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HIND LIMB MUSCULATURE AND HABITS OF A PALEOCENE MULTITUBERCULATE

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INTRODUCTION

The Order Multituberculata is a great group first appearing in the Triassic and ranging through the Jurassic, Cretaceous, and Paleocene into the base of the true Eocene. Highly characteristic of the Mesozoic and Paleocene wherever mammals are found, it was very widespread throughout at least the best known phases of its history. The most various opinions as to the affinities of the Order have been expressed. A recapitulation of this complex taxonomic history does not enter into the present discussion—it suffices to say that the view to which we subscribe and which we believe most in accordance with the additional data here published is that fully expressed by one of us elsewhere (Simpson 1928; see also Granger 1915, Matthew 1928, Granger & Simpson, in press). According to this opinion, the multituberculates represent an entirely extinct, quite separate mammalian side line, not ancestral to any later forms and related to other mammals only through an ultimate common ancestry in the Triassic or earlier. Despite the fact that the multituberculates thus appear to have little direct bearing on the phylogeny of Tertiary and recent mammals, this exceptionally long-lived and once dominant group is perhaps of even greater morphological interest because of its evolutionary isolation. Within the limits of the now available material, it offers an almost unparalleled occasion for the testing and application of the recently developed methods of reconstituting the anatomy, movements, and adaptations of an extinct group of animals.

This problem was first approached in a previous paper (Simpson 1926) in which the food habits, particularly, were studied on the basis of dental, cranial, and mandibular characters. The present paper is chiefly devoted to a second phase of the same subject, to the attempted reconstruction of the more essential elements of hind limb musculature and to an analysis of this musculature and of the osteology from a functional point of view. The material upon which this is

based is largely a single specimen of nearly complete hind limbs and pelvis from the oldest Paleocene (Puerco) of the San Juan Basin in northwestern New Mexico. This unique and invaluable specimen (Amer. Mus. No. 16325) was found by Walter Granger in 1913 and briefly referred to by him in an abstract published in 1915. A complete morphological description is being given elsewhere (Granger and Simpson, in press).

This hind limb is referred to the genus Eucosmodon with much probability. Coming from the oldest known Paleocene horizon, its bearing on the habits of the Jurassic, or, still more, of the Triassic multituberculates is dubious as no skeletal remains certainly referable to the latter forms are yet known. There is, however, reason to believe that conclusions based on the Eucosmodon hind limb are applicable in a general way to all members of its family, the Ptilodontidae of the Cretaceous, Paleocene, and lowest Eocene. Various limb fragments are known from the upper Cretaceous, others are known in a different species of Eucosmodon from the Torrejon (in this case associated with lower jaws), and parts of the pelvis, femur, tibia and fibula of Ptilodus gracilis from the Fort Union of Montana have been described (Gidley 1909). All of this material agrees rather closely with the present more perfect specimen in general functional characters.

In restoring the musculature, accurate restored models, three times natural linear dimensions, were made of the whole pelvis and of the right femur, tibia and fibula. These were mounted in a natural standing pose and the muscles were then fashioned in red modeling clay and affixed in the inferred original positions. Constant reference was made to the original bones, on which the chief muscle attachments are clearly visible, to numerous dissections of recent mammals by Elftman, to the large literature on recent myology, especially of the marsupials and monotremes, and also to the small but important literature on paleomyology (especially Gregory, Camp, Romer, etc.). The completed restoration was then studied, drawn, and dissected as if it had been a recent mammal.

LIMB POSTURE AND MOVEMENTS

The mechanical effect of the limb musculature depends in large part on the normal posture of the various bony elements. This posture is to be inferred chiefly from the osteology itself, the relative sizes of the different segments, the morphology of the individual bones

and, especially, the shape and extent of each articular surface. As all of these surfaces are preserved in the specimen here especially studied, the limb posture is known with a reasonable degree of certainty and serves as a point of departure for a functional analysis of the musculature. The femur had unusual freedom of motion in all directions, but in the normal standing position of the animal it was nearly horizontal, inclined forward, outward, and slightly downward. The angle between the femur and tibia could never have exceeded 90° in life and was usually considerably less—the leg could not be straightened and the crus was usually drawn well backward and could be made almost parallel with the upper limb. Normally the tibia and fibula would thus be directed backward, inward, and downward. The foot, as clearly shown in its almost completely known osteology. is unusually primitive. It is pentadactyl and plantigrade, of grasping type with partially opposable hallux. The digits are strong, the functional length formula 3>4=2>5=1. The terminal phalanges carried claws of moderate size, somewhat compressed transversely.

