THE ENDOCRANIAL CAST AND ENCEPHALIZATION QUOTIENT OF *PTILODUS* (MULTITUBERCULATA, MAMMALIA)

by

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ABSTRACT

Simpson (1937a) reconstructed the brain of the Paleocene multituberculate *Ptilodus* as having the olfactory bulbs widest anteriorly, an unusual condition among mammals. Slight preparation and reexamination of the endocast specimens of *Ptilodus* reveals that the olfactory bulbs in fact taper anteriorly, as in the recently-described endocranial casts of three multituberculate species from the Late Cretaceous of Asia, and as in those of other mammals. The brain of *Ptilodus* was therefore essentially of the same general pattern as in other multituberculates. *Ptilodus* differs, however, in having the vermis more deeply inserted between the cerebral hemispheres. Other details concerning the endocast morphology of *Ptilodus* are clarified.

The encephalization quotient (EQ) of *Ptilodus* is recalculated from revised estimates of both endocranial volume and body mass to fall somewhere within a broad range of values; from 0.41 to 0.62 if the olfactory bulbs are included and from 0.37 to 0.55 if they are not. In any case, the relative brain size of *Ptilodus* is roughly equivalent to that of *Chulsanbaatar*, the only other multituberculate for which EQ has been calculated, but considerably smaller than that of an average extant mammal.

RESUME

Dans la reconstitution de l'encéphale du multituberculé paléocène *Ptilodus* donnée par Simpson (1937a), les bulbes olfactifs sont élargis antérieurement, ce qui représente une condition inhabituelle chez les mammifères. Une préparation minutieuse ainsi qu'un réexamen du moulage endocrânien de *Ptilodus* révèlent qu'en fait les bulbes olfactifs s'effilent antérieurement comme chez trois espèces de multituberculés récemment décrites du Crétacé supérieur d'Asie, et plus généralement comme chez les autres mammifères. Si l'encéphale de *Ptilodus* avait donc la même structure générale que les autres multituberculés, il en diffère par un vermis plus profondément inséré entre les deux hémisphères cérébrales. D'autres détails concernant la morphologie du moulage endocrânien ont été précisés.

Le coefficient d'encéphalisation (EQ) de *Ptilodus* a été recalculé à partir de nouvelles estimations du volume endocrânien et du poids de l'animal; ce coefficent se situe dans un large intervalle de valeurs: de 0,41 à 0,62 si les bulbes olfactifs sont pris en compte, sinon, de 0,37 à 0,55. Dans les deux cas, la taille relative de l'encéphale de *Ptilodus* est sensiblement celle de *Chulsanbaatar*, le seul autre multituberculé pour lequel un coefficient d'encéphalisation a été calculé, mais elle est considérablement plus petite que celle d'un mammifère actuel moyen.

INTRODUCTION

Simpson (1937a) described the endocranial cast and reconstructed the brain of the ptilodontoid multituberculate *Ptilodus montanus* DOUGLASS on the basis of four fragmentary specimens from the middle Paleocene of the Crazy Mountains Basin, south-central Montana. *Ptilodus* is the only North American multituberculate genus and the only member of the suborder Ptilodontoidea for which endocranial casts have been described. Simpson (1937a: 752-753) noted that the olfactory bulbs are "enormous, relatively larger than in any other mammalian brain known to me" and are "peculiar in shape, being pyriform but with the greatest width anterior."

Since Simpson's paper, endocranial casts have been described and reconstructed

for cynodonts (Hopson 1979; Quiroga 1979, 1980, 1984), Cretaceous eutherian mammals (Kielan-Jaworowska 1984, 1986; Kielan-Jaworowska & Trofimov 1986), and Jurassic and Cretaceous multituberculates. Hahn (1969) reconstructed the endocranial cast for the Late Jurassic paulchoffatoid *Paulchoffatia delgadoi* from Portugal. Kielan-Jaworowska (1983, 1986) and Kielan-Jaworowska *et al.* (1986) described and reconstructed endocranial casts of two taeniolabidoid multituberculate species, *Chulsanbaatar vulgaris* and *Nemegtbaatar gobiensis*, from the Late Cretaceous of Mongolia. (Kielan-Jaworowska [1983] also mentioned a partial endocranial cast of *Kamptobaatar kuczynskii* and Kielan-Jaworowska & Dashzeveg [1978] illustrated but did not describe the endocranial cast of *Tugrigbaatar saichanensis*, both also taeniolabidoids from the Late Cretaceous of Mongolia.) These papers give much information that is new on the evolution of the brain at the reptilian-mammalian transition and in early mammals. In all of these multituberculates, as well as in previously described triconodonts (Simpson 1927, 1928; see also Hopson 1979 and Kielan-Jaworowska 1986), the olfactory bulbs are large and taper anteriorly; they are not abruptly truncated anteriorly as reconstructed for *Ptilodus* by Simpson (1937a, fig. 9; see also fig. 1a of this paper).

