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FURTHER NOTES ON MONGOLIAN CRETACEOUS MAMMALS[1]

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In 1923 the Third Asiatic Expedition discovered a mammal skull in the Cretaceous Djadokhta Formation of Mongolia—the second partial Mesozoic mammal skull ever to be described.[2] Upon learning the importance of this specimen, which was still in the matrix and of doubtful relationships as it left them, the members of the expedition turned with renewed energy to searching for further material of the same sort. Their persistence was richly rewarded with no fewer than six additional partial skulls, as well as fragments indicating two other individuals. These specimens, found in 1925, were described the following year.[3]

Further collecting has been impossible, but in cleaning up the material already obtained from the Djadokhta an important new find was made. Imbedded and almost completely hidden in a sandstone nodule collected in 1925 was a partial skull representing a new species of *Zalambdalestes*. This skull shows the characters of the upper cheek teeth much more plainly than any of the earlier material and also is the first in which the complete posterior part of the mandible, with the important angular region, is preserved. There are also associated with the skull a broken femur and part of a pelvis—fragmentary but very welcome additional information as to the structure of this genus. Preparation of the first mammal discovered has also revealed some skeletal remains of *Djadochtatherium* which were not available at the time of the original description and which prove to be of considerable importance. Description of this additional material and its correlation with what was already known are the aims of the present paper.

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[1]Publications of The Asiatic Expeditions of The American Museum of Natural History. Contribution No. 84.

[2]Simpson, G. G. 1925. A Mesozoic Mammal Skull from Mongolia. American Museum Novitates, No. 201.

[3]Gregory, W. K. & Simpson, G. G. 1926. Cretaceous Mammal Skulls from Mongolia. American Museum Novitates, No. 225.

There are now known from the Djadokhta Formation eight partial skulls with associated portions of lower jaws, one skull without jaws, a fragment of a maxilla, and part of a mandible, the remains of eleven individuals in all. These have been assigned to five genera and six species, as follows:

MULTITUBERCULATA
Ptilodontidae
Djadochtatherium matthewi Simpson.
INSECTIVORA
Deltatheridiidae
Deltatheridium pretrituberculare Gregory & Simpson.
Deltatheroides cretacicus Gregory & Simpson.
Hyotheridium dobsoni Gregory & Simpson
Zalambdalestidae
Zalambdalestes lechei Gregory & Simpson
Zalambdalestes grangeri Simpson.

The affinities of the members of this small but unusually important fauna have already been briefly discussed and are to be taken up later in more detail.

The new material, like that already described, was discovered by the Third Asiatic Expedition under the leadership of Roy Chapman Andrews, Walter Granger in charge of paleontology, and has been skillfully prepared by Albert Thomson. The drawings in this paper are by John Germann.

Zalambdalestes grangeri, new species

TYPE.—Amer. Mus. No. 21709. Most of facial portion of skull with right cheek teeth, associated with fragment of lower jaw and with partial pelvis and femur.

HORIZON.—Djadokhta Formation, Upper Cretaceous.

LOCALITY.—Shabarakh Usu, Outer Mongolia. 1925.

SPECIFIC CHARACTERS.—P^{3-4} about as in *Z. lechei*, but molars all more robust and longer relative to their widths.

Although the specimen cannot be made to enter into the genotypic species, it is unquestionably closely related and belongs to the same genus, the characters of which it helps to establish more definitely.

DENTAL FORMULA: One of the most valuable contributions of the new skull is that it clears up some doubts as to the homologies of the teeth and as to the dental formula. The latter may now be given as $\frac{?3.1.3.3}{3.1.3.3}$. The upper incisors were most doubtful, and they remain so, as this region is lacking in No. 21709. There is a large caniniform tooth preceded and followed by diastemata and inserted at a point

nearly two-thirds of the distance from the anterior end of the premaxilla to its suture with the maxilla. This must be an incisor, and from its position is probably not I^1. We indicated the possibility of their being a small I^3 close to the posterior end of the premaxilla and therefore tentatively called the enlarged tooth I^2. It should, however,

