smaller carpal articulations, the curvature of II and IV, the somewhat expanded distal ends of these bones and the limitation of the keels on their distal articulations to the plantar surfaces. In none of this is there any approach to the short, squat metacarpals of the manids. Lamberton suspected that Mc. I was lacking, as in orycteropodids and in contrast to manids, and in this he was probably right. One proximal phalanx is known and this is long and orycteropodid-like. The unguals are long, deep and bear a large plantar tuberosity. They are apparently more compressed laterally than those of *Orycteropus*, a point of resemblance to *Myorycteropus*. They differ from those of manids in not being fissured.

Posterior extremity. The pelvis is relatively shorter than in *Orycteropus* and has a rather "squared-up" appearance when viewed from above or below. The ilium is not expanded dorsally to any extent. There is some similarity to *Manis* in these features, but the basic structure is orycteropodid, as Lamberton noted. The outwardly curving ilium does not terminate anterolaterally in an expanded, blunt area, the ischium is concave medially above the obturator foramen, the pubis is directed medially as well as ventrally and posteriorly so that much of the acetabulum is visible in ventral view, the acetabular notch is wide and deep and the several processes —ischial tuberosity and spine, pectineal process, tubercle for M. rectus femoris—are well developed. The area around the ischial tuberosity is much more compact, and the ischium as a whole shorter than in *Orycteropus* as the preacetabular portion of the innominate is longer than the postacetabular. A decided point of resemblance to *Orycteropus* and of contrast to manids is to be seen in the stout, laterally projecting process from the area of the greater tuberosity. In *Plesiorycteropus* the process arises from this area; in *Orycteropus* it is anterior to the area, left behind so to speak as the ischium expanded posteriorly. Unfortunately, it is not clear from published accounts what muscle or muscles attached to the process. The sacroiliac articulation is set well forward, and is wholly anterior to the tubercle for M. rectus femoris rather than largely medial to it as in other orycteropodids. The femur is distinctive, having a small head set on a well differentiated neck, a very high great trochanter, no pectineal tubercle and a relatively enormous second trochanter that merges distally with the center of the posterior surface of the shaft. There is a certain resemblance to the rodent femur in all this, so much so that Grandidier (1912) described one of these bones as the type of his *Hypogeomys boulei*. Lamberton pointed out that a number of these femora had been found in various deposits together with pelves and lower leg bones, "with which they accord perfectly," and, just as tellingly, that no other bones of appropriate size that could represent a very large rodent have ever been found in Madagascar. His conclusion that the bones are attributable to *Plesiorycteropus* seems inescapable. The femur agrees with that of the manids in the possession of a wide, shallow rotular groove and in the lack of a pectineal tubercle but otherwise differs decidedly in the possession of a medianly placed third trochanter,[1] a deep digital fossa and a large pit in the head for the ligamentum teres, characters present in orycteropodids. The neck of the femur in *Myorycteropus* is better developed than in the living form. At first glance, the tibia and fibula look rather peculiar, but careful examination reveals that the peculiarity, from an *Orycteropus* point of view, is mainly due to three things: the lateral compression of the proximal half of the tibia, the prominent tubercle at the distal

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[1] In Tertiary manids (Emry, 1970: 498, fig. 30) the third trochanter progressively moves distally until in the living forms it disappears and M. gluteus maximus comes to insert on a swelling above the lateral condyle.

end of the cnemial crest, and the extensive distal fusion of the two bones. As regards the fusion, due to ossification in the interosseous membrane, *Plesiorycteropus* has simply carried to conclusion a tendency latent in the family (cf. Fig. 13). *Myorycteropus* approaches the Malagasy form in its possession of a cnemial tubercle and a compressed proximal portion of the shaft. The structure of the manid tibia and fibula, which never fuse either proximally or distally, is very different. The astragalus of *Plesiorycteropus*, conforming to the short, comparatively shallow, distal articulation of the tibia, is short proximodistally, with the head and the relatively short neck directed much more medially than in *Orycteropus* and *Myorycteropus*; an astragalar foramen is lacking and the trochlea is shallower. The facet for the internal malleolus of the tibia is comparable to but better developed than that of these two forms; it extends medially on to the neck and is shaped to receive the forwardly facing part of the articular surface of the malleolus. The head, although convex, is less rounded than in *Orycteropus* and the navicular facet extends farther proximally on the medial side. The manid astragalus also lacks a foramen, at least in the living forms,[1] but is otherwise quite dissimilar. The neck is long and directed distally, and the head is largely concave. The manid tibia has no internal malleolus, strictly speaking, and hence there is no medial facet on the dorsal side of the astragalus.[2]

To sum up, it would appear that *Plesiorycteropus* displays few resemblances to and many differences from the Manidae. Such similarities as exist are not of a kind that would suggest relationship. On the other hand, there is a pervasive similarity to the Orycteropodidae, which is most evident in the axial skeleton and pelvis, less so in the leg and foot bones. Even in these, however, the basic structure on which the various specializations have been superimposed is an orycteropodid one. I believe there can be no doubt as to the ordinal affinities of the Malagasy form.

PHYLOGENY AND MAJOR TAXONOMY

The Tubulidentata are sometimes cited as an example of an essentially monophyletic order. As *Plesiorycteropus* plainly demonstrates, such is not the case. Furthermore, in addition to this major cleavage within the group, it is now apparent that the African and Eurasian genera, while closer to each other than to the Malagasy one, do not stand in any ancestor-descendant relationship. Each of them represents a distinct lineage.

Leptorycteropus, tooth structure apart, is a rather primitive eutherian. While recognizeably an orycteropodine, it is less specialized than the other forms. Structurally it could represent the ancestry of *Orycteropus* and *Myorycteropus*, but its late survival indicates that its predecessors had been independent of theirs since at least Oligocene time.

Orycteropus makes its earliest certain appearance with *O. mauritanicus* of the "Vindobonian" of Algeria. This is a smaller species than the living one, and, as Arambourg emphasized (1959: 46), all the known limb bones are somewhat more slenderly constructed. This is also true of the yet smaller *O. gaudryi*. From available evidence it would thus appear that there has been a modest and late increase in overall robustness of the limb bones, together with reduction of Mc. V and the fifth digit of the pes, and a relative increase in the size of the manus within *Orycteropus*. Progressive enlargement of the olfactory area and lengthening of the facial region occurred.

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[1] Grassé (1955: 1273) unaccountably stated it to be present; it is known only in an unnamed Aquitanian specimen referred to the order by Helbing (1938· 300).

[2] There is a posteromedial styloid process, separated by a groove from the medial side of the bone, but this articulates with the astragalar trochlea, which continues proximomedially to the plantar surface.

An increase in body size accompanied by a proportionately smaller increase in head size is also evident. *O. afer* is about twice as large as the known species of the other genera, and even the comparatively small *O. gaudryi* is decidedly larger. Relationships between the described species of *Orycteropus* are not clear. Tubulidentates first reached Eurasia at some time in the Miocene (assuming an African origin for the order, see p. 232) and there may have been independent evolution within the genus in the north. I doubt if *O. gaudryi* was involved in the ancestry of *afer*, which conceivably could have come from *mauritanicus*, but whether *depereti* descended from *gaudryi* or, as such, reached Eurasia from Africa is uncertain. Progress here must await discovery of more complete materials in both continental areas.

Compared to *Orycteropus*, *Myorycteropus* is precociously specialized for digging and, as MacInnes stresses, could not have been involved in the ancestry of the living genus. The fossorial features present in the fore legs of the latter are by no means as pronounced as those of *M. africanus.* The known bones of the manus of the early Miocene form are relatively larger than those of *O. afer*, not to mention *O. gaudryi*, and Mc. V is relatively long. Specializations apart, however, the structure of the fore limb is basically similar in *Myorycteropus*, *Orycteropus* and *Leptorycteropus*. In the hind limb the femur and tibia stand somewhat apart in structure from those of *Leptorycteropus* and the living form.

In summary, both the *Orycteropus* and the *Myorycteropus* lineages trended toward acquisition of a fossorial habitus, but they did so in somewhat different ways at different times, the *Myorycteropus* lineage going farther in this direction at an earlier date, at least as regards the fore limb. The *Orycteropus* and *Leptorycteropus* lineages may be more closely related to each other than either is to the *Myorycteropus* one.