In an attempt to ascertain whether or not *Ptilodus* did indeed have olfactory bulbs differently shaped from those in cynodonts and all other known early mammals, we reexamined all of Simpson's specimens. Slight preparation and examination of one specimen (USNM 9710) demonstrated that the shape of the olfactory bulbs is not "peculiar" relative to those of either cynodonts or other mammals, or particularly, relative to those of Late Cretaceous Asian multituberculates.

We also take this opportunity to make other comparisons of the endocranial cast of *Ptilodus* with those of more recently discovered multituberculate endocranial casts and to provide a recalculated estimate of the encephalization quotient (EQ) of *Ptilodus montanus*. The latter is based on revised estimates of both brain size and body size for the species.

We employ the following abbreviations:

AMNH   American Museum of Natural History, New York

UA   University of Alberta, Edmonton

USNM   United States National Museum, Washington, D.C.

ZPAL   Institute of Paleobiology, Polish Academy of Sciences (Instytut Paleobiologii), Warsaw.

STRUCTURE OF THE ENDOCRANIAL CAST

The specimens studied by Simpson (1937a) consisted of AMNH 35490 (crushed skull with only a part of the cerebral hemispheres exposed – illustrated in Hopson *et al.* 1989, fig. 1), AMNH 35491 (part of cerebral hemispheres and cerebellum), USNM 6076 (cerebrum and cerebellum – illustrated in Wall & Krause, 1992, fig. 2), and

USNM 9710 (olfactory bulbs and anterior part of the cerebral hemispheres). We reexamined all of the specimens upon which Simpson based his reconstruction of the brain; USNM 9710 and AMNH 35491, in particular, provide new information and are illustrated here for the first time (pl. 1).

The endocranial casts of the olfactory bulbs in USNM 9710 were somewhat obscured by overlying matrix, which was carefully removed to reveal the dorsal borders of the olfactory bulbs (pl. 1, fig. 1). This procedure permits a revised reconstruction of the olfactory bulbs (fig. 1b). The olfactory bulbs in USNM 9710 taper anteriorly, with their greatest width being at about mid-length, not far anteriorly as reconstructed by Simpson (1937a). They are separated from the cerebral hemispheres by a wide transverse fissure. The olfactory bulbs are of similar shape in other multituberculates (e.g., *Nemegtbaatar gobiensis* – see Kielan-Jaworowska *et al.* 1986, pl. 6, fig. 18B; and *Chulsanbaatar vulgaris* – see Kielan-Jaworowska 1983, pl. 1, figs. 1-4) and are not atypical among mammals in this regard.

As noted and emphasized by Simpson (1937a), the olfactory bulbs of *Ptilodus* are indeed large but, relative to the cerebral hemispheres, not as large as originally reconstructed (fig. 1). Large olfactory bulbs have been noted for other multituberculates as well (Kielan-Jaworowska 1983, 1986; Kielan-Jaworowska *et al.* 1986). The presence of large olfactory bulbs in the brain of *Ptilodus* is concordant with other evidence indicating that this genus and at least some other multituberculates were small-eyed, olfactory-dominated, nocturnal forms (e.g., Krause 1986).

AMNH 35491 contains the cast of the posterior part of the cerebral hemispheres and the anterior part of the central lobe of the cerebellum (vermis) (pl. 1, figs. 2, 3). The cross-section of the left fossa subarcuata (housing the paraflocculus) and the section of the posterior semicircular canal is also preserved on the left side of the specimen (pl. 1, fig. 3). The vermis is strongly convex dorsally and more deeply inserted between the cerebral hemispheres than in other multituberculate endocranial casts. The cast of the transverse sinus is very distinct. In the shape of the vermis, *Ptilodus* resembles more closely *Tugrigbaatar* (the endocranial cast of which is still to be described, but see Kielan-Jaworowska & Dashzeveg 1978, pl. 3, fig. 1b) than it does other genera. The paraflocculus appears roughly spherical, as in *Nemegtbaatar*, rather than transversely elongate as in *Chulsanbaatar* and *Tugrigbaatar* (pl. 1, fig. 3).

It follows from the foregoing descriptions that the brain, particularly the olfactory bulbs, of *Ptilodus* does not differ fundamentally in structure from those of other multituberculates, as it appeared to do from Simpson's (1937a) original reconstruction. It has a typical multituberculate pattern, with large olfactory bulbs that taper anteriorly, cerebral hemispheres that diverge strongly posteriorly, no dorsal midbrain exposure, and a cerebellum that consists of a large vermis and prominent parafloculli. Cerebellar hemispheres, as in other multituberculates, are not developed.