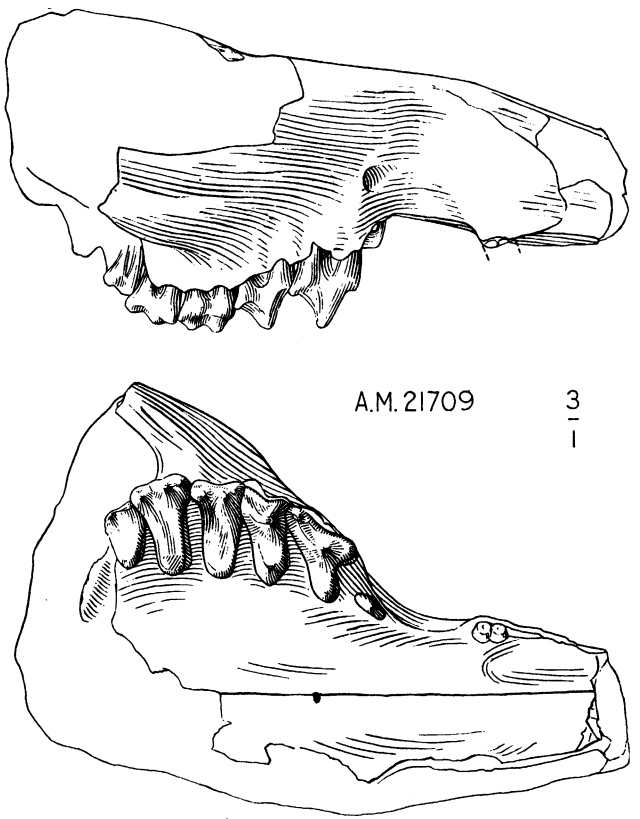

Fig. 1. *Zalambdalestes grangeri*, new species. Right lateral and palatal views of type skull. Three times natural size.

be stated that this region is obscure in the two specimens which show it (21708 and 21704) and that the presence of the tooth called I^3 is not certain. Further discussion would be futile and the only positive fact is the presence of a large lateral caniniform incisor.

CANINE: In the earlier paper the small two-rooted tooth in the middle of the diastema was considered as either P^2 or the canine but

comparison was especially with P^2 of other insectivores. For a canine it is aberrant, although not altogether unique, in its position far back of the maxillo-premaxillary suture. P^2 is now definitely recognized posterior to it, however, so that it must be the canine or P^1. It is rather small, two-rooted, and relatively posterior, hence much like a premolar, but in the most nearly comparable later mammals P^1 is often lacking, while the canine is never lacking, is often two-rooted, relatively small and premolariform, and is occasionally some distance back of the suture, so that it seems necessary to consider this tooth as the canine.

PREMOLARS: The real P^2 was not previously distinguished, but it is clearly shown in the present skull and, with this help, is now also found to be indicated in the previous material. It is a very small tooth close to P^3 and immediately below the infraorbital foramen. The palate narrows abruptly here and the long axis of the tooth follows the oblique dental border, running anterointernal—posteroexternally. The crown is simple, compressed, with but a single cusp and no cingula.

The five large cheek teeth, although somewhat worn, are better preserved than in any other known Djadokhta mammal and their structure may now be definitely set forth for the first time. Our earlier conjectures are, on the whole, well confirmed.

P^3 has a high, piercing, main cusp surrounded by three lesser cusps. The main cusp is not central, but nearer the external border. Directly anterior to it is the small parastyle, while the metastyle, equal in height to the ps but more distinctly separate from the main body of the tooth, projects posteroexternally as a spur. A similar spur of equal length but somewhat lower projects internally and somewhat anteriorly from the main cusp. This heel-like cusped spur is clearly the equivalent of the protocone of the molars.[1]

P^4 is similar to P^3 in structure, but is wider, with the parastyle anteroexternal to the main cusp and the protocone spur larger. This tooth is closely similar to the true molars in form, but is sharply distinguished by the fact that there is only one main external cusp instead of two and that this cusp is somewhat farther from the external border than the paracone and metacone of the molars and larger than either.

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[1]The Osbornian cusp terms are accepted without reference to theories as to order of development but as morphological terms applicable to molars and molariform premolars alike. This usage is becoming established in the literature and its advantages seem obvious.