The foot was clearly a rather flexible structure capable of much movement in all usual ways. The motion of the crus, aside from possible relatively slight rotation, was chiefly simple flexion and extension. The most complex and important movements are those of the femur. These movements are of two quite distinct sorts: rotation of the femur in all directions about a fixed point, the head, and rotation about a linear axis—a line through the center of the head and the middle of the distal end. Further analysis shows that all possible movements of the femur may be resolved into six components, as follows:

- A. Rotation about head of femur:
 - a. Horizontal components (protraction):
 - 1. Forward—protraction of limb.
 - 2. Backward—protraction of body.
 - b. Vertical components (levation):
 - 3. Upward—levation of limb.
 - 4. Downward—levation of body.
- B. Rotation about linear axis:
 - Counterclockwise as viewed from distal end of right femur— —positive rotation.
 - Clockwise as viewed from distal end of right femur—negative rotation.

In considering a single limb during ordinary straightforward locomotion two effects alternate: (1) the distal end of the femur

moves forward relative to the pelvis, and (2) the pelvis then moves forward relative to the distal end of the femur. It is clear that these effects are purely relative and that the resultant motion, involving as it does some lateral motion of the pelvis relative to the substratum,

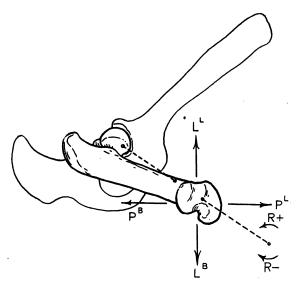


Fig. 1. Eucosmodon. Diagramatic lateral view of right femur and pelvis, showing normal position and components of femoral motion. Not to scale. LB, levation of body. LL, levation of limb. PB, protraction of body. PL. protraction of limb. R+, positive rotation. R—, negative rotation.

is actually rather more complex. The pelvis, and hence the body, is furthermore moving forward at a nearly constant rate, as protraction of the limb against the body on one side is simultaneous with protraction of the body against the other limb. Each of these two phases of the motion of a single limb involves three of the six components of femoral movement:

First Phase:
Protraction of limb.
Levation of limb.
Positive rotation.

Second Phase: Protraction of body. Levation of body. Negative rotation.

As will appear in the subsequent functional classification of the individual muscles, the majority of the muslces are involved in more than one of the six components. In most cases, however, a given

muscle is involved in only one of the two groups above, that is, in only one of the two phases of the normal stride. Exceptions are seen in the femoro-coccygeus, which is a protractor of the body but also a levator of the limb, and in the obturator externus, which is a protractor and levator of the body but also a positive rotator.

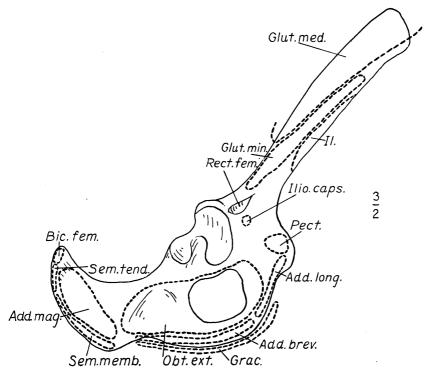


Fig. 2. *Eucosmodon*. Right lateral view of restored pelvis, showing hypothetical areas of muscle attachment. For abbreviations see page 19.

The terms "protractors of limb or body" and "levators of limb or body" seem to us preferable for use in functional analysis to the anatomical terms "flexors," "extensors," "adductors" and "abductors" which consider the body as if it were suspended in space (or laid out on the dissecting table).