As sufficiently emphasized above, *Plesiorycteropus* stands far apart from the other members of the family, so much so as to leave little doubt that its ancestry has had a long independent history. Mahé (1972: 356) suspected that its predecessors may have reached Madagascar sometime in the Eocene, at about the same time as the ancestral lemuroids arrived there. I would agree.[1] Evolution within the *Plesiorycteropus* lineage has resulted in a terminal form so distinctive as to merit subfamilial distinction. This taxon may be defined—and contrasted with the Orycteropodinae—as follows:

Plesiorycteropodinae subfam. nov.

Skull with short facial region, no postorbital process, glenoid articulation low, on ventrally directed process of squamosal. Sacrum with seven vertebrae, relatively narrow anteriorly and wide posteriorly. Humerus with deltopectoral area confined to proximal half of shaft and inclined laterally, supinator crest evenly decreasing proximally, medial epicondyle not greatly expanded proximodistally. Shaft of radius much compressed transversely, linea obliqua very salient. Ulna decreasing markedly in size distally, articulating only with cuneiform, olecranon long, straight. Metacarpals with keels of distal articulations limited to plantar surfaces, proximal ends of Mc. II and Mc. IV small, Mcs. IV and V not notably reduced in length relative to Mc. II. Pelvis relatively short, ischium with very large tuber ischii, area of sacral attachment situated well forward, anterior to level of large, elongate, crested tubercle for M. rectus femoris. Femur with small head; well defined neck; large, high great trochanter; large second trochanter extending far medially, merging distally with center of shaft; third tro-

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[1] He also suggested that the ancestors of *Cryptoprocta* crossed at about the same time. Here I must differ and concur with those (e.g. Cooke, 1972: 125) who regard as probable a late Oligocene or early Miocene date for the arrival of viverrids in the island.

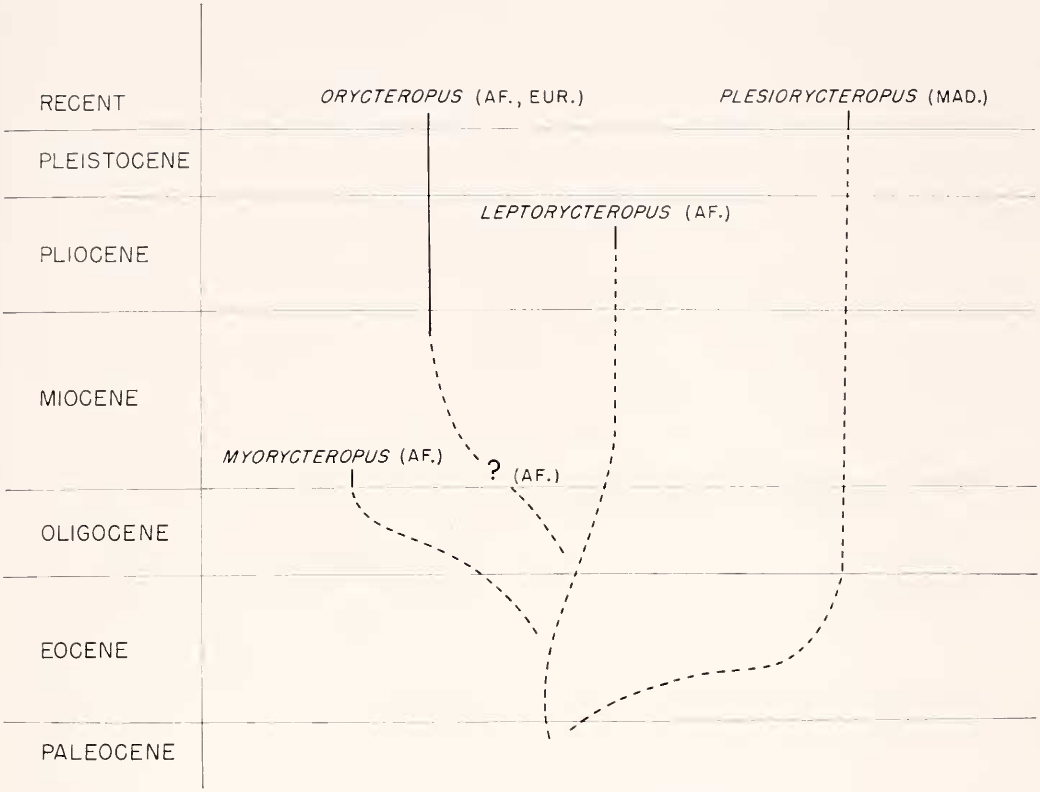

Figure 16. Suggested relationships of the known tubulidentate genera.

chanter merging proximally with crest running from great trochanter; shallow rotular groove. Tibia-fibula fused distally as well as proximally, distal articular surface short anteroposteriorly, proximal portion of tibia compressed laterally. Astragalus short proximodistally, neck short and inclined medially, facet for internal malleolus of tibia large, foramen lacking.

Sole known representative: *Plesiorycteropus madagascariensis* Filhol 1895; Recent superficial deposits, Madagascar.

Figure 16 presents an interpretation of tubulidentate phylogeny that seems reasonable on the available evidence. The plesiorycteropodines, be it noted, as descendants of waif immigrants from Africa, are a splinter group from, *not* the "sister group" of, the Orycteropodinae.

ADAPTATION AND BEHAVIOUR

Orycteropus afer

The living aardvark is a nocturnal animal and hence difficult to observe, a difficulty compounded by its partially subterranean habits. Nevertheless something, although by no means enough, is known of its biology (Fitzsimons, 1920: 233–247; Frassati, 1937; Bigourdan, 1950; Hediger, 1951: 61–73; Verheyen, 1951: 94–98; Urbain, 1954; Verschuren, 1958: 89–100; Rahm, 1961b; Kingdon, 1971: 376–387; Pagès, 1970).

An inhabitant primarily of savanna grasslands, although extending into forested (Rahm, Pagès) and more arid areas, it is a powerful digger that constructs burrows in which the daylight hours are spent.

Verheyen records that after a cold night an individual may sun itself outside the burrow during the early morning hours; aardvarks lack an insulating layer of subcutaneous fat. The temperature and humidity within the burrow during the day are essentially the same as those at the surface of the ground during the night (Verschuren). The animal digs a burrow with great rapidity, excavating with the fore feet and shifting the earth back by powerful movements of the hind feet and tail. An aardvark enters its burrow head first; accounts of its method of exit vary. Bigourdan described it as first poking its head out of the entrance, listening and sniffing the air, then bounding a short distance and repeating the process, and finally bounding in a semicircle around its hole before moving off. Harroy (reported in Verschuren) observed an individual emerging stern first, thrashing its tail about and stirring up clouds of dust as it did so. When hard pressed within the burrow an aardvark can literally erupt out head first from a new opening (Verschuren). Its fast gait is bounding but not rapid; Urbain so described it, but he was apparently observing aardvarks dashing from one hole to another. Shortridge (1934: 66) has stated that: "On suspicion of danger, the Ant-Bear—like the Pangolin—is in the habit of raising itself on its hind quarters and gazing [sniffing, surely] around, sometimes even shuffling along in this position, balanced by its stout kangaroolike tail." Fossati has observed similar behaviour.

Escape from mammalian predators—lions, leopards, hyaenas, dogs—is accomplished mainly by digging, and the burrow also serves as a protection from grass fires, at which times aardvarks play host to a wide variety of uninvited guests, ranging from arthropods through frogs, lizards and snakes to those mammals who can enter. Fitzsimons wrote of aardvarks dealing adversaries powerful blows with their shoulders by means of rapid and sudden turning movements. Kingdon remarked that "... when attacked by dogs it has been seen to turn a somersault. This effectively throws off the attackers, after which it proceeds throwing somersaults whenever touched." Sometimes, he goes on to note, an aardvark will do this when only startled. Behaviour of these kinds would serve to gain time for digging. In an extremity it may, so Verheyen records, throw itself on its back and prepare to defend itself with all four feet.[1] That this reaction is not universal is attested to by Fitzsimons who once observed an aardvark attacked by a leopard: "The intended victim bunched its body up, and keeping its head out of harm's way between its front legs, it shook the Leopard off repeatedly, and actually dug itself into the earth and escaped." He further remarks that in leopard infested districts "..... sometimes the entire back is a mass of healed scars inflicted by the teeth and claws of a Leopard." Accounts of the thickness of the skin are surprisingly conflicting. Hedinger describing it as thin—"... je fus frappé par le minceur et la souplesse de la peau (pas de tout genre couenne!)"—and Fitzsimons going to the opposite extreme: "... skin . . . thick, tough and fibrous, and the blade of penknife will usually snap if an attempt is made to drive it through . . . ." For me, at any rate, the matter is set at rest by one of the earliest studies of the anatomy of *Orycteropus.* Jäger (1837: 12) described the skin as "... überall sehr stark und an manchen stellen ½″ dick, ähnlich der der Pachydermen ...", and added, in agreement with an observation made over a century later by Verheyen, "... sie war durch ein dünne Lage sehr dichten Zellgewebes mit dem Hautmuskel verbunden."