M^1 and M^2 are of the same structure save that M^2 is wider transversely and has the parastyle the more external instead of the metastyle, as in P^{3-4}, or instead of having both nearly equally external as in M^1. These teeth are tritubercular but are very short and wide, being more elongate transversely than in any other known insectivore and approached in this respect only by some of the zalambdodonts (cf. *Ericulus*, *Chrysochloris*). The structure, however, is quite different from that of any recent zalambdodont. The paracone and metacone are lateral in position, separated only by the narrow cingulum from the external border of the tooth. They are subequal and are rather more distinct than the earlier material suggested. The bases are to a certain degree confluent, but hardly more so than in *Ictops*, for example. The parastyle and metastyle are small and are united across the outer face of the crown by a narrow cingulum. Internally there is a stout protocone, much worn in this individual but apparently originally not quite as high as the paracone and metacone. The crown between the outer and inner cusps is hollowed out by wear. There is no trace of a hypocone or of an anterior cingulum.

Fig. 2. *Zalambdalestes grangeri*. Diagram of right upper cheek teeth. Arrow follows the main apices of premolars and molars. Twice natural size.

M^3 is a small tooth, not so wide in proportion to its length as the preceding molars. The paracone is larger than the metacone and there appears to be no metastyle.

Lower Dentition: No new material of the lower dentition has been found and the figures accompanying the earlier paper reveal what is known. A few words must be added to the verbal description. The hypoconulid cannot be distinguished on M_{1-2} in the available material but in M_3, as mentioned, it is distinct and close to the entoconid. The paraconid is internal on all the molars and is probably slightly lower than the metaconid, although this is not certain. Paraconid and metaconid are closely approximated. On P_4 the paraconid is more distinct and slightly more external, but is lower than on the molars. The heel of P_3 has but a single cusp and seems to slope downward externally.

As seen in No. 21704, P_2 occludes just posterior to the upper canine, hence well in advance of P^2 and not in contact with it. The

tip of P_3 seems to pass just internal to P^2. A wholly incisiform semi-procumbent tooth, which must be the homologue of the lower canine, passes just anterior to the upper canine and comes lightly in contact with it.

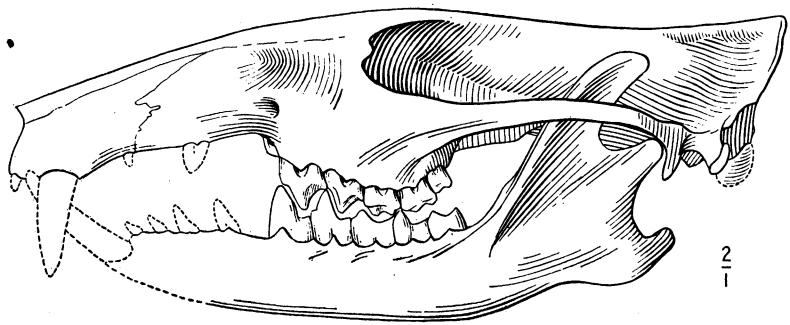

Fig. 3. *Zalambdalestes lechei* Gregory and Simpson. New composite reconstruction of skull and jaws, left lateral view. Twice natural size.

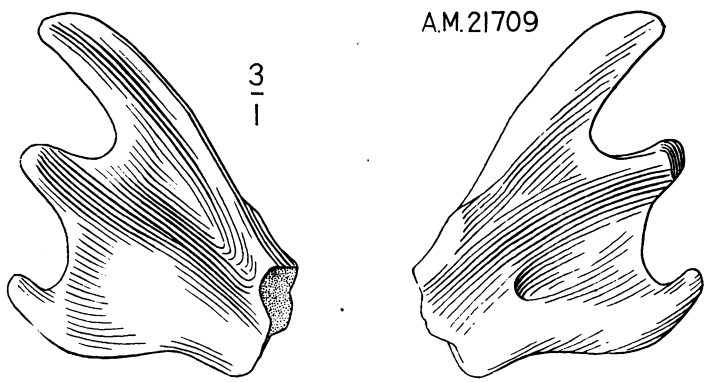

Fig. 4. *Zalambdalestes grangeri*. Posterior part of right lower jaw of type, external and internal views. Three times natural size.