Rotation of the femur about a linear axis is unusually important in *Eucosmodon*. The muscles bringing about this rotation are powerful and their origins, courses, and insertions are such as to make their action more effective than it is in most mammals. As brought out

below, the lesser trochanter serves almost wholly for the insertion of positive rotators and is strongly developed and specialized in such a way as to give strong leverage for this motion. The greater trochanter, chiefly for insertion of the glutei, is analogously developed for negative rotation. It results from the nearly horizontal femur and the acute angle between thigh and crus that positive rotation of the femur,

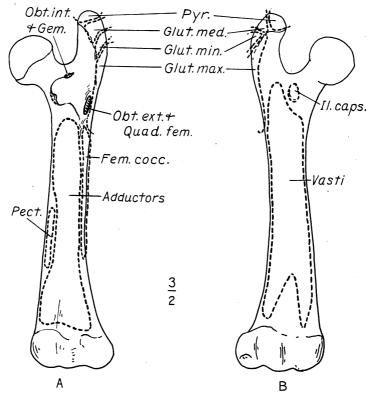


Fig. 3. Eucosmodon. Right femur, showing hypothetical areas of muscle attachment. A, ventral view. B, dorsal view. For abbreviations see page 19.

without other simultaneous movements, would cause movement of the foot forward and somewhat inward. Negative rotation, with the foot planted on the ground, would result in moving the body forward and slightly away from this foot.

The position of the femur together with this strong adaptation for rotation distinguishes *Eucosmodon* rather sharply from most other

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mammals and from most reptiles. In the majority of mammals the distal end of the femur was drawn more anteromedially beneath the body and rotation, while often present, is generally much more limited than in *Eucosmodon*. An essential difference between *Eucosmodon* and most other mammals is that the muscles which are primarily protractors in the former become involved also in levation in the

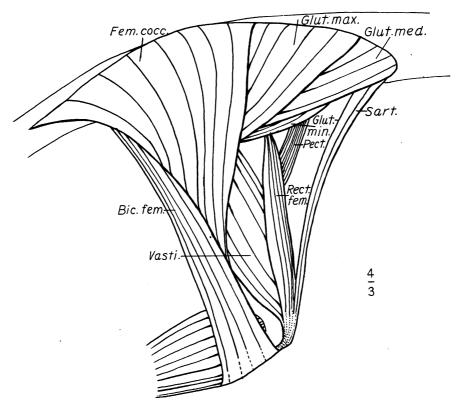


Fig. 4. *Eucosmodon*. Hypothetical restoration of muscles of right hind limb. Superficial dorsal view. For abbreviations see page 19.

latter, due to the changed position of the femur. The disadvantages of retaining a somewhat more reptilian posture were compensated in *Eucosmodon* to a considerable degree by the freedom of rotation.

The actual movements of the animal, whether in the simplest case of normal straightforward locomotion or in its more irregular activities, such as turning or moving backward or laterally, would

obviously each involve a complex combination of the muscular activities here analyzed into their simplest components. The limb was no doubt occasionally used also for purposes other than locomotion (scratching, seizing objects, etc.) but the chief movements involved would be the same except for being related to the pelvis as a fixed point.

MUSCULATURE

TOPOGRAPHY.—Detailed verbal descriptions of the individual muscles are unnecessary. All of the muscles which have been restored and their inferred attachments on the pelvis and femur are seen in the accompanying figures. The following table presents a résumé of the probable conditions:

NAME	Origin	Insertion
Rectus femoris	Small pit anterior to acetabulum.	With vasti on tibia.
Sartorius	Probably anterior tip of ilium.1	With vasti and rec-
	•	tus on tibia.
Biceps femoris.	Ischial tuberosity.	Proximal portion of
		lower limb.
Iliacus.	Inferior border of ilium.	With psoas major.
Psoas major.	Lumbar vertebrae.	Lesser trochanter.
Psoas minor.	Lumbar vertebrae.	Pectineal process.
Pectineus.	Pectineal process.	Ventral surface of
		femur.
Femoro-coccygeus.	Fascia lata.	Distal continuation
		of gluteal crest.
Gluteus maximus.	Fascia lata and upper border of anterior end of ilium.	Gluteal crest.
Gluteus medius.	Dorsal portion of lateral surface of	Greater trochanter.
Citieus meurus.	ilium.	0.100.001 0.100.001
Gluteus minimus.	On lateral face of ilium between	Greater trochanter.
	gluteus medius and iliacus.	
Ilio-capsularis ²	Depression below origin of rectus	Tuberosity on dor-
ino capatana	femoris.	sal face of femur at
		base of neck.
Obturator internus.	Internal surface of pubis and ischi-	Upper digital fossa.
	um around obturator foramen.	
Gemelli.	Dorsal border of ischium.	Upper digital fossa.
Obturator externus.	Outer surface of pubis and ischium	Fossa lateral to les-
	around obturator foramen.	ser trochanter.
Quadratus femoris.	Dorsal border of ischium.	Probably in fossa
		lateral to lesser tro- chanter.

¹The origin of the sartorius is in doubt, but there is no evidence that it originated from the pectineal process as does the supposedly homologous muscle in *Ornithorhynchus*.

²Ilio-capsularis=scansorius or ilio-femoralis of authors.

Name	Origin	Insertion
Gracilis.	Along pubo-ischiatic symphysis.	Tibia.
Semi-membranosus.	Posteroventral border of ischium	Tibia.
	below semi-tendinosus.	
Semi-tendinosus.	Posterior border of ischium below	Tibia.
	biceps femoris.	
Adductor magnus.	Broad depression on posterior part	Ventral surface of
	of lateral surface of ischium.	femur.
Adductor brevis.	Lateral surface of ischium and	Ventral surface of
	pubis near inferior border.	femur.
Adductor longus.	Anterior part of lateral surface of	Ventral surface of
	pubis.	femur.
Pyriformis.	Caudal vertebrae.	Tip of greater tro-
		chanter.

FUNCTIONAL CLASSIFICATION

In the following table the muscles are placed in different categories according to their functions in producing the various components of femoral and body movement discussed in a preceding section. The probable relative importance of each muscle in producing the given effect is indicated by the type, the most important muscles for each category being in capitals, those of somewhat less importance in italics, and the least important in roman lower case.

PROTRACTORS

Rectus femoris
Sartorius
Iliacus
Psoas major
PECTINEUS

OF LIMB

Adductor Longus

OF BODY

Biceps femoris Femoro-coccygeus Gluteus medius Gluteus minimus Obturator internus

Gemelli

Obturator externus Quadratus femoris Semi-membranosus Semi-tendinosus Adductor Magnus

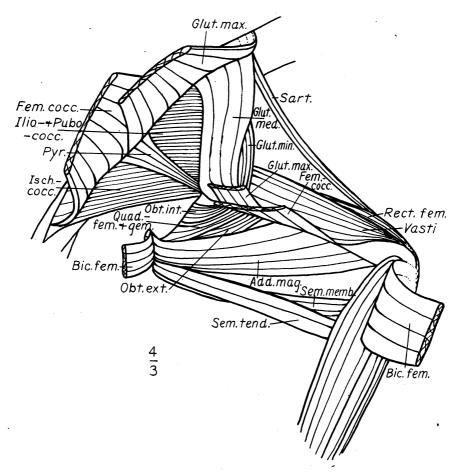


Fig. 5. Eucosmodon. Hypothetical restoration of muscles of right hind limb. Posterolateral view. For abbreviations see page 19.

LEVATORS

OF LIMB

RECTUS FEMORIS Sartorius Femoro-coccygeus

OF BODY

Biceps femoris

Gluteus medius Gluteus minimus Obturator externus GRACILIS Semi-membranosus Semi-tendinosus ADDUCTOR MAGNUS ADDUCTOR LONGUS ADDUCTOR BREVIS

Pvriformis

ROTATORS

POSITIVE

ILIACUS PSOAS MAJOR Ilio-capsularis Obturator externus

NEGATIVE

GLUTEUS MAXIMUS GLUTEUS MEDIUS GLUTEUS MINIMUS

The columns correspond to those on page 4, the left hand column including the muscles concerned chiefly in moving the limb forward, the right hand column those concerned chiefly in moving the body forward. The latter, which must move and support the much greater weight of the body, are more numerous and, in the aggregate, much more powerful than those concerned chiefly with moving and lifting the limb alone.