It has been reported (Verheyen) that aardvarks in the course of their nightly wanderings are capable of covering distances of between 10 and 30 kilometers, and

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[1] Kingdon, but no one else, states that it will stand erect and strike at an adversary with the claws of the fore feet in the manner of the myrmecophagids.

may return to a former burrow or construct a new one at daybreak. The animal is fully capable of swimming. Aardvarks, especially the males, are solitary for parts of their lives. Males and females consort in the same burrow during the mating season and the one (rarely two) young remains with the mother for six months or so after. Smell and hearing are the dominant senses.

All accounts agree that the primary food of aardvarks in the wild consists of termites and, to a much lesser extent, of ants, although, in common with other myrmecophagous mammals, they vary their diet to some degree (p. 226). *O. afer* exploits the large ground termite nests that form so conspicuous a feature of the tropical African landscape, its area of distribution, according to Grassé (in Pagès), almost exactly corresponding to that of the Macrotermitinae. Aardvarks make excavations 30 cm. wide and 40 deep in the sides of the hills, and may drive even deeper holes into the interiors (Verschuren), to a depth of 3 meters or more (Pagès). According to Bigourdan, the aardvark rotates its visits to nests, following a circuit of 2 to 4 kilometers around its burrow and visiting individual hills at intervals of 5 to 8 days, thus allowing the colonies, whose powers of recuperation are immense, a rest between raids. As he observed, the relationship is amusingly reminiscent of that of a bee keeper to his hives. Pagès, on the other hand, reports destruction of nests due to repeated visits.

On the evidence there can be no doubt that *O. afer* is a well-adapted, fully committed myrmecophage. The several extinct species of the genus in all probability resembled it in most behavioural respects, at least their known hard parts strike no discordant note. Within the genus there was certainly an increase in the digging capability and there may have been some increase of the olfactory sense. As befits an animal apparently capable of detecting fruits and grubs 30 cm. or more underground, *O. afer* is highly macrosmatic. It has 10 endoturbinals (including the nasoturbinal)[1], the highest number recorded in the Mammalia, and richly developed ectoturbinals, which, again, are more complex than in other mammals (Coupin, 1926). The sinus system within the skull is extensive, with all components except the sphenoidal intercommunicating to form what Coupin calls the "sinus générale", into which the ectoturbinals extend. In *O. gaudryi* the ethmoidal area and the "sinus générale" are less expanded than in *afer* (cf. figures in Colbert, 1941, especially 21). *O. depereti*, to judge from Helbing's figures, is somewhat more advanced than *gaudryi* in these respects, which suggests that the turbinal system, especially the ectoturbinal portion, was enlarging.

To what extent may the extinct genera have resembled *Orycteropus*? Before taking up the question, the nature of the myrmecophagous adaptation requires consideration.

The Myrmecophagous Adaptation

Ants first appear in the fossil record in early late Cretaceous time and termites in the mid-Cretaceous; since the earliest known termite, a hodotermitid, is not a member of the primitive family Mastotermitidae the origin of the order obviously goes back to an earlier date (Wilson, 1971: 31, 105–8). The colonies of numerous termite and of some ant species are enormous, with individuals numbering in the hundreds of thousands and even millions (Wilson, 1971: 436–9). The highly successful radiations of these two great groups of social insects, which approximately coincide with those of metatherian and eutherian mammals, have made available rich, concentrated sources of food. Among the vertebrates, numerous omnivorous, insectivorous and carnivorous forms take advantage of this resource, the majority of them

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[1] Weber (1904: 416) reported 11 and Le Gros Clark (1926) 9; Coupin found 10 in each of twelve specimens.

opportunely by taking foragers or alates during nuptial flights.[1] To penetrate to the interiors of the colonies, to tap the riches at their source and to depend upon them as the major articles of diet—in other words to become a fully committed myrmecophage—requires the evolution of special equipment.

The nature of this equipment has been admirably summarized by Griffiths (1968: 230–246). In brief, in eutherian mammals, it consists of a very extensible, vermiform or ribbonlike tongue lubricated by sticky secretions from greatly enlarged salivary glands, a highly developed olfactory sense, a stomach with a very muscular pyloric area that acts as a "gizzard" for grinding the food, and limbs of fossorial type to breach the walls of nests. In the echidnas there is no specialization of the pyloric area, the food being ground by the spiny base of the tongue acting against spines on the palate. As usual when convergent evolution is involved, the adaptive complex has been attained in somewhat different ways in the several myrmecophagous groups, but the function of the whole is similar throughout. It is a device for the rapid transfer of small prey to the stomach in large quantities—Griffiths (1968: 40) reports that an "echidna of about 3 kg. weight can ingest 200 g. wet weight of termites . . . in a matter of 10 min."

Teeth are superfluous to the adaptation. With the conspicuous exception of *Orycteropus,* fully committed myrmecophagous mammals have either lost their teeth entirely (echidnas, pangolins, myrmecophagids) or have reduced them greatly (*Stegotherium* and, probably, *Plesiorycteropus* and the myrmecophagous palaeanodont *Patriomanis*—Emry, 1970: 468). The masticatory musculature in these forms is accordingly much reduced, with accompanying reduction of the temporal fossa, postorbital process and, in some cases, the zygomatic arch. The ramus of the jaw becomes diminished to a straight or nearly straight rodlike structure with little or nothing by way of an ascending portion, and the condyle and glenoid articulation are in one way or another brought down nearly or completely to the level of the palate. This combination of osteological characters (cf. Anthony, 1929), together with a median groove in the bony palate (not present in myrmecophagids), permits ready recognition of any extinct myrmecophage possessing it, but it must be observed that on these criteria one could not be sure that *Orycteropus* was a committed myrmecophage were it known only in the fossil state. The genus has fully functional molars and posterior premolars and a high ascending ramus, which resembles, as Frechkop (1937:18) has noted, that of the camels; it stands in striking contrast to *Plesiorycteropus* with its rather pangolin-like jaw articulation. This very curious anomaly is discussed below (p. 226).

There would appear to be at least two avenues of approach to full myrmecophagous specialization: either from fairly generalized insectivorous-carnivorous ancestors or from insectivorous-omnivorous ancestors with moderate to marked fossorial adaptation. In either case an increasing dependence on termites and ants for food would have provided the base for further specialization. (An ability to extend the tongue and to scratch or scrape earth—the essential requirements for a beginning—are of course characteristic of terrestrial mammals generally.) Certain living forms illustrate these approaches.

Myrmecobius fasciatus, the numbat (Fleay, 1942; Calaby, 1960), is an example of the first. Termites constitute its main diet, with ants forming about 15 percent; Calaby suspects that most of the latter, together with the very small beetles whose

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[1] Once, rounding a corner in Turkana, I came upon a towering termite hill in full nuptial eruption at midday. Gathered about was a variety of birds, ranging, to my surprise, up to hawks and eagles, all eagerly feasting on the temporary bounty provided by the myriads of alates on the ground in the vicinity of the nest.

remains are sometimes found in the scats, are taken together with the termites. The animal "... appears to swallow its food without chewing," (Calaby). Fleay observed that a captive specimen did chew large termites, but Calaby notes that such species do not occur within the numbat's present range. Concordant with this degree of dietary specialization, the tongue can be extended for approximately 100 mm. (condylobasal length of skull 54.0 to 58.3 mm.—Tate, 1951), the facial region is elongated, the palate is long, unfenestrated and grooved medially, the mandible is moderately, although not extremely, reduced and the cheek teeth, evidently little used, are notorious for their variability (as Calaby remarks they seem to be escaping from selection pressure). On the other hand the stomach displays no modification in the pyloric area and the limbs lack fossorial specializations other than some enlargement of the fore claws (Griffiths). The numbat seeks its food by scratching in the upper few inches of the soil or by turning over pieces of wood. It does not attack nests except to scratch in their upper surfaces when these have been softened by rain. Grinding of the food in the stomach is no doubt aided by coarse sand ingested with the prey.[1] *Myrmecobius* is an animal in transition—an "amateur anteater" in Griffith's words—that could be on the way to full commitment, or "professional" status. It has attained a morphological threshold at which any genetic changes leading to pyloric thickening, further fossorial specialization, etc., would be selectively advantageous.