SKULL: The new skull fully confirms our belief that the large opening in the base of the anterior end of the zygoma of No. 21708 is artificial. In the present specimen this region is better preserved and a thin plate of bone is here seen, slightly hollowed out, probably for the origin of well developed snout muscles.

MANDIBLE: In our earlier material the angular process of the mandible was lacking and the coronoid process, while apparently complete, had probably lost its apex. With No. 21709, however, is

associated the completely preserved postdental portion of the right mandible, and the earlier restoration must be modified. The coronoid is long and slender, extending farther back than the condyle. The angle is a small, pointed, hook-like process, not at all inflected. The external surface of the base of the coronoid is excavated. On the internal surface, the region anteroinferior to the condyle is broadly concave and near the anterior end of this shallow excavation is the large dental foramen. Although distinctive, this whole posterior part of the mandible finds fairly close comparison with *Potamogale* among zalambdodonts or with some of the erinaceomorphs, such as *Necrolestes* or *Galerix*.

SKELETAL REMAINS

In the same nodule of reddish sandstone which yielded skull No. 21709 were a number of skeletal fragments. Besides some indeterminate fragments, distal caudal vertebrae, etc., there were found parts of a pelvis and femur and, at a little distance from these, another pelvis nearly complete with the sacrum, anterior caudals, and some limb bones. On further development the second pelvis and associated material proved to belong to a small reptile, but the other pelvis and femur are mammalian and their size and general characters strongly confirm the natural inference that they belong to the same individual as the skull.

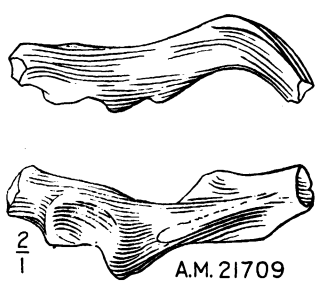

Fig. 5. *Zalambdalestes grangeri*. Pelvis associated with type. Superior and external views of right ilium and part of ischium. Twice natural size.

PELVIS: The pelvis is clearly of insectivore type, but is rather peculiar in detail. The acetabulum is deep and about one third of it was apparently formed by the pubis, which is lacking. The ischium just back of the acetabulum is a stout bone nearly oval in section. The ilium, which is complete save for a very small portion of the anterior end, is not blade-like or compressed laterally and is triangular in section throughout. The crista lateralis is prominent and divides the lateral aspect of the bone into nearly equal dorsal and ventral portions. The iliopectineal tubercle is well marked, purely ventral in position, and close to the ilio-pubic symphysis. The anteroinferior iliac spine is also quite distinct and is at the posterior end of the crista

lateralis, immediately anterior to the acetabulum. The ventrolateral face of the ilium is concave throughout. The dorsolateral face is convex posteriorly, above the spina anterior inferior ilii and the posterior portion of the crista lateralis, but anteriorly, in the region for the origin of the gluteus medius, it becomes hollowed out. Just at the anterior portion of the sacro-iliac joint the dorsal (or dorsoposterior) edge of the ilium is produced into a relatively large plate-like crest, similar to that common in the Creodonta but usually less prominent or absent in the Insectivora. Anterior to this crest and to the sacroiliac joint the ilium turns sharply outward and projects anterolaterally and somewhat upward, free of the vertebral column. This pelvis, basically primitive but with strongly marked muscle insertions and a certain peculiar aspect of its own, suggests a strong pelvic musculature. It is far the oldest mammalian pelvis so far discovered

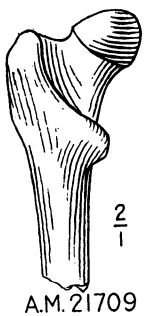

Fig. 6. *Zalambdalestes grangeri*. Semidiagramatic restoration of proximal portion of left femur associated with type. Posterior (ventral) view. Twice natural size.

FEMUR: Only the proximal portion of the *femur* is preserved and this is imperfect, but can be restored with certainty. It is at a definitely higher evolutionary level than any of the known Jurassic femora and agrees with the rest of the evidence in marking *Zalambdalestes* as a member of the basic true placental stock. The head projects at an angle to the shaft, but the neck is not markedly constricted. The greater trochanter projects nearly as high as the head, from which it is separated by a very shallow notch. It is compressed transversely, and a strong curving crest runs downward and then internally from it to the lesser trochanter which is large and quite internal in position. Just beneath this crest is the deep digital fossa. The presence or absence of a third trochanter cannot be determined.

