CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

VOL. 31, NO. 8, PP. 185-195 December 15, 2005

BRAIN OF *PLESIADAPIS COOKEI* (MAMMALIA, PROPRIMATES): SURFACE MORPHOLOGY AND ENCEPHALIZATION COMPARED TO THOSE OF PRIMATES AND DERMOPTERA

BY

PHILIP D. GINGERICH AND GREGG F. GUNNELL

MUSEUM OF PALEONTOLOGY
THE UNIVERSITY OF MICHIGAN
ANN ARBOR

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

Philip D. Gingerich, Director

This series of contributions from the Museum of Paleontology is a medium for publication of papers based chiefly on collections in the Museum. When the number of pages issued is sufficient to make a volume, a title page plus a table of contents will be sent to libraries on the Museum's mailing list. This will be sent to individuals on request. A list of the separate issues may also be obtained by request. Correspondence should be directed to the Publications Secretary, Museum of Paleontology, The University of Michigan, 1109 Geddes Road, Ann Arbor, Michigan 48109-1079 (paleopubs@umich.edu).

VOLS. 1-31: Parts of volumes may be obtained if available. Price lists are available upon inquiry.
See also: www.paleontology.lsa.umich.edu/Publications/publicationIntro.html

BRAIN OF *PLESIADAPIS COOKEI* (MAMMALIA: PROPRIMATES): SURFACE MORPHOLOGY AND ENCEPHALIZATION COMPARED TO THOSE OF PRIMATES AND DERMOPTERA

BY

PHILIP D. GINGERICH[1] AND GREGG F. GUNNELL[1]

Abstract — *Plesiadapis* is a Paleocene mammal known from Europe and North America that has long been important in discussion of the origin of Primates. A well preserved skull and associated postcranial skeleton of the large North American species *Plesiadapis cookei* was found in 1986 that includes a partial brain endocast. The brain of *Plesiadapis* was small and narrow, with a smooth neocortex and considerable midbrain exposure. Encephalization is about one-quarter that expected for a living mammal of its size (EQ ca. 0.25) and half or less that of any known primate or dermopteran. *Plesiadapis* and other Proprimates may be related to Primates or possibly Dermoptera, but new evidence from the brain shows *Plesiadapis* to be more primitive than both and doubtfully included in either.

INTRODUCTION

Plesiadapis is a member of an archaic group of plesiadapiform mammals that diversified in the Paleocene and Eocene of North America and Europe (Russell, 1964; Gingerich, 1976; Gunnell, 1989). There are scattered early Paleogene records of plesiadapiforms in Asia (Beard and Wang, 1995; Smith et al., 2004), and possibly North Africa (Tabuce et al., 2004). The ordinal relationships of plesiadapiforms are uncertain, with some scholars arguing for inclusion in a broadly defined order Primates (Bloch and Silcox, 2001; Silcox et al., 2001; Bloch and Boyer, 2002; Tabuce et al., 2004), while others place some members of the group within Dermoptera (Beard, 1990; Kay et al., 1992). Reference to Proprimates (Gingerich, 1990a) is intended to reflect the ambiguity of limited similarity by associating plesiadapiforms nominally with Primates, but at the same time recognizing that they may not be closely related phylogenetically. Whatever their relationships ultimately prove to be, plesiadapiform Proprimates have been important in discussion of the origin of Primates (Simpson, 1935; Russell, 1964; Cartmill, 1972, 1974; Szalay et al., 1975; Gingerich, 1976; Martin, 1986; Gunnell, 1989; Bloch and Boyer, 2002; Kirk et al., 2003).

A new specimen of *Plesiadapis cookei*, University of Michigan Museum of Paleontology (UM) 87990, includes the skull and much of the skeleton of a young adult. This has all permanent teeth fully erupted and slightly worn. Epiphyses are partially fused or free on some long bones, but the long bones have reached adult size. Preliminary notice of the skeleton was published by Gunnell and Gingerich (1987) and Gingerich and Gunnell (1992), and several replicas of the skeleton have been mounted at the University of Michigan and elsewhere (Fig. 1).