The evolutionary history of the development of the neocortex has attracted the interest of paleontologists (Quiroga 1980, Kielan-Jaworowska 1986), as well as zoologists and neuroanatomists (see Ebbeson 1980 and numerous references therein, and Jerison 1990 for recent reviews). In fossil material the presence of the neocortex is usually inferred from the cast of the rhinal fissure, which is taken to indicate the boundary between paleocortex (below) and neocortex (above). In some Recent
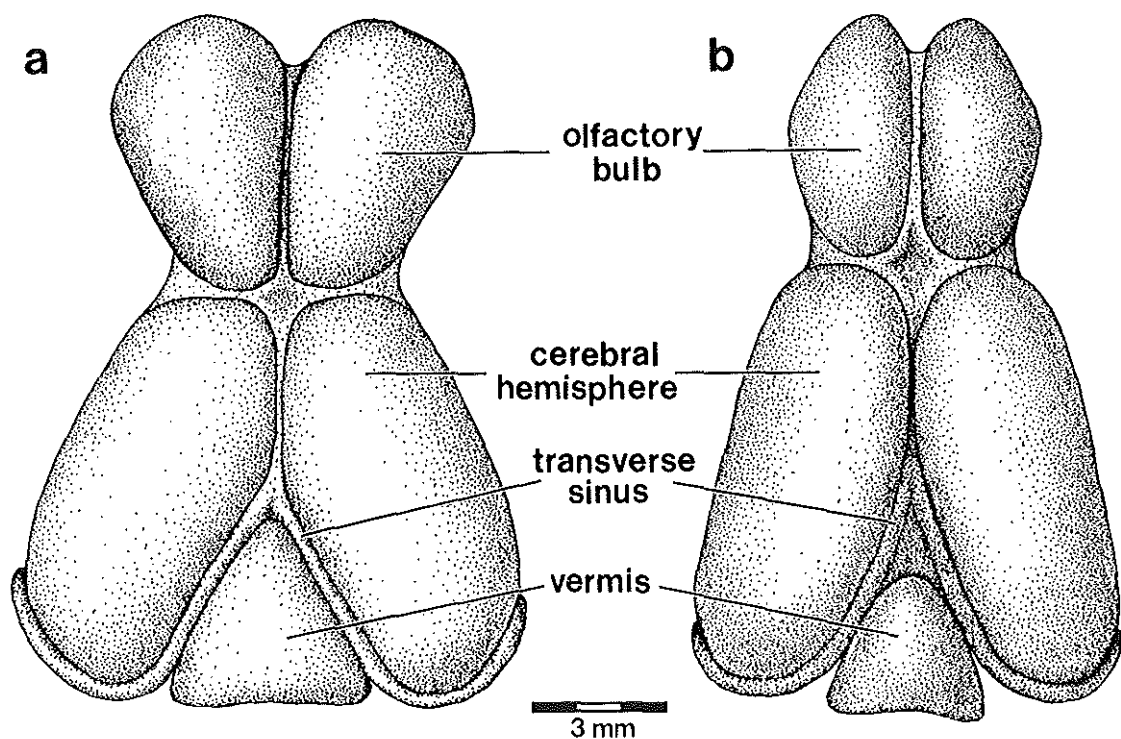
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Fig. 1.— Reconstruction of the endocranial cast of *Ptilodus montanus* DOUGLASS in dorsal view: a: according to Simpson (1937a); b: this paper. Note abrupt truncation anteriorly of olfactory bulbs in a and anteriorly tapering nature of olfactory bulbs and relatively large cerebral hemispheres in b.

mammals, however, the rhinal fissure is perceptible only microscopically (Schneider 1968); as a consequence, its identification in fossil endocranial casts is, at best, difficult.

Unfortunately, none of the specimens of *Ptilodus* has the lateral and ventral sides of the cerebral hemispheres preserved, and whether the rhinal fissure was present or absent in this genus therefore cannot be determined. Even in endocranial casts of Late Cretaceous multituberculates from Mongolia that preserve this region, the rhinal fissure is not obvious (Kielan-Jaworowska 1983, 1986; Kielan-Jaworowska *et al.* 1986). Nevertheless, Kielan-Jaworowska (1983, 1986) reconstructed it tentatively for *Chulsanbaatar*, indicating that the dorsolateral, convex part of the cerebral hemispheres might correspond to the extensive neocortex. Jerison (1990, fig. 3) argued that the rhinal fissure in one endocranial cast of *Chulsanbaatar vulgaris* (ZPAL MgM-I/88) was visible and reconstructed it in a much higher position than shown by Kielan-Jaworowska. We have reexamined this specimen and have been unable to duplicate Jerison's observation. In addition, we have reexamined all of the other specimens of *Chulsanbaatar* in which endocranial casts are preserved. In all of them faint furrows are present but they are differently shaped, not only on particular specimens but also on left and right sides of the same specimen.