The aardwolf, *Proteles cristatus,* has also gone some distance along the route to myrmecophagy. It subsists very largely on harvester termites (*Trinervitermes*), although other insects, carrion, small vertebrates and vegetable food have also been recorded as items in the diet (Ewer, 1973: 204, 205). The small, peglike cheek teeth are reduced and variable in number $(\frac{4-3}{4-2})$ and display little wear in specimens available to me. Stomach structure is consistent with this reduction, the walls being "very thick and muscular, especially towards the pyloric end" (Flower, 1869:486). For the rest, *Proteles* would seem to be less modified in response to myrmecophagy than *Myrmecobius.* The tongue is apparently not notably protrusile. Rather surprisingly, in view of the greatly reduced cheek teeth, the lower jaw is strongly built, with a high coronoid process, and the postorbital process is prominent. The canines, however, are large, somewhat peccary-like teeth that develop extensive mutual wear surfaces. As Ewer has suggested (p. 60), retention of a strong masticatory musculature and associated bony structures may be related to use of these teeth, perhaps for defense—and, it may also be supposed, for killing small vertebrates. The feet are not adapted for proficient digging—there is less disparity in size between the unguals of the fore and hind feet than in *Myrmecobius*—and the animal is not able to open termite mounds (harvester termites, the principal food item, forage very extensively on the surface of the ground and are hence readily accessible).[1]

Examples of the second and, I suspect, more usual avenue of approach are provided by the armadillos, a family that had evolved a fully committed myrmecophagous representative, *Stegotherium* (Scott, 1903: 12–40; 1937: 680), by early Miocene time. The Dasypodidae are in the main fossorial and omnivorous, and ants and

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[1] This naturally happens with any terrestrial myrmecophage but grit is not essential to comminution in the fully committed ones with "gizzards", as is shown by the fact that small pebbles are only rarely encountered in the stomachs of the arboreal forms that attack colonies of tree-nesting termites.

[1] In its retention of strong canines and relatively robust mandible *Proteles* resembles the Eocene palaeanodont *Metacheiromys.* The latter and its relative *Palaeanodon* have median palatal grooves, which suggest possession of extrusible tongues, and their cheek teeth are greatly reduced. These fossorial forms may have subsisted to a considerable degree on termites.

termites are known to be eaten by some of them. The only species whose food habits have been studied in any detail is *Dasypus novemcinctus*. From field observations and analyses of the stomach contents of 169 individuals collected over 10 months of the year in Texas, Kalmbach (1944: 15–18, 23–50) found that 488 species contributed to the diet. Animal food averaged 93.3% of the stomach contents, vegetable food 2.1% and vegetable debris, presumably ingested with the prey, 4.6%. Invertebrates averaged 91.7% and vertebrates 1.65%, with insects forming 77.6%, arachnids and myriapods 7.9%, and miscellaneous invertebrates (worms, molluscs, crayfish) 6.2%. Beetles, 41.6%, form the major article of diet, with one family, Scarabeidae, contributing 27.9% to the whole. Hymenoptera, mainly ants, form 14% and termites 4.5%. Enormous numbers of termites and ants may be taken, however. One stomach contained "at least 40,000 ants of several species" and another "some 13,000 termites." The vegetable food consists of fruits, berries, mushrooms and seeds, although some of the latter may have been ingested accidentally; Kalmbach remarks (p. 52): "Field observations indicate that under some conditions armadillos may subsist on vegetable matter to a far greater extent than has been disclosed by stomach examination." Among the vertebrate food items are salamanders, frogs, lizards and their eggs, small snakes and snake's eggs, young birds and bird's eggs, young rodents and rabbits, and carrion. "Small insects are swallowed whole and unmutilated and many of the larger but soft bodied creatures such as cutworms, earthworms and some beetle larvae are handled in the same manner. Larger hard-shelled insects, and salamanders, lizards and batrachians are subjected to a chewing process, and their remains in the stomach usually are mutilated if not dismembered. Vegetable items including berries and mushrooms are subjected to considerable mastication before being swallowed" (p. 18). Young rabbits are " . . . killed and mutilated by thrusts of the . . . front feet . . . actual eating was accomplished by continued chewing until the food was softened and torn enough to be swallowed" (p. 44). Eggs if small enough are taken entire and crushed in the mouth; if too large they are broken by the claws and the contents lapped up. The percentages of the various prey groups that make up this highly varied diet change with the seasons—and no doubt over the range of the species. In the tropics *D. novemcinctus* probably consumes a higher percentage of termites, although data are lacking.

The scattered and scanty information available on the diets of other armadillos reveals food items similar to those recorded for *D. novemcinctus*, e.g., beetles, termites, ants, maggots, caterpillars, worms, small snakes, carrion, vegetable matter, etc. *Dasypus* and *Cabassous* do dig for ants and termites (Kalmbach; Ingles, 1953: 268) and take them with their moderately extrusible tongues. The salivary glands extend back along the underside of the neck (Kühlhorn, 1939: 81). The pyloric areas of the stomachs of *Dasypus, Euphractus* and *Tolypeutes* are known to be somewhat thickened (Owen, 1831: 142, Kalmbach, 1943: 28–29; Owen, 1832: 155; Murie, 1874: 86), although evidently not to the extent seen in a committed myrmechophage. Nevertheless, such thickening would aid in the comminution of prey items swallowed whole and in the further reduction of those chewed. The arrangement in fact exemplifies the essential base from which, in eutherians, the transfer of the grinding function from the teeth to the pyloric "gizzard"[1] could progressively proceed.

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[1] A highly muscular pylorus is not confined to myrmecophagous forms among the Mammalia, although, apart from them, it is very rare. Böker (1937: 177), who calls stomachs of this type Kaumagen, records them as occurring in certain squid eating odontocetes and in *Dugong*. Such a structure is also present (Davis, 1964: 207), in conjunction with very large, crushing cheek teeth, in the Giant Panda, *Ailuropoda melanoleuca*, which feeds on bamboo shoots.

None of these three armadillos is committed to myrmecophagy to any great extent—much of their food is chewed, their jaws are not reduced, their glenoid articulations are rather high on the skull, and their teeth do not exhibit the marked variability that accompanies loss of function. Nevertheless such forms as *Dasypus*, *Cabassous* and *Tolypeutes* would appear to stand poised near the beginning of the road to it.

The living species that seems to have gone farthest toward myrmecophagy is the giant armadillo, *Priodontes maximus*. Little is actually known of its feeding habits. Accounts of stomach contents record caterpillars, beetle larvae, maggots and worms (Kappler in Heck, 1920: 520), but the animal is reputed ("... verschiedener Beobachter berichten . . . "—Kühlhorn, 1939: 59) to be very partial to termites. Several anatomical features are to an extent consistent with this. The animal is a very powerful digger that constructs burrows; as such it could make short work of termite hills. The tongue is vermiform and can be extruded for a considerable distance—Kühlhorn found that in a recently dead individual it could be pulled out some 160 mm (length of head 172–200 mm—Krumbiegel, 1940: 54); the salivary glands extend back to the sternum. Nothing is known, apparently, about stomach structure; it would be interesting to learn if the thickening of the pyloric area has gone beyond that encountered in other armadillos. The glenoid articulation is low on the skull, not as low as in the Miocene *Stegotherium* but lower than in other living armadillos, and the posterior portion of the mandible has undergone some reduction. The numerous teeth, small in proportion to the size of the skull, are highly variable in number; in the upper jaw they fluctuate between 14 and 20 on a side and in the lower between 17 and 21[1] (Kühlhorn, 1939: 76). Like those of *Myrmecobius*, they may be escaping from selection pressure. As Kühlhorn concluded, the giant armadillo stands part way between the omnivorous *Dasypus, Cabassous* and *Tolypeutes* and the fully specialized myrmecophagous xenarthrans. (*Stegotherium*, one of these, is related to *Dasypus*, while *Priodontes* is allied to *Cabassous* and *Tolypeutes*—[Patterson and Pascual, 1972: 265, fig. 6].) The animal is an "amateur" anteater to about the same extent as the numbat despite the different routes the two have followed and the different degrees of specialization each has attained in one component or another of the adaptation.