CORRELATION WITH SOME OSTEOLOGICAL FEATURES

Most of the many osteological peculiarities of the Eucosmodon pelvis and femur are apparently directly related to the arrangement and action of the muscles and we here propose to deal briefly with some of the more striking instances of this correlation.

Pelvis.—The sacro-iliac angle in Eucosmodon is remarkably large. This results in the acetabulum being lower relative to the blade of the ilium than in most other mammals, which in turn is associated with greater levatorial powers. The relatively great depth of the pelvis and its large lateral surface are probably to be correlated with the more horizontal position of the femur. The pectineal process is well developed, with a strong roughened area for muscular origin. The insertion of the pectineus also indicates its strength. It is a limb

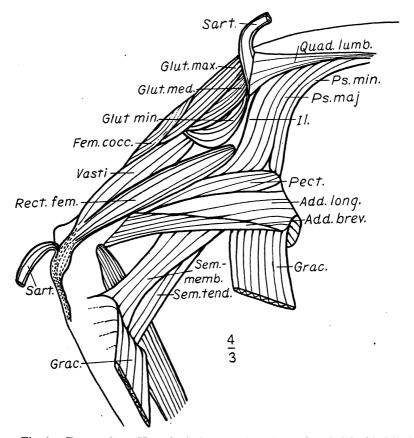


Fig. 6. Eucosmodon. Hypothetical restoration of muscles of right hind limb. Anterolateral view. For abbreviations see page 19.

protractor and its development is correlated with the relative mechanical disadvantage of its short lever arm in this animal.

The acetabulum is large and it was closely applied to the almost spherical femoral head, indicating great freedom of action at this joint. The anterior part of the articular surface is large and overhanging, while the posterosuperior border is weak and emarginate. This, too, is related to the large sacroiliac angle and more horizontal femur, the maximum stress being more nearly parallel to the iliac axis than in mammals with small sacro-iliac angles and more vertical femora.

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Greater trochanter.—The muscles inserting on the greater trochanter, glutei medius and minimus and pyriformis, cause the femur to function as a lever of the third order in profracting and levating the body, the distal end of the femur being the fulcrum. general, as the trochanter becomes longer the speed of action (that is, the amount of body movement caused by a given muscular contraction) of these muscles becomes less and their effective power becomes greater. As the trochanter shortens, the speed becomes greater but the power becomes less until, if the head of the trochanter is in line with the axis of the head of the femur, these muscles will have no power for protraction or levation. In Eucosmodon the length of the greater trochanter, which is considerable, must be nearly at an optimum for rapid protraction. When the femur is far forward, at the beginning of the body protractive movement, the chief single protractor, the adductor magnus, is nearly parallel to the femur and hence weak in The muscles inserting on the greater trochanter here serve efficiently in starting protraction rapidly, while the adductor magnus would finish it powerfully. The impression is that of a capacity for darting movements or for sudden leaps to safety when startled. The strength of the trochanter and the insertions of the glutei along its extended lateral border also make these muscles effective in negative rotation.

Lesser trochanter.—The usual and, in all probability, the primitive position of the lesser trochanter is near the anterior border of the femur, a position in which the iliopsoas would have little or no rotatory effect. In Eucosmodon the great size and strength of the lesser trochanter and its strongly lateral position would make this muscle mass a powerful positive rotator. The smooth and rounded head of the trochanter is apparently due to the fact that in this position the broad obturator externus must pass over it.