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On the other hand, as pointed out by Kielan-Jaworowska *et al.* (1986), the endocranial cast of *Nemegtbaatar* is roughly similar in cross-section to that of *Chulsanbaatar* in having a dorsally expanded convex part (tentatively interpreted by Kielan-Jaworowska [1983] as a lissencephalic neocortex), and ventrally a less expanded paleocortex. We therefore confirm that "... in neither genus [*Chulsanbaatar* or *Nemegtbaatar*] is the rhinal fissure preserved, and only the line of change of curvature can be used as a guide" (Kielan-Jaworowska *et al.* 1986: 554).

ENCEPHALIZATION QUOTIENT

Encephalization quotients (EQs) provide a means for quantifying relative brain size, that is, the ratio of observed brain mass to expected brain mass for a given body mass. Jerison (1973) calculated for *Ptilodus montanus* a brain mass of 1.09 g minus the olfactory bulbs, and a brain mass of 1.36 g with the olfactory bulbs using the technique of graphic double integration. Since only the dorsal and posterior views of the endocranial cast of *P. montanus* are exposed, he estimated the lateral dimensions by comparison with the marsupial *Didelphis*, the rodent *Rattus*, and the insectivorans *Neurogymnurus*, *Setifer*, and *Echinosorex*. Jerison (1973) calculated a body mass of 200 g for *P. montanus* using the equation

$$M = k L^3 \qquad (1)$$

where M is body mass in g, L is body length in cm, and k is an empirically determined coefficient. He estimated body length to be four times skull length (40 mm in the case of *P. montanus*) from a series of regressions of data from modern mammals, and assumed a stout body build (k = 0.05) rather than an average body build (k = 0.025) for the species. Jerison (1973) noted, however, that large errors in his estimate of body mass were possible since, at that time, there were "no useful data" on the postcranial skeleton of *Ptilodus*.

Jerison (1973) employed the following equation to calculate the EQ of *P. montanus*:

$$EQ = \frac{E}{0.12 \, M^{0.67}} \qquad (2)$$

where E is brain mass and M is body mass in grams (g). Preferring to not include the olfactory bulbs in his estimate of brain size, Jerison calculated an EQ of 0.26 for the species. Including the olfactory bulbs and assuming a heavy habitus, the EQ for *P. montanus* is 0.33; excluding the olfactory bulbs and assuming an average habitus (100 g), it is 0.41; and including the olfactory bulbs and assuming an average habitus, it is 0.52.

According to other studies on modern mammals (e.g., Bauchot 1978; Eisenberg & Wilson 1978, 1981; Eisenberg 1981; Martin 1981; Hofman 1982, Armstrong 1982, 1983; Martin & Harvey 1985), the allometric exponent value in measuring EQ is about

0.74 and the proportionality coefficient is not 0.12 but 0.055. Thus,

$$EQ = \frac{E}{0.055 \, M^{0.74}} \qquad (3)$$

Kielan-Jaworowska (1983), using Jerison's (1973) estimate of body mass but applying equation 3 and measuring the brain mass including the olfactory bulbs (1.36 rather than 1.09 g), estimated the EQ for *P. montanus* to be 0.49. Excluding the olfactory bulbs and assuming a heavy habitus, the equation (3) EQ for *P. montanus* is 0.39; excluding the olfactory bulbs and assuming an average habitus, it is 0.66; and including the olfactory bulbs and assuming an average habitus, it is 0.82.

Kielan-Jaworowska (1983), however, questioned the methodology that Jerison (1973) employed to estimate endocranial volume in *P. montanus*. As revealed by more recently described endocranial casts from the Late Cretaceous of Asia (Kielan-Jaworowska 1983, 1986; Kielan-Jaworowska *et al.* 1986), endocranial shape in multituberculates is more irregular than in primitive therian mammals. The simple application of a formula for the volume of an ellipsoid, which was used by Jerison (1973), is therefore inappropriate for multituberculates. Although only the dorsal and posterior aspects of the endocranial cast of *P. montanus* are observable, the lateral and ventral aspects can now be approximated by comparisons with the Asian material.