The Extinct Orycteropodid Genera

Turning to what can reasonably be reconstructed regarding the adaptations of the extinct aardvarks, it can be said at once that *Leptorycteropus* was not specialized for myrmecophagy. What is known of the structure of the skull reveals nothing of the osteological combination associated with that method of feeding. The temporal fossa and postorbital and jugal processes are relatively well developed, the palate is not grooved, the mandible has an extensive, firm symphysis, and a rather large canine is present, together with a full complement of cheek teeth. The limb bones indicate an animal capable of digging but not highly specialized for it; *Leptorycteropus* may have dug its own burrows but was certainly not as proficient as *Orycteropus* in doing so. Like *Dasypus*, it may, in addition to going to ground, have escaped its enemies by quick dashes into dense thickets. A thick and tough hide, supposing this to have been common to the order, would, like the armadillo carapace, have protected it from plant spines and thorns. The impression conveyed is of an omnivorous form that was a faster runner than the living species. Like other omnivores it no doubt ate termites and ants, but was not dependent on them to a major degree.

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[1] I doubt if the acquisition of so great a number of teeth was in any way associated with myrmecophagy. Better knowledge of the behaviour and food habits of *Priodontes*, which has no fossil record, may provide a clue to their function.

Since *Leptorycteropus* had the characteristic tubulidentate tooth structure I would judge that acquisition of this had nothing to do with myrmecophagy. Like the dental structure of the Xenarthra it may have evolved early in the Tertiary.[1]

Myorycteropus was as far ahead of *O. afer* in fossorial adaptation as *Leptorycteropus* was behind it, at least as regards the fore limb. The pelvis and hind leg bones are not as robustly constructed as those of *Orycteropus* (Figs. 12–13), which suggests that the hind legs and tail were not as much employed in digging. In all probability it constructed burrows. It was beyond any doubt perfectly capable of attacking termite and ant nests, but its degree of commitment to myrmecophagy is at present impossible to assess. Nothing is known of the skull other than a maxillary fragment, and this is not complete enough to reveal whether or not a median groove was present on the palate. The ascending ramus of the mandible slopes posteriorly considerably more than does that of *Orycteropus* and the condyle is lower. On this very scanty evidence one might suspect that *Myorycteropus* was some way along the road, but there can be no certainty on this. The jaw, dentition aside, is not as a whole very different from that of *Dasypus*, and there is nothing to indicate that the diet of *Myorycteropus* could not have been comparably diverse. Only if remains of possible descendants are found in later Miocene or Pliocene deposits will it be possible to determine whether or not a trend toward marked reduction of the jaw and elimination of the dentition was under way in the lineage.

There is much less uncertainty regarding the diet of *Plesiorycteropus.* Alone among tubulidentates, it displays cranial characters associated with a definite commitment to myrmecophagy, of which the most significant is the carrying down, somewhat in the pangolin manner, of the glenoid articulation on a descending zygomatic process of the squamosal. This implies that the posterior portion of the ramus was much reduced and the teeth diminished or perhaps lost entirely. Whatever the factor or factors that operate to maintain the size of the mandible and the persistence of fully functional teeth in *Orycteropus* may be (see below), they were not involved in the evolution of the Malagasy form.

The leg bones differ in numerous respects from those of orycteropodines (Figs. 10–13) and exhibit points of similarity to those of other groups, especially to armadillos—and within that family to *Dasypus.* The similarities to this genus,[1] which include the general structure of the humerus, the long and straight olecranon, the relative lengths of the fore and hind leg bones and the general structure of the femur and the tibia-fibula, are striking. *Plesiorycteropus* was certainly capable of digging and hence of breaking into nests. In one character, the tapering distal end of the ulna, it differs decidedly from both armadillos and orycteropodines, but agrees well enough with other accomplished diggers, such as *Phascolomis* and *Marmota.* The very high great trochanter of the femur common to both *Dasypus* and *Plesiorycteropus* is a very interesting point of resemblance. Marked elevation of the trochanter above the head of the femur is a character encountered in various mammals that are proficient jumpers and in which the main propulsive force is supplied by the hind legs—the higher the trochanter the more rapidly contraction of

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[1] The teeth of these two groups are often spoken of as degenerate. As far as loss of enamel is concerned this is true, but, as Röse (1892: 508), for one, has emphasized, in losing it they have attained new orders of specialization, involving hypselodonty and modifications of the dentine. One advantage of such teeth, which are well suited to herbivorous, omnivorous and insectivorous diets, is that they can rapidly adjust to the jaw movements of individuals, as may be observed in adequate series of various xenarthrans.

[1] The bones figured as *D. novemcinctus* by Emry (1970) are not of that species but of *Euphractus sexcinctus.*

M. gluteus medius can act in extending the femur (cf. Smith and Savage, 1956: 612–613). The very large size of the M. rectus femoris origin may also be interpreted as indicating jumping abilities (cf. Gazin, 1968: 63). Kalmbach recorded that *D. novemcinctus* frequently jumps upward when disturbed. This is a useful defensive reaction. I have seen, in motion pictures taken in the Venezuelan llanos under the direction of Dr. R. Marlin Perkins for the television series "Wild Kingdom", two individuals of *D. novemcinctus* being harassed by a couple of bush dogs (*Speothos venaticus*). The armadillos were paying little attention to them, but whenever the activities of the dogs became too annoying they would jump straight up, spilling their tormentors. In more serious situations such behaviour would gain time for a dash to safety—and *Dasypus* is capable of good bursts of speed over short distances (Roosevelt, 1914: 85). A capacity for jumping no doubt also serves *Dasypus* well in the course of its daily rounds.[1] I suspect that much of the behaviour of *Plesiorycteropus* on the ground was similar to that of the armadillo.

At all localities yielding its remains *Plesiorycteropus* occurs together with various lemurs, some of which are or were arboreal. At least one of these localities, Ampasambazimba, was situated in a densely forested area at the time the sediments there were deposited (Tattersall, 1973a: 10–16, 24). Could *Plesiorycteropus* have been at least partially arboreal, as Lamberton (1946: 47), in describing the unguals, seems to have thought? Simpson (1931: 315–319), calling attention to osteological characters possessed in common by various fossorial and arboreal mammals, pointed out that a shift from one habitus to the other could readily occur. Certain living myrmecophagous mammals exemplify this. Among both anteaters and pangolins intermediates between one habitus and the other exist. *Tamandua* is both arboreal and terrestrial, attacking tree and ground termite colonies, while *Myrmecophaga* is terrestrial and *Cyclopes* arboreal. Of the manids, *Phataginus tetradactyla* and *P. tricuspis* are primarily arboreal, excellent climbers that sleep in trees (Pagès) while other species sleep on the ground in burrows or holes. Of these, *P. gigantea* is almost exclusively terrestrial, but some, e.g., *P. temmincki* and *Manis pentadactyla*, are also capable of climbing and of attacking tree colonies (Rahm, 1961a). There is nothing in the known parts of *Plesiorycteropus* that would rule out a similar capability. The humerus resembles that of the arboreal phalangers as well as that of *Dasypus*. The lack of expansion of the distal end of the ulna would be consistent with, although not necessarily evidence of, climbing habits. The rather shallow crurotarsal articulation, together with the shape of the astragalus and the medial extent of its navicular facet (cf. *Phascolarctos*), suggest a foot less confined than those of orycteropodines to movements in the sagittal plane. Fusion of tibia and fibula is no bar to arboreal habits (cf. myrmecophagids), and an ability to jump would be advantageous. The termite fauna of Madagascar includes tree as well as ground nesting species (Paulian, 1970: 289–290); *Plesiorycteropus* could have taken advantage of both. It may well have been the most versatile of the aardvarks.

The tubulidentates were evidently more varied in adaptation and behaviour than has been supposed. As concerns the locomotor apparatus the order included forms both less and, in the fore limb, more fossorial than the living representative and one that seems to have been partially arboreal. As regards diet, at least one and possibly two were omnivores, and two otherwise differently adapted lineages in-

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[1] And in unusual situations too. Once, while a guest in a household that included two partially grown *D. novemcinctus*, I heard a clatter one morning and on investigating found that the pair had jumped up on the dining room table where they were happily consuming the breakfast.

dependently evolved to full myrmecophagous commitment, each, I suspect, via the second or "armadillo route" to that specialization. It begins to appear that aardvarks played roles in Africa and Madagascar analogous to those of the armadillos and anteaters in South America. (Pangolins, on the other hand, may have been more circumscribed by an early commitment to myrmecophagy, but their fossil record is unfortunately too scanty to throw much light on the matter.) During the early Tertiary tubulidentates were perhaps more numerous and diversified than during the later. Earlier they would have encountered little competition in the omnivore zone, and their only mammalian predators then were hyaenodontid creodonts in Africa. With the arrival of the Carnivora around the end of the Oligocene they would have been faced not only with new predators but in all likelihood with direct competition as well. A number of the smaller Carnivora of present day Africa are insectivorous-omnivorous, and some are fossorial in addition (Bigalke, 1972: 161–166); conditions in the later Tertiary may well have been similar.