DIGITAL FOSSA.—One of the most unusual features of the Eucosmodon femur is the apparent division of the digital or intertrochanteric fossa into two smaller fosae, one high up between the neck of the femur and the greater trochanter, and one considerably lower, between the lesser trochanter and the gluteal crest. After many comparisons and after trials of the effects of the muscles with various insertions, we believe that the lower fossa lodged the insertions of the obturator externus and probably also of the quadratus femoris, while the gemelli and obturator internus were inserted into the upper fossa. Comparison with Didelphis, for example, shows that the relative positions of these insertions are not greatly different save for their separation into two groups. This separation seems to be related to, possibly to depend on, the buttressing of the powerful lesser trochanter, from which a ridge curves upward toward the greater trochanter. In other mammals a somewhat similar but generally weaker buttress may be present, but it passes below the whole group of intertrochanteric insertions. The beginning of these divergent developments probably lay in a stage when the lesser trochanter was anterior in position and these various muscle insertions were widely spread on the proximo-ventral surface of the femur, as they are in the monotremes and in the known Jurassic mammalian femora.

FUNCTIONAL ADAPTATION

Broader paleobiological conclusions must involve the correlation of these new data with what is known as to habits and habitat from other sources. This latter evidence has already been given in a general way (Simpson 1926) but it remains to sum up this evidence in the light of continued research and in respect to the specific problem of Eucosmodon.

DENTITION.—Evidence as to food habits is derived chiefly from the dentition as correlated with cranial and mandibular osteology and myology. The multituberculates generally are somewhat rodent-like in habitus, although with very numerous detailed differences due to their widely distinct heritage. One pair of incisors in each jaw is enlarged and the molars are of grinding and crushing type, broad, low-crowned, generally with numerous tubercles. The premolars, in most cases, are chiefly adapted to powerful shearing. In addition, the anterior upper premolars, when present, are of use in grasping food and pressing it against the shearing apparatus. The general jaw functions are thus three: (1) the selection and obtaining of food by the incisors, with the mandible in its extreme anterior position; (2) the preliminary comminution of food or removal of undesirable husks, etc., by the posterior premolars, the mandible in its posterior position, the motion chiefly vertical; and (3) the grinding of this food and its preparation for deglutition by the molars, the mandible moving chiefly anteroposteriorly. All of the dental features and of the adaptations of skull and jaws show that the food was certainly largely vegetable.

Turning to *Eucosmodon* in particular, it shares with the other ptilodontids a very powerful shearing apparatus, provision for holding the food firmly while it was being cut, and very complex but low

crowned molars. The outstanding individual peculiarly of the genus is the fact that the lower incisiors had very long crowns with the enamel limited to an anterior band. Wear was much as in rodents. the softer dentine being worn away rapidly leaving a continuously sharp protruding edge of enamel. There are several marked differences from the usual rodent type, however. The lower incisors are strongly compressed transversely; the tip is rounded, although sharp, and not transverse or chisel-like. Growth was not continuous, roots being formed in the adult, although the incisors did move forward in the jaw following wear, as they do in rodents. Such incisors are markedly different from those of *Ptilodus*, for example, which did not alter in position once fully erupted, had completely enameled crowns, and were not subjected to heavy wear. The Ptilodus type of incisor was suitable for picking up small objects for food and for piercing them, but not for gnawing. The Eucosmodon type of incisor, on the contrary, has the added function of true gnawing, although less exclusively directed toward this purpose than are the corresponding teeth of rodents.

Comparison with other multituberculates and with the most nearly analogous later mammals thus indicates for Eucosmodon a regimen largely herbivorous and including fibrous or woody substances, such as bark or roots, as well as such fruits as were present. Although certainly not predaceous, Eucosmodon also gnawed bones when these were accidentally available (see below).

OSTEOLOGY.—Knowledge of the limbs of Eucosmodon is largely limited to the posterior appendages considered earlier in this paper. Of the fore limbs nothing is known in the Puerco species and only a few fragments in a smaller species from the later Torrejon. These fragments are sufficient, however, to indicate close similarity to Ptilodus gracilis, the fore limbs of which are somewhat better known (Gidley 1909, p. 620). As previously pointed out (Simpson 1926, pp. 247-9), the ratio of femur length to humerus length in Ptilodus is 1.33, showing that it was "probably a swiftly moving and agile quadruped." The ratio gives no positive index as to whether the animal was terrestrial or The humerus is not that of a fossorial animal.