Kielan-Jaworowska (1983) also expressed the opinion that Jerison (1973) "highly overestimated" the body mass of *P. montanus* but added that, since skeletal material of this species is known (Gidley 1909, Simpson 1937b, Krause & Jenkins 1983), direct comparisons of that material with the skeletons of modern mammals should be undertaken to assist in the estimation of body mass. Unfortunately, most of the isolated limb elements of *P. montanus* are either too fragmentary or too crushed to provide reliable measurements; the only direct measurements that can be obtained for *P. montanus* are the diameters of the humerus and femur. The recently described postcranial skeleton of *Ptilodus kummae* (Jenkins & Krause 1983; Krause & Jenkins 1983), however, adds significant new information for estimating the body mass of *Ptilodus*. Basing body size estimates of multituberculates on measurements of postcranial elements is more appropriate than basing them on dental elements. Although allometric equations have been developed from which body size in eutherian mammals can be predicted from tooth size (e.g., Gingerich *et al.* 1982; Legendre & Roth 1988; Legendre 1989), these cannot be applied to multituberculates owing to the grossly different construction of their teeth. By contrast, a number of workers (e.g., Gidley 1909; Rowe & Greenwald 1987; Sereno & McKenna 1990) have noted at least general similarities in postcranial morphology between multituberculates and therians.

Thus, revised estimates of both endocranial volume (i.e., brain mass, since brain tissue has a density close to unity) and body mass for *Ptilodus montanus* are possible. These can be used to calculate revised estimates of the EQ of *Ptilodus*.

REVISED ESTIMATE OF BRAIN MASS

The lateral and ventral aspects of the endocranial casts of *Chulsanbaatar vulgaris*

and *Nemegtbaatar gobiensis* have been illustrated and the brains reconstructed by Kielan-Jaworowska (1983, 1986) and Kielan-Jaworowska *et al.* (1986). Although the brain of *Ptilodus montanus* cannot be assumed to have been identical to those of *C. vulgaris* and *N. gobiensis*, both of which are members of a different suborder, the Taeniolabidoidea, it is assumed here that their endocranial structure is more similar to that of *P. montanus* than is an ellipsoid based on marsupials, rodents, and insectivorans (Jerison 1973). This assumption is supported by the basic similarities of the dorsal and posterior aspects of the brains of *P. montanus* to those of *C. vulgaris* and *N. gobiensis*. Given this assumption, we constructed a clay model of the brain of *P. montanus*, enlarged to five times natural size (in linear dimensions). The size and morphology of the dorsal and posterior aspects of the brain were reconstructed from USNM 9710 and AMNH 35491 (pl. 1) while the lateral and ventral aspects were patterned after the most recent reconstruction of the brain of *C. vulgaris* (Kielan-Jaworowska *et al.* 1986, fig. 7).

The volumetric displacement of the brain of *P. montanus*, based on this model, is 1.48 ml and, without the olfactory bulbs, 1.32 ml. Our estimates of brain mass, both with and without the olfactory bulbs, are therefore substantially greater than Jerison's estimates of 1.36 g and 1.09 g, respectively. Furthermore, our estimate of the mass of the olfactory bulbs relative to that of the rest of the brain is 12.1%, less than one-half Jerison's estimate of 24.8%. This is perhaps to be expected in light of the fact that: 1) the dorsal surface area of the olfactory bulbs is considerably less than originally estimated by Simpson (1937a) (compare Figs. 1a and 1b), and 2) Jerison estimated the lateral and ventral dimensions from an elliptical model whereas the skulls from the Late Cretaceous of Asia indicate that the olfactory bulbs of multituberculates were shallow anteriorly, and even somewhat concave (not convex) in the anterior part of the ventral surface.

REVISED ESTIMATE OF BODY MASS

Gingerich (1990) recently developed a computer program that predicts body mass using coefficients derived from individual and multiple regressions. These regressions were based on the length and midshaft diameter of the humerus, ulna, longest metacarpal, femur, tibia, and longest metatarsal from 36 species of mammals ranging in size from shrew (*Sorex minutus*) to elephant (*Loxodonta africana*).

The diameters of the humerus and femur of *Ptilodus montanus* were measured directly from USNM 6076 (Table 1), but other dimensions of postcranial elements had to be obtained by extrapolation from the much better known skeleton of *P. kummae* (UA 9001). In order to do so, it was necessary to utilize the best-known comparable parts of both species, namely teeth. The dental elements associated with the partial skeleton of *P. kummae* (UA 9001) from the Upper Paleocene Ravenscrag Formation of southeastern Saskatchewan include left i1 and P4 and right p4, m1, and P2-4; of these, the only complete teeth are right m1, P2-4 and left P4. The cranial material studied by Simpson (1937a), and from which Jerison (1973) estimated brain mass and skull length, included seven specimens of *P. montanus*, one from Silberling Quarry and the others from Gidley Quarry. Both quarries occur in the Middle Paleocene Lebo Formation of