The Retention Of Functional Teeth in Orycteropus

The intriguing question as to why *Orycteropus*, alone among committed myrmecophagous mammals, should possess fully functional cheek teeth and a high ascending ramus remains for consideration. The masticatory musculature (Edgeworth, 1924; Sonntag, 1925: 339–340; Frick, 1951) is of the sort usual for the kind of jaw possessed by the animal. In the adequately known extinct species four or five antemolar teeth are present; in *O. afer* the more anterior of these drop out as growth proceeds, but there is no reduction of the more posterior teeth. On the contrary these are similar in size to or even larger than those of the extinct species (see measurements in Colbert, 1941: 322–3). They display none of the extreme variability associated with a dentition on the decline. Their retention, together with the structure of the posterior portion of the mandible, is surely related in some way to diet.

Other than termites and ants very little in the way of animal food has been recorded. Fitzsimons mentions "locusts and other odd insects", Frassati, scarabaeid larvae, and Mitchell (1965), "beetles and other insects." Kingdon reports that "locusts are occasionally eaten", larvae are taken in quantity, "over 40 scarabaeid pupae eaten in a single night were found in one stomach," and "there is a single report of a mouse being taken." The teeth of *O. afer* are no doubt employed in the comminution of some of these, but to judge from other myrmecophagous mammals they would not be essential—the pyloric "gizzard", which is well developed (Jäger, Sonntag, Allison, 1947), could perform the task without them. Pangolins, for example, are known to eat adult beetles,[1] and captive specimens of *Manis pentadactyla* have eaten mice and young rats, which were "sucked in wholesale . . . there seemed to be no endeavour or need to chew" (Adam, 1932). Unless the aardvark's animal diet is far more varied than all reports indicate the explanation does not lie here.

The only possible clue is provided by a vegetable item in the diet. *O. afer* is known (Verheyen, 1951: 96–97; Meeuse, 1962: 62–63, 1963; Mitchell, 1965; Leakey, 1969: 113) to eat the fruit of a cucurbitaceous plant, *Cucumis humifructus* Stent, called in South Africa the "aardvark-cucumber." So close is the association between the two species that Meeuse has described it as symbiotic to some degree. The recorded distribution

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[1] Pagès records them in seats of *Phataginus giganteus*, and Leakey (1969: 122) has a delightful note of a Temminck's pangolin squatting partially submerged on the shore of Lake Victoria and floating its sticky tongue out on the surface of the water to trap beetles (presumably Gyrinidae) swimming there.

of the cucurbit—South Africa, South West Africa, Rhodesia, Zambia, Tanzania and Zaire (Republic of the Congo)—coincides with that of the aardvark, and the plant is "almost exclusively found near old ant-bear holes" (Meeuse). Alone among the Cucurbitaceae, *C. humifructus* is geocarpic, the globose fruits, 5 to 9 cm in diameter, being developed at the ends of long peduncles that penetrate the ground to a depth of 30 cm or more (Meeuse). Loose soil is essential, for the peduncles, if damaged during growth, do not bear fruit; such soil is present around aardvark workings. The numerous seeds, or some of them, at any rate, pass through the animal's alimentary tract undamaged. Aardvarks bury their feces in holes about 10 cm deep, frequently in the earth excavated from their burrows, and the holes are carefully filled in (Verheyen). The seeds are thus planted in suitable soil enclosed in a packet of manure. Passage of the seeds through the animal may facilitate germination, Meeuse having noted "that it is very difficult to get seeds of *C. humifructus* to germinate in contradistinction to those of other species of the genus *Cucumis*." He goes on to state "that the aardvark is, for practical purposes, the most important if not the only dispersing agent of the seeds." So great a degree of specialization and of dependence on the part of the plant argues for a long history of its evolving association with the animal.

The advantage to the plant seems evident, but for such a relationship to come into being the benefits should be reciprocal. Since aardvarks are very partial to the fruits and actively excavate them (Verheyen) some attraction obviously exists. The pulp of the fruit "is a very juicy somewhat gelatinous soft substance with a faintly sweet cucumber taste and no appreciable flavour." For this reason Meeuse doubts that the fruit is eaten for taste or flavor if aardvark and human palates are comparable (which they may not be; for example, I do not find termites obnoxious although I would not care to subsist on them). There may perhaps be a nutritional advantage since some cucurbits are known to be rich in various vitamins, but *C. humifructus* has apparently not been investigated in this connection. Meeuse and Leakey have suggested that the fruit is a source of water. This would be decidedly beneficial even if nothing else was gained by eating it. *O. afer* has been observed to drink (Verheyen), but its range includes areas, such as the Kalahari, with prolonged dry seasons. The fruits of *C. humifructus* are protected against desiccation by a waxy covering. Such a resource would permit aardvarks to penetrate regions rich in termites that might otherwise be denied to them. Leakey's observations are to the point here: "The first seven specimens we studied [in 1945] included the seeds of a wild cucumber that grows underground. We set to work to find a reason for this. Some of our staff members located an area with several aardvark burrows and a single water hole. Each morning for a number of weeks they studied the night tracks leading to this water hole, and never saw any trace of an aardvark going to water. Apparently the aardvark often meets his needs for liquid by eating wild cucumbers."

Do aardvarks employ their cheek teeth to break up the fruit? I suspect that they do, although the only published account would suggest otherwise. Verheyen reported that one of his Congolese assistants, F. Kibwe, informed him that the fruit was broken by pressure of the muzzle and the contents licked up by the tongue ("font sauter la capsule en la pressant avec la pointe du museau, pour ensuite à l'aide de la langue, la vider complétement"). In view of the wariness of aardvarks and their nocturnal habits it seems doubtful that anyone could approach close enough to observe such fine details in the field. That a fruit with a "tough firm outer layer" (Meeuse) could be so broken also seems unlikely, particularly as the aardvark's muzzle is soft (Kingdon). On the other hand the gape and the nature of the jaw articulation of *O. afer* would permit taking the fruit into the mouth, where it could be crushed with the teeth.[1] I have no other suggestion to offer, and the matter obviously requires further investigation. No one, it would seem, has presented a captive aardvark deprived of water with its "cucumber" and recorded how the animal dealt with it.

RELATIONSHIPS AND ORIGIN OF THE TUBULIDENTATA

The affinities of aardvarks have long been debated, the opinions put forward falling into three main categories: the group forms a division of an order or superorder Edentata, together with xenarthrans and pangolins; it is a very isolated order whose origin lay somewhere among the Mesozoic mammals; its relationships are with the ungulates and its ancestry was condylarthran (for the history of opinion and further references see Jepsen, 1932: 270–274; Simpson, 1945: 190, 191, 239).

Little need be said at this date regarding the first of these views, now universally abandoned. The evidence reported and reviewed above brings nothing to its support. *Plesiorycteropus* does resemble armadillos and pangolins in certain skeletal features not present in orycteropodines, but convergence, not relationship, is involved.

Broom (1909 a, b) was prominent among proponents of the second school. He saw in the primitive nature of Jacobson's organ an indication of probable marsupial affinities and of very early divergence from the eutherian stock, while in the milk dentition (interpreted by him as di$\frac{3}{3}$, dc$\frac{1}{1}$, dm$\frac{6}{6}$) "the evidence of six premolars would . . . . . suggest the possibility of its being related to some of the Mesozoic mammals, a number of which have probably an identical dental formula." It may be observed that a primitive Jacobson's organ would not be incompatible with condylarthran ancestry and that the presence of numerous tooth germs in the premolar area does not necessarily link *Orycteropus* to any Mesozoic group. A number of papers about the dentition of the aardvark and its tooth germs have been written. Despite the intrinsic interest of this subject it has nothing to do with the problem of relationships. *Leptorycteropus* reveals that a rather generalized tubulidentate had a functional canine and the normal eutherian cheek tooth number. The additional tooth germs of *Orycteropus* have no more relevance to the origin of the order than the numerous teeth of *Priodontes* have to the origin of the Edentata. Jepsen (1932), in referring *Tubulodon* from the North American early Eocene to the order, concluded that the ancestry did not lie among the Condylarthra and "must be sought in the Mesozoic." The principal evidence for his ordinal assignment of *Tubulodon* lay in the presence of tubular structures in the dentine. Discoveries made since Jepsen wrote have revealed that *Tubulodon* is a member of the palaeanodont family Epoicotheriidae (Gazin, 1952: 32–46; Simpson, 1959). Here, then, if the tubular structures are at all comparable, might be evidence in favor of the old, inclusive edentate group. However, they are surely not. Colbert (1941: 348) pointed out that they were unlike the tubules of *Orycteropus*. Gazin observed tubular structures in the teeth of the related *Pentapassalus*, but he also detected them not only in teeth but also in bones of other forms occurring in the same deposits as *Pentapassalus*. His conclusion was that they were certainly post-mortem in nature. Whatever the relationships of the palaeanodonts may be—to Xenarthra, to Pholidata or to both (Matthew, 1918: 620–657; Simpson, 1931; Emry, 1970; Patterson, 1975) they do not lie with the Tubulidentata.