---

[1] Museum of Paleontology and Department of Geological Sciences, The University of Michigan, Ann Arbor, Michigan 48109-1079

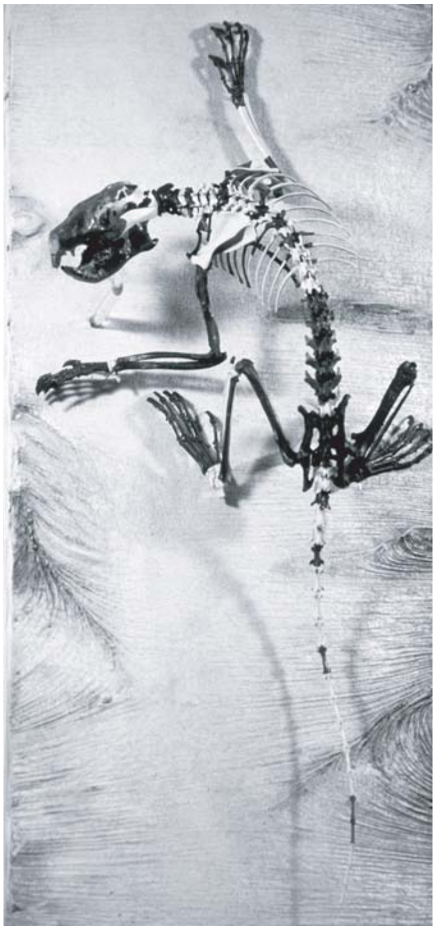

FIG. 1 – UM 87990 skeleton of *Plesiadapis cookei* as mounted in the University of Michigan Exhibit Museum. Parts in light gray are reconstructed. For scale, skull length, femur length, and ulna length are all approximately 9 cm.

The specimen was found in 1986 by graduate student J. G. M. Thewissen while working as a member of a University of Michigan field party. It was found in a freshwater limestone at UM locality SC-117, in the Clarks Fork Basin of northwestern Wyoming (Fig. 2). *P. cookei* is itself a diagnostic guide to the middle Clarkforkian part of the late Paleocene epoch (biozone Cf-2, approximately 56 Ma; Rose, 1981; Gingerich, 2001; Lofgren et al., 2004).

NEW SKULL OF *PLESIADAPIS COOKEI*

The new skull of *Plesiadapis cookei,* UM 87990, resembles those of *P. tricuspidens* described previously from Europe (Russell, 1959, 1964; Gingerich, 1976), but it is unique and important in preserving the first good endocast of a plesiadapid brain. Study of the endocast is enhanced by its association with a postcranial skeleton.

FIG. 2 – University of Michigan locality SC-117 where the UM 87990 skeleton of *Plesiadapis cookei* was found. Collector is kneeling at the discovery site; view is toward the west.

The skull of UM 87990 is in five pieces, comprising (1) a slightly crushed palate and splanchnocranium, with part of the cribriform plate and impressions of the olfactory bulbs of the brain; (2) a separate neurocranium, with a partial natural endocast of the brain exposed on its dorsal surface, and the basicranium and auditory bullae nearly intact on its ventral side; (3) a frontal-parietal piece of skull roof fitting firmly onto both the splanchnocranium and the neurocranium, and preserving a clear impression of the dorsal profile and surface of the brain from the olfactory bulbs to the cerebellum; (4) a left dentary with roots for the incisor and all cheek teeth, and an intact ascending ramus, condyle, and angle; and (5) a right dentary with an enlarged incisor, well preserved cheek teeth, and an intact angle. Fitting these together, the reconstructed skull (Fig. 3) measures 90 mm in condylobasal length and 58 mm in bizygomatic breadth.

BRAIN OF *PLESIADAPIS COOKEI*

The brain of *Plesiadapis cookei* is long and relatively narrow. Its total length is 42 mm, and its maximum width across the piriform lobes of the cerebrum is 22 mm. Maximum depth cannot be measured, but this appears to have been about 12-13 mm. Olfactory bulbs are large, with each measuring 10 mm anteroposteriorly and about 5 mm transversely. There is a strong median fissure dividing the olfactory bulbs dorsally. The cribriform plate reaches rostrally as far as the border between the orbital and temporal fossae, resembling recent lipotyphlan insectivores (Butler, 1956), but unlike tupaiids or euprimates. The frontal is thick over the olfactory bulbs.

The cerebrum is 22 mm long and 22 mm wide, with a smooth dorsal surface. Anterior lateral surfaces are not preserved. Posteriorly, there are distinct swellings on the natural endocast for transverse sinuses and for a dorsal sagittal sinus. Lateral to the dorsal sinus is a faint depression interpreted as a marginal sulcus. A second sulcus is more clearly defined on the dorsolateral surface of the cerebrum, lateral to the marginal sulcus, and this appears to be the rhinal fissure delimiting expansion of neocortex or neopallium over the piriform lobe of the cerebrum. If the rhinal fissure is correctly interpreted (dashed line in Fig. 3), it indicates that neopallium in *Plesiadapis* was expanded to about the same extent as it is in living *Tenrec* (Le Gros Clark, 1932), which is considered a "basal insectivore" (basal insectivores are "olfactory" insectivores with other sensory centers of the brain little developed; Stephan, 1967).