MEASUREMENTS

	Zalambdalestes grangeri No. 21709	*Z. lechei* No. 21708
P^{3-4} ant.-post., ext.	5.3 mm.	5.3 mm.
M^{1-3} a.-p., int.	5.3	4.5
M^{1-3} a.-p., ext.	6.3	5.4
P^3-M^3 a.-p., ext.	10.8	ca. 9.9
M^1 a.-p., ext.	2.5	2.1
M^1 transverse	4.1	4.0
M^3 a.-p, ext.	1.7	ca. 1.4
M^3 trans.	2.7	ca. 2.6

Measurements of teeth so small and irregular may differ even several percent if taken at different times or by different observers. The above were taken with proportional dividers under a microscope and repeatedly checked and compared. Reasonable allowance has been made when necessary for the more eroded teeth of No. 21708, so that, if anything, the differences between the two are minimized.

Djadochtatherium matthewi Simpson

When the type skull of *Djadochtatherium* was described, preparation of the associated fragments was not complete. Mr. Thomson has since completed his skillful work, revealing several associated foot bones, five fragmentary vertebrae, the lower end of a scapula, a large part of a humerus, ribs, and several other fragments. These were all found in direct association with the skull and jaws and there is every reason to consider them as parts of the same individual. Incomplete as they are, these remains are of great interest and significance and this occasion is taken to describe them in some detail.

The proximal epiphysis and much of the shaft of the right *humerus* are preserved. While it agrees in a general way with the only other multituberculate humerus so far described,[1] that of *Ptilodus*, it differs somewhat in detail and permits a more thorough description of the known parts than that given by Gidley. As he has pointed out, the humerus in this Order is entirely unlike that of the monotremes and stands at the same evolutionary level as that of the most generalized placentals and marsupials.[2]

The head is large, the articular surface forming part of a sphere and only slightly elongated anteroposteriorly. The tuberosities are

[1]Gidley, J. W. 1909. Notes on the Fossil Mammalian Genus *Ptilodus*, etc. Proc. U. S. Nat. Mus., XXXVI, 611–26. Humerus, p. 620.

[2]Gidley states that it is "eutherian throughout" and with this all would agree if by "eutherian" evolutionary status and not positively indicated relationship were meant. Broom has criticised this statement, apparently overlooking the fact that the term "Eutheria" as originally proposed by Gill included *both* marsupials and placentals and that Gidley was obviously using the term in this sense.

widely separated and neither is enlarged. The bicipital groove is broad and shallow and merges imperceptibly into the anterodistal face of the shaft. The crest of the lesser tuberosity is moderately prominent and becomes gradually lower and more rounded as it passes distally. The deltoid ridge is, as stated by Gidley for *Ptilodus*, "well developed but not highly specialized." Proximally it bears a triangular flattened surface, about 3 mm. wide near the greater tuberosity and narrowing distally so that the apex of the ridge becomes