The structure of the hind foot in Eucosmodon indicates great flexibility, grasping power with opposable hallux, and presence of sharp Neither in its proportions nor morphological features does

¹The upper incisors are not yet certainly known.

this hind foot show fossorial or saltatory adaptations. This and other known characters definitely suggest a quadrupedal animal, well adapted for possible arboreal life but also capable of rapid progression on the ground.

Environments.—Multituberculates occurred in a variety of environments. The Mesozoic forms are found in littoral marine deposits (Stonesfield), swamps or freshwater littoral lagoons (Purbeck), marshy flood plains (Morrison), arid uplands (Djadokhta). Distribution of the order was wide not only in time and space but also in facies. As in the case of other orders, such as the Rodentia, the fundamental adaptation was everywhere the same but specific habitats varied widely. Each case would demand some individual consideration.

The genus *Eucosmodon* has been found in several distinct deposits, but these are generally of similar facies. The particular specimen here studied in most detail is from the lower Puerco. Its relation to its environment, like that of any fossil animal, is to be inferred from the following data:

- I. Conditions of deposition of sediments in which found.
- II. Associated Flora-
 - A. As indicative of physical environment.
 - B. As providing a possible specific habitat.
 - C. As providing possible food.
- III. Associated Fauna-
 - A. As indicative of physical environment.
 - B. As including possible enemies.
 - C. As including possible competitors.
 - D. As providing possible food.
- IV. Possible direct traces of activity. (E.g., foot prints, tooth marks, coprolites).

Sinclair and Granger (1914, p. 309) conclude that the Puerco sediments were formed by water, that they were accumulated "on river flood plains or on the surface of broad, low-grade, coalesced alluvial fans," that bogs were locally present, that there was a "heavy growth of vegetation along the streams and, presumably, in the interstream areas also," and that there are no indications of aridity. This is also true, broadly at least, of the other formations in which Eucosmodon has so far been positively identified and these conditions are clearly those under which Eucosmodon lived, although perhaps not the only ones in which various species could exist.

The flora of the Puerco itself is very incompletely known but certainly included fig, bread-fruit, viburnum, plane, and Paliurus

(Sinclair and Granger 1914, p. 306). Slight as this list is, it suggests a warm, fairly moist climate and proves that ample facilities for arboreal life were at hand. Even these few species would also provide highly nutritious food. More broadly, the floral facies is similar to that of the Raton and Denver formations, with their large floral lists, and the age, although not quite the same, is not sufficiently different to vitiate analogies. Study of various lists (Knowlton) indicates a probable rich flora at this time and place. Palms, beeches, ivies, laurels, grapes, willows, poplars, oaks, figs, bread-fruits, walnuts—to mention only a few outstanding and probably common types—were surely present in regions inhabited by *Eucosmodon*.

The fauna, as almost always when relatively well known, indicates several different local habitat groups or cenobiotas. There is an aquatic cenobiota: fish, turtles (including Trionyx), champsosaurs, crocodiles. A second group includes most of the known mammals: browsing herbivores, omnivorous terrestrial mammals, and predaceous carnivores (with probably some carrion feeders). Fossorial types are absent so far as certainly known, although several mammals, such as the multituberculate Txiolabis, might belong here. Of the known Puerco mammals only Eucosmodon is strongly suggestive of arboreal life, although other small tree-living forms were probably present.

Possible enemies are numerous. None of the terrestrial carnivores was too large to scorn *Eucosmodon*, which was as large as a large squirrel or small rabbit, and none was too small to overcome it. In the streams crocodiles and champsosaurs endangered it. Probable close competitors, on the contrary, are quite unknown in this formation. There are no other gnawing animals save *Tæniolabis*, which was much larger, differently adapted, and has not been found at the same level as the pelvis and hind limbs here discussed although it occurs in association with *Eucosmodon* in the upper Puerco. Rodents, which would have been most closely competitive, were quite absent.