Posterior to the cerebrum, just behind the transverse sinuses, the tectum of the midbrain is broadly exposed with two small but distinct swellings representing the caudal or auditory quadrigeminal colliculi. Rostral or visual colliculi may have been exposed on the midbrain as well, but neither the endocast nor the frontal-parietal piece of skull roof preserves any clear indication of these. Relative size of the quadrigeminal colliculi suggests that acoustic reflexes were better developed than visual reflexes in *Plesiadapis*. Posterior to the midbrain, the profile of the cerebellum is well defined, but little surface detail of the vermis or lateral hemispheres is preserved. The foramen magnum measures about 8.5 by 6.0 mm.

Endocranial volume cannot be measured directly for the *Plesiadapis cookei* endocast, but the size of the brain can be estimated using a full-scale model molded to fit the endocranial profile of the articulated splanchnocranium, parietal-frontal skull roof, and dorsal neurocranium, and augmented to reflect other important dimensions. Dorsoventral depth of the model was determined by comparison with a range of endocasts of similar living mammals. Water displacement indicates that the model has a volume of 5 cc. This number is much smaller than the estimate of 18.7 cc derived as an upper limit using double integration of a graphic representation of the brain in similar-sized *Plesiadapis tricuspidens* (Gingerich, 1976). The new smaller volume is based on a specimen providing much greater control over the size of all major components of the brain, and we now expect that *P. tricuspidens* had an endocranial volume of about 5 cc also. Assuming brain tissue has the density of water, with negligible error, an endocranial volume of 5 cc indicates a brain weight of 5 gm in *P. cookei*.

BODY SIZE OF *PLESIADAPIS COOKEI*

The absolute size of the brain of *Plesiadapis cookei* is less interesting than brain size in relation to body size. Body weight can be estimated from the skeleton. Alexander et al. (1979) provided highly correlated shrew-to-elephant regressions of long bone length and diameter on body weight for living mammals. Their objective was better understanding of skeletal allometry, however their measurements can be used in reverse to predict body weight from long bone lengths and diameters (Table 1; Gingerich, 1990b).

Each length and diameter can be used to generate a body weight prediction for *Plesiadapis cookei* independently. These are highly variable and range from 1,338 g, for metatarsal diameter, to 3,343 g, for humerus diameter. The geometric mean of the individual estimates is 2,176 g. The broad range of the individual estimates means that *Plesiadapis* was not proportioned like the average mammal in the Alexander et al. data set. We can get a sense of how it differed by comparing individual estimates to their average. Clearly *Plesiadapis* had a longer humerus, a longer ulna, a longer femur, and a greater midshaft diameter of the humerus than expected. Further, it had a shorter tibia, a shorter longest metatarsal, and many long bones of smaller midshaft diameter than expected. In simplest terms, *Plesiadapis* was longer-limbed and lighter-limbed than the mammalian average.