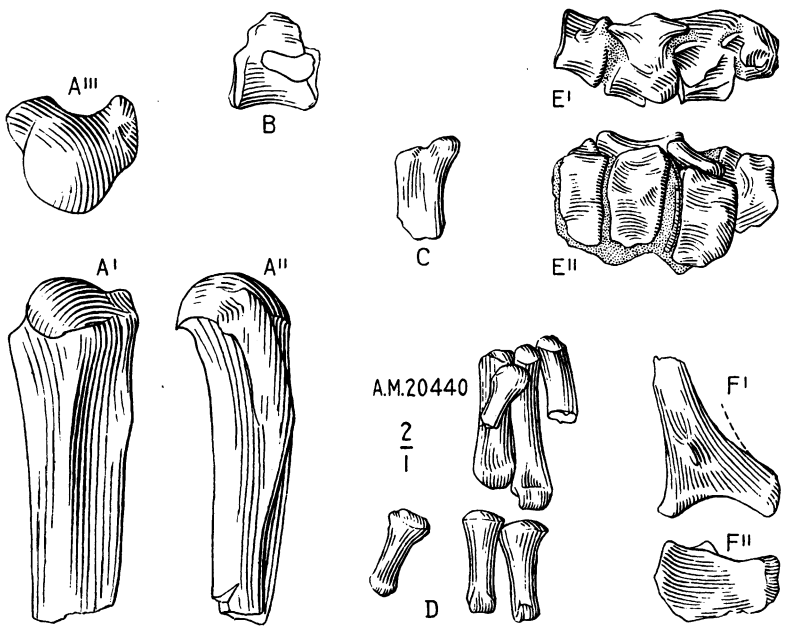

Fig. 7. *Djadochtatherium matthewi* Simpson. Skeletal fragments associated with type. A', right humerus, posterior view. A'', same, external view. A''', same, proximal view. B, Lumbar vertebra, lateral view. C, Head of rib. D, Metacarpals and proximal phalanges, palmar view. E', Articulated dorsal vertebrae, lateral view. E'', same, ventral view. F', Right scapula, lateral view. F'', same, inferior view of glenoid cavity.

single and sharp at a point estimated to be about 15 mm. from the top of the greater tuberosity. About 6 mm. of the ridge is preserved below this point and in this distance, which must carry it well below the middle of the shaft, it becomes only slightly less prominent and remains sharp, bordered by concave surfaces on both sides. There

is also a ridge, quite definite and fairly sharp at first but becoming rounded distally, extending down the posteromedian part of the humerus from below the head to the end of the part preserved. This ridge, the crest of the lesser tuberosity, and the deltoid ridge make the shaft definitely triangular in section, dividing it into a broad, slightly concave anterior face, a narrow concave posteroexternal face, and a still narrower posterointernal face which is concave proximally but becomes somewhat convex distally.

Only a fragment of the right scapula is preserved but it is at present the only multituberculate scapula known and is therefore important. The glenoid cavity is complete, but only a portion of the blade remains. The relationship of glenoid cavity to blade is exactly that of higher mammals and fundamentally unlike that in monotremes. The blade narrowed just above the glenoid and was backwardly directed—another point of marked resemblance to higher mammals and marked dissimilarity to monotremes. The glenoid cavity is elongate anteroposteriorly and somewhat wider posteriorly. The posteroexternal angle projects slightly and is pointed. The cavity fits the head of the preserved right humerus perfectly, allowance being made for the thin articular cartilage, and confirms their natural association.

The importance of this scapula is that it seems to settle much discussion as to the multituberculate shoulder girdle and agrees with much other evidence in showing that the multituberculates were in at least a metatherian[1] stage of evolution and cannot possibly have been ancestral or closely related to the monotremes. In 1889 Marsh described under the name *Camptomus amplus* a scapula, interclavicle, and other fragments (the association of which with the reptile-like shoulder girdle was admitted to be doubtful). This clearly reptile-like shoulder girdle was considered as probably, or possibly, allotherian (multituberculate)[2] and as such, without due regard for the hesitation which Marsh himself expressed and for the fact that reptiles to which parts of this dissociated shoulder girdle could well belong are known to occur in the same formation, it has become firmly fixed in the literature, popular and scientific. Thus Broom cites it in the course of his valuable discussion of multituberculate affinities.[3] Broom also believed the pectoral girdle to be known in *Ptilodus*, so identifying the

[1]This does not mean that they were related to the Marsupialia.

[2]Marsh, O. C. 1889. Discovery of Cretaceous Mammalia. Am. Jour. Sci., (3) XXXVIII, 81–92. *Camptomus*, p. 87.

[3]Broom, R. 1914. On the Structure and Affinities of the Multituberculata. Bul. Am. Mus. Nat. Hist., XXXIII, 115–134. *Camptomus*, p. 125.

element called the pelvis by Gidley.[1] Further discoveries quickly showed that Gidley was correct with regard to *Ptilodus*.[2] and the present specimen shows that Marsh and those who have followed him were probably incorrect in referring the *Camptomus* fragments to a multituberculate. *Djadochtatherium* is a typical multituberculate, older than the Lance, whence *Camptomus* was derived, and it certainly can have had neither reptile-like coracoid nor interclavicle, although of course rudiments of the more typically reptilian elements may have been present as they are in many primitive marsupials and placentals.