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the eastern Crazy Mountains Basin, Montana. Krause (1982) demonstrated that the lengths and widths of m1 in large samples of species of *Ptilodus* generally exhibit less variability than do the length and width dimensions of premolars. It seems logical therefore to compare the relative sizes of *P. montanus* and *P. kummae* on the basis of the dimensions of m1. If this is a reliable assumption, then *P. montanus* from Gidley Quarry is 1.04 to 1.16 times (x = 1.10) the size of *P. kummae* (UA 9001) in linear dimensions, based on length and width dimensions of m1, respectively (data from Krause 1977, 1982). Using this adjustment, the lengths and diameters of the femur, tibia, and metatarsal III of *P. montanus* were estimated from those of *P. kummae* (Table 1). It is noteworthy that the only parameter that could be both directly measured from USNM 6076 of *P. montanus* and extrapolated for *P. montanus* from UA 9001 of *P. kummae*, the diameter of the femur, is similar in value. That the value for USNM 6076 is, in fact, slightly lower than that extrapolated from UA 9001 is consistent with the observation that USNM 6076 represents a relatively small individual of *P. montanus* (Simpson 1937b; Krause 1982).

Employing Gingerich's (1990) program, body mass estimates derived from the measurements of postcranial elements listed in Table 1 range from 79 to 561 g for *P. montanus* (Table 2). The low body mass estimate that is based on the length of the tibia and the high value that is based on the length of the femur are both due to the unusually low crural index (length of the tibia relative to the length of the femur x 100) of 79 in *P. montanus*, an arboreal, scansorial quadruped (Jenkins & Krause 1983; Krause & Jenkins 1983). This is very low when compared to most modern scansorial mammals, which have proximal and middle limb segments that are approximately equal in length

	Dimension (*P. kummae*) UA 9001	Dimension (*P. mont.*) USNM 6076	Estimate (*P. mont.*)
Diameter of L humerus		2.6	
Length of L femur	36.0*		39.60
Length of R femur	36.4*		40.04
Diameter of L femur	3.8		4.18
Diameter of R femur	3.9	4.0	4.29
Length of R tibia	28.8*		31.68
Diameter of R tibia	2.0**		2.20
Length of L metatarsal III	11.8		12.98
Diameter of L metatarsal III	1.1**		1.21

* Measurements from Krause & Jenkins (1983)
** Measurement approximate

Table 1.— Measurements in millimeters of the diameters and lengths of the long bones and metatarsals preserved in specimen UA 9001 of *Ptilodus kummae*, USNM 6076 of *P. montanus* (a relatively small individual for the species – Simpson 1937b, Krause, 1982), and estimates of the same measurements for *P. montanus* based on those from UA 9001 of *P. kummae* (see text). L = left, R = right.

(Hildebrand 1974). For further comparison, among sciurids crural indices range from 0.98 to 1.18 (x = 1.05, N = 25 species) in arboreal forms, from 0.98 to 1.16 (x = 1.07, N = 11 species) in volant forms, and from 0.90 to 1.07 (x = 0.96, N = 8 species) in non-saltatory terrestrial forms (Table 3). Among a diversity of extant mammals (including marsupials, edentates, macroscelideans, primates, rodents, lagomorphs, carnivorans, perissodactyls, artiodactyls, and proboscideans) sampled by Howell (1944), Taylor (1976), and Jungers (1980, 1985), only hippopotami (63), rhinoceroses (68), lions (77), and hyaenas (77) exhibited crural indices lower than that of *P. montanus*.

The largest body mass estimate (561 g), based on the diameter of the femur, is almost twice that (313 g) estimated from femoral length. This indicates that Jerison (1973) may have been correct when he suggested, for reasons that were not specified, that *Ptilodus* was of heavy habitus. Although metatarsal III length and diameter yield approximately equal body mass estimates (112 g and 109 g), tibial diameter also yields a body mass estimate (129 g) that is substantially greater than that based on tibial length (79 g). Similarly, although the length of the humerus in USNM 6076 cannot be measured, it appears to be a relatively robust bone (Krause & Jenkins 1983, fig. 11H). There are thus indications that the long bones of *Ptilodus* are of unusual proportions and of generally greater robusticity than those of most modern mammals of roughly the same size.

At least one other estimate of body mass is possible. Thewissen & Gingerich (1989) recently predicted body mass from skull length for *Eoryctes melanus*, an Early Eocene palaeoryctid insectivoran. This was based on data from 64 species of extant insectivorous mammals including members of the Chrysochloridae, Erinaceidae, Macroscelididae, Potomagalidae, Solenodontidae, Soricidae, Talpidae, Tenrecidae, and Tupaiidae. The body mass of *P. montanus* estimated from the regression of body mass and skull length for these taxa is 116 g, substantially less than the majority of the estimates derived from postcranial elements.