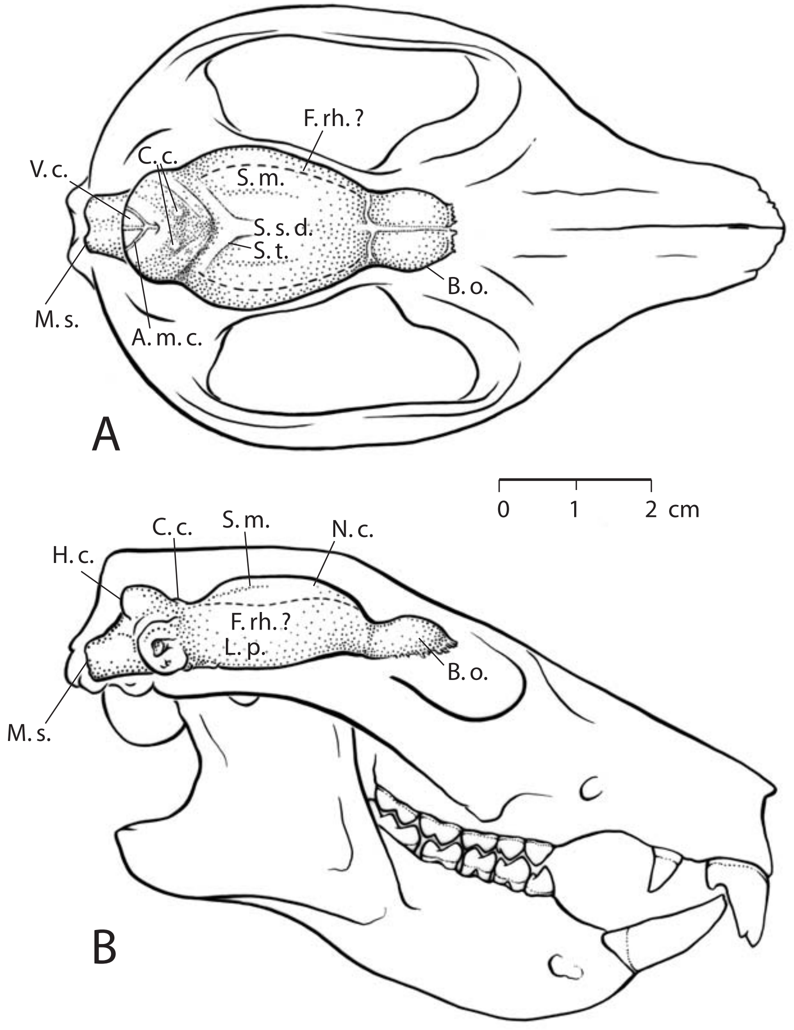

FIG. 3 – Brain and skull of late Paleocene *Plesiadapis cookei*, UM87990, from locality SC-117 in the Clarks Fork Basin, Wyoming. A, dorsal view. B, right lateral view. Note small size of brain as a whole, relatively large olfactory bulbs, long and smooth cerebrum, and extensive exposure of the midbrain with distinct impressions of caudal colliculi. Abbreviations: *A.m.c., Arteria cerebellar caudalis. B.o., Bulbus olfactorius. C.c., Colliculus caudalis. C.r., Colliculus rostralis. F.rh., Fissura rhinalis. H.c., Hemispherium cerebelli. L.p., Lobus piriformis. M.s., Medulla spinalis. N.c., Neopallium cerebri. S.m., Sulcus marginalis. S.s.d., Sinus sagittalis dorsalis. S.t., Sinus transversus. V.c., Vermis cerebelli.*

We can approach estimation using multiple regression. All of the Alexander et al. long bone lengths and diameters taken together yield a body weight estimate for *P. cookei* of 2,135 g. Long bone measurements alone yield a body weight estimate of 2,796 g. This discrepancy is minimized if long-limbed artiodactyls are removed and the multiple regression recalculated. With artiodactyls removed, long bone lengths and diameters yield a body weight estimate for *P. cookei* of 2,239, and long bone measurements alone yield a very similar body weight estimate of 2,255. Combining the four best estimates, 2,176, 2,135, 2,239, and 2,255, a pooled estimate of 2,200 g seems reasonable.

TABLE 1 – Body weight estimate for *Plesiadapis cookei* based on lengths and anteroposterior midshaft diameters of long bones in UM 87990. Estimation is explained in Gingerich (1990b). Abbreviations: *CI*, confidence interval; *D*, diameter; *ER*, encephalization residual; *L*, length; *N*, sample size.

Dimension	Measurement (mm)	Predicted body weight (g)	95% CI for prediction ($k = 1$) Min. (g)	 Max. (g)
Single-variable regression				
Humerus length	76.6	3,039	902	10,245
Ulna length	92.0	3,077	976	9,698
Metacarpal length	24.1	2,272	364	14,188
Femur length	88.8	2,635	723	9,603
Tibia length	87.0	1,741	473	6,406
Metatarsal length	32.4	1,848	281	12,143
Humerus diameter	7.8	3,343	1,845	6,057
Ulna diameter	5.6	—	—	—
Metacarpal diameter	2.3	1,492	615	3,621
Femur diameter	6.6	2,043	1,075	3,883
Tibia diameter	6.2	2,083	818	5,303
Metatarsal diameter	2.8	1,338	358	4,999
N, geom. mean, max., min.	11	**2,176**	1,845	3,621
Multiple regression				
All species	11 L&D:	**2,135**	6 L:	**2,796**
Artiodactyls removed		**2,239**		**2,255**
Brain weight:body weight of 5 g:2,176 g				
Jerison EQ		**0.248**	0.276	0.176
ER = Log_2 EQ		**-2.012**		
Brain weight:body weight of 5 g:2,200 g				
Jerison EQ		**0.246**		
ER = Log_2 EQ		**-2.023**		

For comparison, regression of body weight on skull length in insectivores (Thewissen and Gingerich, 1989) yields a body weight for *Plesiadapis cookei* of 2,299 gm. Regression of body weight on tooth size in prosimian primates has been used to estimate the body weight of *P. cookei* (Conroy, 1987) , but the tooth size estimate of 3,067 g is substantially larger than estimates calculated here based on the postcranial skeleton. If the greater body weight were used, the relative size of the brain would be even smaller than calculated here.