The preserved foot bones probably belong to the right manus and consist of four *metacarpals*, two of them complete, and three proximal *phalanges*. The proportions and general aspect of these bones are quite comparable to those familiar in primitive marsupials and placentals. Metacarpal II is 9.1 mm. long; Met. III, 10.8 mm.; 1st phalanx II, 6.9 mm.; 1st phal. III, about 7.0 mm. The middle portion of the shaft of met. III measures 2.0 mm. in transverse diameter. The bases of metacarpals II and III are closely appressed, somewhat narrowed transversely, and the articular surfaces for the carpals are nearly featureless, approaching simple sections of transverse cylinders and extending, at least on met. II, somewhat farther on the dorsal than on the volar side. The external overlap of the proximal ends common in primitive mammals is either very slight or absent. The shafts of these bones are gently arched, their dorsal surfaces nearly straight and volar surfaces slightly concave. The heads (distal ends) are very little expanded. The surfaces for the phalanges are also transversely cylindrical and extend farther on the volar than on the dorsal side. Keels are absent or, possibly, very faintly indicated at the volar end of the articular surface.

The proximal end of met. I lies in the specimen below that of met. II. Its base is more equidimensional, the carpal articulation rounded The shape of this surface, the absence of any evidence of pressure against met. II, and its displacement in a foot which was articulated when buried all point to the first digit as being more freely movable than the others and very probably opposable to them.

The first phalanges are expanded proximally and the articular surfaces for the metacarpals are simple and only slightly concave. The distal ends are slender and not expanded. The articular surfaces

[1]Gidley, *loc. cit.* sup., p. 621.
[1]Note by Walter Granger to Broom's paper, *loc. cit.*, p. 134.

for the second phalanges also extend farther on the volar side and each has a shallow median groove ending in a slight notch at this end.

These foot fragments definitely suggest a mobile, slender forefoot with an opposable pollex.

The vertebrae include four partial anterior dorsals in articulation and a single isolated vertebra of different character. These are all poorly preserved and their description provisional. The centra of the four associated vertebrae are depressed and are wider than long. On the second and third of the four there is a small posteromedian process on the lower part of the centrum and also small posterolateral processes. These all appear to be absent on the first preserved vertebra and this region is broken off on the fourth. There appear to be no true transverse processes. The nerves probably issued through posterior notches in the bases of the neural arches. The zygapophyses are simple, their articular faces plane and nearly horizontal, but facing a little outward on the post- and inward on the prezygapophyses. The upper parts of the neural arches are broken off. The isolated vertebra, which was found in the same nodule, has a higher and narrower centrum, slightly longer than broad, concave and slightly keeled on the lower surface, and has strong transverse processes. On the four articulated vertebrae facets for ribs appear to be present, although not clear, and two ribs were found very close to them, but there are no rib facets on the isolated vertebra, which must be a lumbar.

The ribs are exemplified by numerous fragments, showing little beyond the fact that capitulum and tuberculum are distinct, close together but separated by a notch, and that the main body of the rib is compressed anteroposteriorly and elliptical in section.

Corrections for Novitates No. 225

This occasion is taken to correct the following errors in our former paper, Novitates No. 225.

p. 1, l. 14 & l. 20. For "1924" read "1923."

p. 1, 1.22. Delete "and family."

p. 4, 1.10 of legend to Fig. 1. Insert "H," before "H'".

p. 9, legend to Fig. 8. For "x1/1" read "x2/1."

p. 9, 1.18–19. Read "The palate is of comparable width throughout internal to the alveoli," etc.

p. 9, 1.2 from bottom. For "P^{2-4}" read "P_{2-4}"

p. 14, 1.21. After "$P\frac{3}{3}$ or ^{2}" insert "$M\frac{3}{3}$."

p. 15, legend to Fig. 13. For "x2/1" read "x slightly less than 2/1."
p. 16, legend to Fig. 14. For "x2/1" read "x3/2."
p. 17, 1.8. For "P_4" read "P_3."
p. 17, 1.9. For "P^4" read "P_4."
p. 20, Fig. 19. The left view is of the internal aspect and would be correctly oriented if rotated clockwise about 150°.