The geometric mean for the seven body mass estimates based on postcranial elements is 172 g. If the body mass estimate (116 g) derived from skull length is also included, the geometric mean is lowered to 163 g.

	Predicted Body Mass	95% Prediction Limits	
		Minimum	Maximum
Femoral length	313	85	1,152
Tibial length	79	21	298
Metatarsal length	112	17	754
Humeral diameter	192	106	351
Femoral diameter	561	295	1,069
Tibial diameter	129	50	333
Metatarsal diameter	109	29	412

Table 2.— Body size estimates for *Ptilodus montanus* based on measurements presented in Table 1. All values in grams (g).

Species	Femoral Length	Tibial Length	Crural Index
ARBOREAL			
Callosciurus erythraeus (N = 8) [1]	—	—	109
Callosciurus notatus (N = 3) [1]	—	—	107
Callosciurus prevosti (N = 5) [1]	—	—	106
Dremomys pernyi (N = 4) [1]	—	—	114
Funisciurus isabelli (N = 1) [2]	36.5	41.9	115
Funisciurus akka (N = 1) [2]	39.4	45.7	116
Microsciurus alfari (N = 7) [1]	—	—	118
Protoxerus aubinnii (N = 2) [1]	—	—	112
Protoxerus stangeri (N = 2) [1]	—	—	107
Ratufa affinis (N = 2) [1]	—	—	101
Ratufa bicolor (N = 4) [1]	—	—	98
Ratufa indica (N = 2) [1]	—	—	104
Sciurus aberti (N = 6) [1]	—	—	112
Sciurus aureogaster (N = 1) [2]	54.8	58.2	106
Sciurus carolinensis (N = 43) [1]	—	—	113
Sciurus deppei (N = 8) [1]	—	—	112
Sciurus griseus (N = 1) [2]	68.7	75.9	110
Sciurus kaibakensis (N = 1) [2]	61.8	65.5	106
Sciurus niger (N = 19) [1]	—	—	112
Sciurus "spadiceus" (N = 1) [2]	59.4	64.1	108
Sundasciurus hippurus (N = 2) [1]	—	—	107
Sundasciurus hoogstraali (N = 2) [1]	—	—	108
Sundasciurus steeri (N = 33) [1]	—	—	106
Tamiasciurus hudsonicus (N = 34) [1]	—	—	113
VOLANT			
Aeromys tephromelas (N = 2) [1]	—	—	102
Eoglaucomys fimbriatus (N = 3) [1]	—	—	109
Glaucomys sabrinus (N = 10) [1]	—	—	116
Glaucomys volans (N = 26) [1]	—	—	115
Hylopetes electilis (N = 1) [1]	—	—	113
Hylopetes nigripes (N = 8) [1]	—	—	112
Petaurista alborufus (N = 1) [2]	101.4	99.0	98
Petaurista hainana (N = 1) [2]	128.3	132.0	103
Petaurista petaurista (N = 9) [1]	—	—	103
Pteromys elegans (N = 1) [2]	93.0	98.0	105
Trogopterus horsfieldi (N = 1) [1]	—	—	105
TERRESTRIAL (Non-saltatory)			
Ammospermophilus leucurus (N = 1) [2]	31.0	33.2	107
Cynomys gunnisoni (N = 1) [2]	46.8	44.9	96
Cynomys ludovicianus (N = 1) [2]	49.6	50.2	101
Marmota bobac (N = 1) [2]	81.4	75.9	93
Marmota caligata (N = 1) [2]	99.0	94.2	95
Marmota himalayana (N = 1) [2]	72.4	65.0	90
Marmota marmota (N = 2) [2]	76.6	72.3	94
Marmota monax (N = 1) [2]	77.3	69.4	90

[1] Data from Thorington & Heaney (1981)
[2] Data from D. Daegling (unpublished)

Table 3.— Lengths of femora and tibiae and crural indices for selected species of sciurid rodents.

We follow Thewissen & Gingerich (1989) in providing two estimates of EQ, one based on equation (2) and another based on equation (3). The Jerison-derived EQ (equation 2) for the revised body mass estimate of 163 g and revised brain mass estimate of 1.48 g, including the olfactory bulbs, is 0.41. The revised brain mass estimate excluding the olfactory bulbs is 1.32 g, which yields an EQ of 0.37. The equation (3) EQ, including the olfactory bulbs, is 0.62 and, excluding the olfactory bulbs, is 0.55. Thus, the relative brain size of *P. montanus* appears to have been substantially less than that of an average extant mammal.