It is interesting to note that many of the Puerco bones have been gnawed (Sinclair and Granger 1914, p. 310). Bones are known from each of the two Puerco fossil levels with tooth marks of exactly the size which would be made by known *Eucosmodon* incisors from the respective levels. No other animal is known which could have made these marks and this direct evidence proves that *Eucosmodon*, like many rodents, varied or supplemented its vegetable diet by gnawing bones.

CONCLUSIONS AS TO HABITS AND HABITAT

The individual here chiefly studied lived in a warm, moist, partly forested region, and this was apparently true of all now known members of the genus. It was not aquatic nor fossorial and the direct evidence of the hind limbs, with the indirect evidence of food habits and environment, strongly suggests that it was chiefly arboreal, although no doubt occasionally descending to the ground. Its food was chiefly vegetable and may have included both fruits and more fibrous material, such as bark, supplemented by gnawed bones. It was an agile animal, capable of rapid locomotion, whether on the ground or in the trees where it was clearly safer from enemies and probably more at ease.

RESUME

- 1. The femur of *Eucosmodon* was held in a nearly horizontal position, pointing outward and slightly forward and downward.
- 2. The restoration of the pelvic musculature shows it to have a degree of differentiation similar to that of other mammals.
- 3. The details of muscular morphology and function are characteristically different from those of other mammals or of reptiles.
- 4. The pelvic musculature, in agreement with all other known anatomical and environmental features, indicates an arboreal mode of life.

REFERENCES

- Cours, E. 1872. Osteology and Myology of *Didelphys virginiana*. Mem. Boston Soc. Nat. Hist., II, 41-154.
- ELFTMAN, H. O. Functional Adaptations of the Mammalian Pelvis. (Manuscript.) GIDLEY, J. W. 1909. Notes on the Fossil Mammalian Genus *Ptilodus*, etc. Proc. U. S. Nat. Mus., XXXVI, 611-26.
- Granger, W. and Simpson, G. G. 1928. Revision of the Tertiary Multituberculata. Bull. Am. Mus. Nat. Hist. (in press).
- Gregory, W. K. and Camp, C. L. 1918. Studies in Comparative Myology and Osteology. Bull. Am. Mus. Nat. Hist., XXXVIII, 447-563.
- MATTHEW, W. D. 1928. The Evolution of the Mammals in the Eocene. Proc. Zool. Soc. London, 1927, 947-985.
- Pearson, H. S. 1926. Pelvic and Thigh Muscles of Ornithorhynchus. Jour. Anat., LX, 152-163.
- ROMER, A. S. 1922. Locomotor Apparatus of Certain Primitive and Mammallike Reptiles. Bull. Am. Mus. Nat. Hist., XLVI, 517–606.
- SIMPSON, G. G. 1926. Mesozoic Mammalia. IV. The Multituberculates as Living Animals. Am. Jour. Sci. (5) XI, 228-250.
 - 1928. A Catalogue of the Mesozoic Mammalia, etc. British Museum (Natural History).

1928] HABITS OF A PALEOCENE MULTITUBERCULATE 19

Sinclair, W. J. and Granger, W. 1914. Paleocene Deposits of the San Juan Basin, New Mexico. Bul. Am. Mus. Nat. Hist., XXXIII, 297-316.

ABBREVIATIONS USED IN TEXT-FIGURES

Add. brev.Adductor brevisAdd. long.Adductor longusAdd. mag.Adductor magnusBic. fem.Biceps femorisFem. cocc.Femoro-coccygeus

Gem. Gemelli

Glut. max. Gluteus maximus Glut. med. Gluteus medius. Glut. min. Gluteus minimus

Grac. Gracilis II. Iliacus

Ilio- and Pubo-coccygei

II. caps. Ilio-capsularis
Isch.-cocc. Ischio-coccygeus
Obt. ext. Obturator externus
Obt. int. Obturator internus

Pect. Pectineus
Ps. maj. Psoas major
Ps. min. Psoas minor
Pyr Pyriformis

Pyr. Pyriformis
Quad. fem. Quadratus femoris
Quad. lumb. Quadratus lumborum

Rect. fem. Rectus femoris
Sart. Sartorius

Sem. memb. Semi-membranosus
Sem. tend. Semi-tendinosus

Vasti Vasti