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[1] A comparable feat is performed by *Dasypus novemcinctus* when it takes a quail's egg into its mouth, crushes it and swallows it shell and all. Leakey has a drawing of an aardvark taking a fruit into its mouth, but whether or not this was based on observation is not stated.

The third view had a gradual growth. As comparative anatomical studies progressed during the 19th century the separation of *Orycteropus* from both manids and xenarthrans became increasingly apparent and resemblances to ungulates began to be noticed. Around the turn of the century, some authors (e.g., Smith, 1898: 387–389; Weber, 1904: 419–420) had come to believe that these resemblances indicated the real affinities, Elliott Smith apparently being the first to suggest a condylarthran ancestry. What might be called the comparative anatomical approach culminated in the work of Sonntag and others. In his summation, Sonntag (1926: 479–484) reviewed the anatomy of *O. afer* system by system, concluded that the affinities were with the ungulate orders (noting resemblances to hyracoids and proboscideans) and, drawing on the paleontological literature then available, strongly endorsed the hypothesis of condylarthran origin. Contemporaneous or subsequent work in the same vein—Woollard (1925) on the brain, Coupin (1926) on the nasal region, especially the endoturbinals,[1] Frechkop (1937) on the feet, Frick (1956) on the muscles of the head—are not in contradiction.

A minor point requires notice here. *Orycteropus* has a mesethmoid and this, according to one view, might exclude it from the ungulate assemblage entirely. Broom (1926, 1927, 1932: 317–318, 1935) split the Mammalia into two grand divisions, "Palaeotherida" and "Neotherida", the former without and the latter with an additional ossification center, the mesethmoid, in the basicranial axis. The eutherian "Palaeotherida" included Chrysochloridae (an order in his opinion), Edentata, Proboscidea, Sirenia, Perissodactyla and Artiodactyla; the "Neotherida" embraced Insectivora, Macroscelidea, Dermoptera, Chiroptera, Primates (including Tupaiidae), Rodentia, Lagomorpha, Pholidota, Carnivora, Cetacea, Hyracoidea and Tubulidentata.[1] "Most probably," he thought (1932: 318), "with the enlarging brain too much cartilage was left to be readily ossified by the presphenoid and the mesethmoid arose as a neomorph," a suggestion that took no account of the possession by various "palaeotheridans" of brains more enlarged than those of numerous "neotheridans" and ignored the likelihood that if this really was the explanation a mesethmoid might well appear independently in group after group as brain size increased. As regards distribution of the mesethmoid among the mammalian orders Broom was on shaky ground; he knew of or examined far too little material and subsequent work has proved him wrong in some instances. Among the "palaeotheridan" Artiodactyla, Starck (1967: 498–502) cites Augier's finding of additional centers of ossification in the basicranial axis of *Sus* and himself figures a clearly defined mesethmoid in a

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[1] A resemblance to certain arctoids in the proliferation of the ectoturbinal system led Coupin to suggest some relationship to the Carnivora also. I believe the resemblance to be due to convergence, the arctoids in question being highly macrosmatic.

[1] Broom was a little given to this sort of thing. Earlier (1897, 1915 a and b) he had proposed two other grand divisions of the Eutheria based on the structure of Jacobson's organ. Chrysochloridae, Tupaiidae, Macroscelidea, Rodentia and Lagomorpha (probably), Edentata and Tubulidentata were included in the "Archaeorhinata"; Insectivora, Chiroptera, Primates, Carnivora, Cetacea and Sirenia (possibly), Hyracoidea, Perissodactyla, and Artiodactyla in the "Caenorhinata" (for want of material some living groups were left out of account and nothing at all was said about how an extinct order could possibly be allocated on this basis to one division or the other). Agreement between the two schemes is, not surprisingly, very far from complete. Only two "archaeorhinate" groups are also "palaeotheridan", artiodactyls and perissodactyls are "caenorhinate" but "palaeotheridan", *Orycteropus* is "archaeorhinate" but "neotheridan", and so on. That such discrepancies worried Broom is not apparent from his writings; he seems to have forgotten about "Archaeorhinata" and "Caenorhinata" by the time he proposed "Palaeotherida" and "Neotherida."

neonate *Hippopotamus* (within this order Broom studied only *Bos*, *Ovis* and *Capra*). A "palaeotheridan" order has thus been shown to include "neotheridan" members, and future findings of a similar nature may confidently be expected. Among the "palaeotheridan" Edentata, Dechaseaux (1971: 17–20) has described a median ossification in the ground sloths *Oreomylodon* and *Hapalops* that, topographically, has the attributes of a mesethmoid, and has cogently commented on the practical difficulties of determining, on the basis of basicranial ossification centers, whether extinct forms belong to one category or the other: "comment, dès lors, établir pour les Mammifères actuels et fossiles une division en *Paleotherida* et *Neotherida* qui ait une valeur assez sûre pour servir de fondement à des hypotheses d'ordre générales." As a further consideration, few would deny the "neotheridan" Hyracoidea a place among the ungulates. Jollie (1958: 274), without mentioning the mesethmoid by name, refers to it under the heading "secondary ossifications in the posterior part of the nasal capsule", i.e., structures of minor significance. I must agree with Roux (1947: 370–376), Starck, and Dechaseaux that the mesethmoid is no guide to higher groupings in the Eutheria. Possession of this bone by *Orycteropus* need not be taken into account in assessing affinities.

Until rather recently the fossil record of the Tubulidentata consisted for all practical purposes—*Plesiorycteropus* being ignored—of a few extinct species of *Orycteropus*, and paleontology was thus in no position to make any direct contribution to the problem of relationships. With the condylarth hypothesis in the air, however, paleontologists familiar with condylarthran osteology could weigh the resemblances and differences between the extinct order and the living genus across the vast intervening time gap. Thus Matthew (1937: 134–144) found the postcranial skeleton of *Orycteropus* to compare closely with that of the Paleocene periptychid *Ectoconus* and used it as the standard of comparison in his description of the latter. The resemblance, he thought, "does not involve any near relationship," a denial that no doubt stemmed from his belief (p. 196) that *Ectoconus*, as a periptychid, was a member of the now generally abandoned order Taligrada (Periptychidae and Pantolambdidae), which he regarded as broadly ancestral to most of the "subungulate" orders. He did, however, state that the tubulidentate pes was perhaps derivable from the condylarthran type (p. 319). Gregory (1910: 337) had earlier called attention to resemblances between the two groups in the astragalus, a point expanded upon by Sonntag (1926: 464–7).[1] Colbert (1941: 343–347), using the technique of deformed coordinates, carried the comparison of *Ectoconus*, which he regarded as a condylarth, further, and on the basis of the resemblances he detected concluded that the two orders ". . . . . . 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." The additional evidence now available, provided by the extinct orycteropodid genera made known since Colbert wrote and by recent additions to knowledge of condylarthran osteology (*Arctocyon*, Russell, 1964: 139–189; Meniscotheriidae and Hyopsodontidae, Gazin, 1965, 1968), may briefly be reviewed.