Using equivalent equations, our revised estimates of the EQ of *Ptilodus* are higher than those previously obtained by either Jerison (1973) or Kielan-Jaworowska (1983) when assuming a heavy habitus. This is owing to the revised higher estimate for brain mass and the revised lower estimate for body mass. Kielan-Jaworowska (1983) had earlier predicted that the EQ of *Ptilodus* was actually higher than previously calculated by either her or Jerison.

Using equivalent equations, the revised EQ for *Ptilodus* is slightly higher than that for *Chulsanbaatar* from the Late Cretaceous of Asia. For instance, the EQ of *Chulsanbaatar* using equation (3) and including the olfactory bulbs was calculated by Kielan-Jaworowska (1983) as being 0.54-0.56 compared to 0.62 for *Ptilodus*. Owing to the various assumptions involved in the calculation of the EQs for the two taxa, this difference is here considered negligible.

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PLATE

PLATE 1

Stereophotographs of partial endocranial casts of *Ptilodus montanus* DOUGLASS from Gidley Quarry, eastern Crazy Mountains Basin, Montana.

Fig. 1.— Dorsal view of USNM 9710, showing the olfactory bulbs and the anterior part of the cerebral hemispheres. Note that the olfactory bulbs taper anteriorly.

Fig. 2.— Dorsal view of AMNH 35491, showing part of the cerebral hemispheres and cerebellum with the vermis deeply inserted between the cerebral hemispheres and the cast of the transverse sinus.
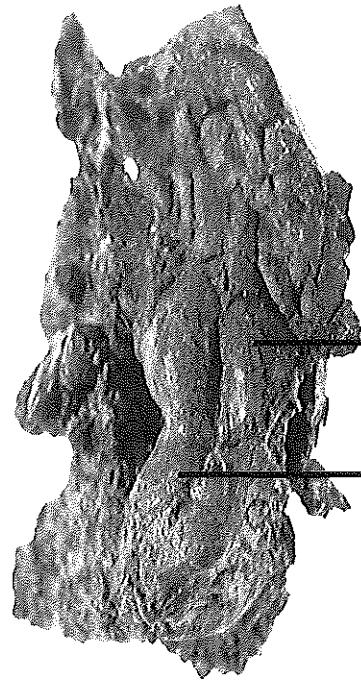
Fig. 3.— Posterodorsal view of AMNH 35491, showing different view of same structures indicated in Fig. 2 as well as better view of left paraflocculus.
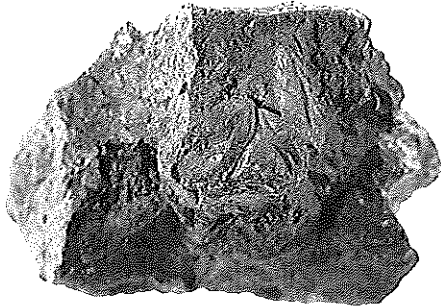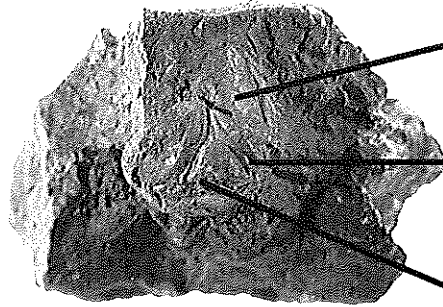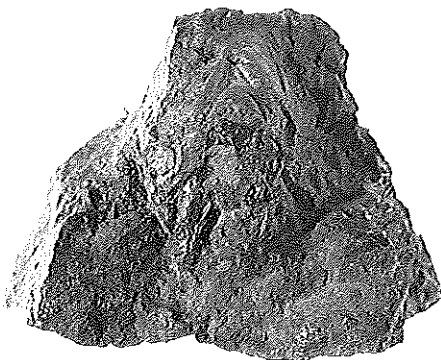
PLATE 1

1

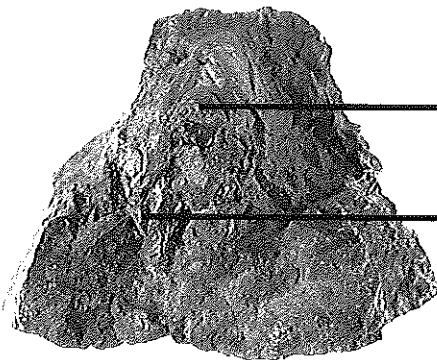olfactory bulb

cerebral hemisphere

1cm

2

cerebral hemisphere

transverse sinus

vermis

2cm

3

vermis

para-flocculus