The skulls of aardvarks and condylarths have been little compared. As far as the facial region is concerned the two groups are of course far apart, but in the cranial certain resemblances between members of the two orders are apparent. The primitive tympanic of *Orycteropus* is not fused to the skull. Its anterior crus attaches

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[1] Matthew made no reference in his monograph of 1937 to this study of *Orycteropus*. The omission was no doubt due to posthumous publication, the major portion of his text having been written in 1916–1917. In 1918 (pp. 655, 656) he favored a condylarthran origin for the Tubulidentata.

to the postglenoid process and to a tubercle anteroventral to it on the squamosal-alisphenoid suture. This tubercle corresponds to the crest posterolateral to the foramen ovale described by Gazin, who suspected that it served for tympanic attachment, in *Meniscotherium* and *Hyopsodus*. The alisphenoid in orycteropodids is a major contributor to the anterior wall of the tympanic cavity, and a similar degree of participation also occurs in condylarths. The latter lack an epitympanic sinus and so does *Plesiorycteropus*. The lateral face of the periotic in *Orycteropus* is deep and nearly vertical whereas that of condylarths is less inclined, but here again *Plesiorycteropus* is closer to the condylarth condition; in neither group is the promonterium conspicuous. The paroccipital process is reduced to the vanishing point in orycteropodids; it is small in *Hyopsodus*. The alisphenoid contributes laterally to the base of the pterygoid plate in aardvarks and to a rather greater extent in condylarths. The posterior margin of the palate in *Orycteropus* is in the form of a very prominent transverse bar; a similar structure occurs in various condylarths. The lachrymal area in the two groups is similar (Gregory, 1920: 171, 176); the foramen is within the orbit in condylarths and *Plesiorycteropus*. A contact between frontal and alisphenoid occurs in *Orycteropus* and *Arctocyon*. The cranial foramina are broadly comparable in the two orders. *Orycteropus* lacks a postglenoid foramen but *Plesiorycteropus* has one. The orycteropodids do not have an alisphenoid canal but neither do all condylarths, e.g., *Hyopsodus*.

The vertebral formula in *Orycteropus afer* is C7, D13, L8, S6, Cd25. In most condylarths for which the count in whole or in part is reasonably well known—*Phenacodus*: C7, D14 or 15, L4 or 5 (not 6 or 7–Gazin), S4, Cd24; *Ectoconus*: C7, D14 ±, L4, S4; *Arctocyon*: C7, D14?, L6?—the number of lumbars is lower, but in *Meniscotherium* it is nine. The marked increase in the sizes of the posterior dorsals and lumbars over those of the anterior dorsals encountered in *Orycteropus* and *Leptorycteropus* also occur in *Meniscotherium*. The solidly built condylarthran sacrum is a structure from which the orycteropodid sacrum could readily have been derived by incorporation of anterior caudals.

Among aardvarks the scapula is known only in *Myorycteropus* and *Orycteropus*, the most fossorial members of the order. It is broad, with large pre- and postspinous fossae, coracoid process and metacromion, and an acromion that descends distally well below the glenoid cavity. No known condylarth was specialized for digging. Despite this, certain resemblances to the orycteropodid scapula occur in one member or another of the order: in *Arctocyon* the bone as a whole is rather wide, in *Ectoconus* the coracoid process is stout and recurved, as in condylarths generally (some recurvature may also occur in aardvarks) and in *Meniscotherium* a prominent metacromion is present. Various resemblances between the two orders in the structure of the humerus are apparent. The proximal end of the bone and the large deltopectoral area in orycteropodids resemble those of *Ectoconus* and *Arctocyon*, with the lesser developed area of *Leptorycteropus* finding a counterpart in *Meniscotherium chamense*. The prominent supinator crest of the orycteropodines is matched among condylarths by those of *Arctocyon* and *Ectoconus*, the lesser one of *Plesiorycteropus* by *Loxolophus* and *Meniscotherium*. Like aardvarks, various condylarths lack a supratrochlear foramen. The entepicondylar and distal articular areas are very similar in both. The radius and ulna and, in particular, the manus are specialized in tubulidentates. Neither the marked distal expansion of the radius and ulna in orycteropodines nor the distal diminution of the ulna in *Plesiorycteropus* is met with in condylarths, but the rather generalized structure of these bones in that group could have provided the base from which such specializations arose. The aardvark manus is fully known only in *Orycteropus*. In this form the virtual elimination of the first digit, the increase in width of the rest of the foot and the concentration on the second and third digits have resulted in a widening of the lunar, a diminution of the magnum, some enlargement of the centrale portion of the scaphocentrale, a marked lateral extension of the trapezium over Mc. II (this carried even further in *Myorycteropus*), and the development of an articulation between the cuneiform and Mc. V. Most of this is on the dorsal side, however. If the manus is viewed from the ventral surface, there is, apart from the extension of the trapezium and the concomitant reduction of the trapezoid, a closer resemblance to the condylarthran carpal arrangement.

The tubulidentate pelvis is peculiar in the possession of a very prominent, laterally projecting process in the region of the ischial tuberosity. *Orycteropus* is further specialized in the extension of the ischium posterior to this process and in the dorsal expansion of the ilium above the sacral articular area. Neither character is to be seen in *Plesiorycteropus*, and the latter would appear to have been less marked in *Leptorycteropus*. Such specializations apart, there is a general resemblance between aardvark and condylarth innominates, including shape and direction of the anterior portion of the ilium, the prominent tubercle for M. rectus femoris and the spina ischiadica. The iliopectineal process, very prominent in *Orycteropus*, is much less developed in *Leptorycteropus*. The condylarth femur is rather closely comparable to that of aardvarks in overall shape, trochanters and digital fossa. The marked lateral extension of the distal end in orycteropodines does not occur in *Plesiorycteropus*. Fusion apart, tibia, and fibula are similar in the two orders as regards such features as the anteroposteriorly expanded proximal and distal ends of the fibula and the wide proximal end and prominent cnemial crest of the tibia. Tibial bowing and an interosseous crest occur in condylarths, e.g., *Meniscotherium*. Basically, the orycteropodine pes is of condylarthran type. The resemblances in the astragalus have been commented on by previous authors (that of *Plesiorycteropus* is presumably specialized). The tarsal articulations, with the exception of the calcaneonavicular facet (a specialization), agree with those seen in meniscotherids and the later phenacodontids and hyopsodontids. The long, transversely compressed tubulidentate entocuneiform is approached in members of these families. In *O. afer* the wedge-shaped ectocuneiform thrusts up between cuboid and navicular, imparting a somewhat alternating appearance to the tarsus in dorsal view. *O. gaudryi*, in which the wedge shape of this bone is less accentuated and the narrower cuboid has a less outwardly and downwardly sloping medial articular surface, suggests that the condition in the surviving species is secondary, related to the widening of the pes within the *Orycteropus* lineage. The relations of the metatarsals to the distal tarsal row and to each other, including the proximal overlap of the dorsal portion of Mt. III over Mt. IV, are again as in the three families mentioned above.

All in all, there is a strong similarity between condylarths and aardvarks in the skeleton, with many of the features seen in the latter either actually occurring in one or more of the families of the former or capable of derivation from a condylarthran base. Available data are consistent with the hypothesis that the one order was derived from the other.

Evidence bearing on the place of origin of the Tubulidentata is indirect yet suggestive. The earliest members of the order so far known occur in Africa. Two extinct lineages of the Orycteropodinae were present there. The divergently specialized *Plesiorycteropus*, whose ancestors reached Madagascar from Africa probably at some time in the Eocene, further tilts the scales. The only evidence that might argue against an African origin is provided by two bones from the Phosphorites, both a little damaged, described by Filhol (1894: 135–6, 140–1). One of these, a humerus, he referred to the Orycteropodidae as *Palaeorycteropus quercyi.* The other, a tibia, which he compared with that of the pangolins, was later made the type of *Archaeorycteropus gallicus* by Ameghino (1905: 223).[1] Neither is convincingly orycteropodid-like. Simpson (1931: 374) considered both to be indeterminate, and Thenius (1960: 196n) concluded that *Palaeorycteropus* " . . . gehört sicher nicht zu den Tubulidentaten." Both, I think, should be listed as Eutheria *inc. sed.*[2]

In agreement with such authors as Lavocat, Arambourg, and Cooke, I believe on present evidence that the Tubulidentata came into existence in Africa, possibly in Paleocene time, one of a number of groups that arose there during the isolation of that continent during the earlier Tertiary. What the relationships of the order may have been to the other distinctively African ungulate groups, all presumably of condylarthran ancestry, is at present quite uncertain. For evidence bearing on this and on numerous other problems concerning the early history of mammals in Africa we must wait upon future discoveries.

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[1] In the same paper he referred a broken distal end of a tibia (now lost) from the early Eocene Casamayor Formation of Patagonia to this "genus", as *A. patagonicus.* Simpson (1948: 94) very justifiably regarded the "species" as a *nomen vanum.*

[2] A third Phosphorites form sometimes mentioned in this connection is *Leptomanis quercyi* Filhol 1894, based on an incomplete dorsal portion of a skull. Filhol believed the specimen to represent a manid showing points of resemblance to myrmecophagids, Simpson regarded it as "indeterminate, possibly an orycteropodid", and Emry, with whom I agree, would include it in the Manidae "with the understanding that its real identity may not be known."

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