RELATIVE BRAIN SIZE

Relative brain size can be calculated as an encephalization quotient (EQ) of observed brain size divided by expected brain size for an average mammal of the same body size, or better as an encephalization residual (ER) on a halving-doubling $\log_2$ scale (where ER = $\log_2$ EQ; Gingerich, ms.). Jerison (1973), Martin (1981), and Eisenberg (1981) proposed three slightly different allometric scaling relationships of brain and body size in mammals. These yield EQ values of 0.25, 0.25, and 0.30, respectively, and ER values of -2.03, -2.03, and -1.72, respectively, for encephalization in *Plesiadapis cookei*. The Jerison and Martin values do not differ for mammals the size of *P. cookei*. EQ values for *P. cookei* are about one quarter the expectation for a mammal this size, and

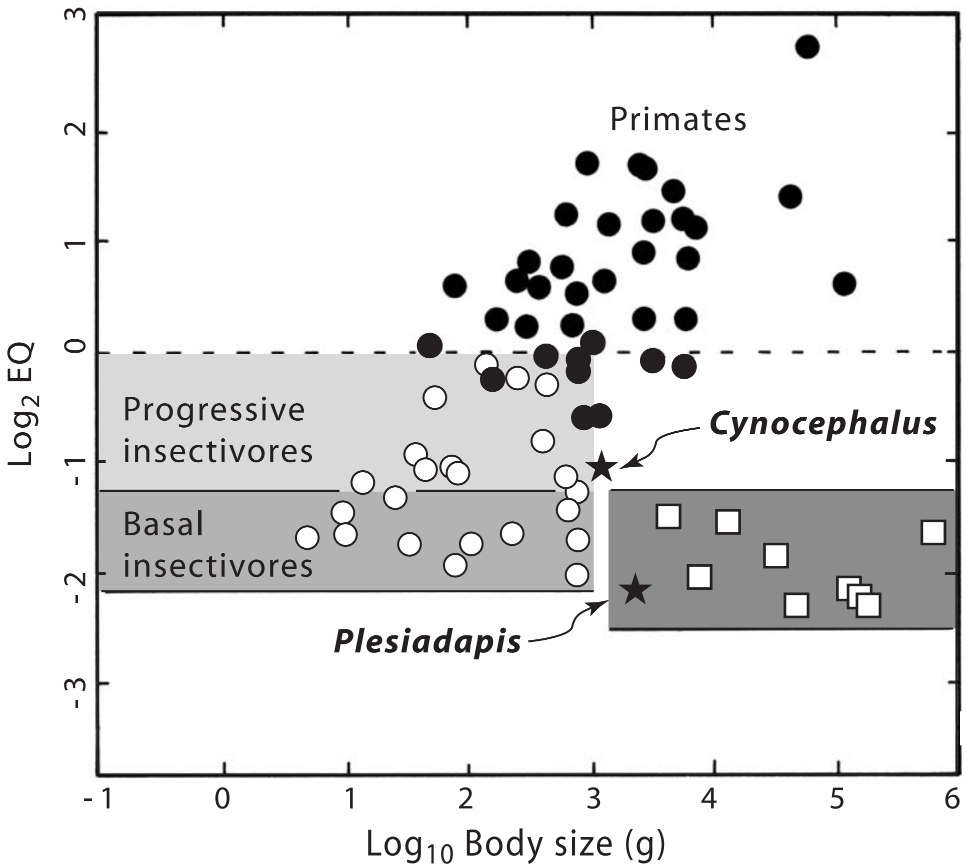

FIG. 4 – Relative brain size in late Paleocene *Plesiadapis* and the living dermopteran *Cynocephalus* compared to that in extant insectivores (open circles), extant primates (closed circles), and early Paleogene archaic ungulates (open squares). Data taken from Stephan et al. (1970) and Radinsky (1978). Abscissa and ordinate both employ proportional scales; ordinate is in doubling units relative to standard encephalization quotient EQ = 1.0 (dashed line; encephalization residual ER = $\log_2$ of standard EQ = $\log_2 1.0 = 0$) for brain size in an average mammal of any body size. Note that *Plesiadapis* falls at the lower limit of basal insectivores and within the range of early Paleogene archaic ungulates (value for *Plesiadapis* is in Table 1). *Cynocephalus* lies well above *Plesiadapis* and within the range of progressive insectivores.

on the order of one-half, those of any living or fossil primate calculated the same way (Conroy, 1987; Eisenberg, 1981; Stephan et al., 1970; Radinsky, 1977; Gurche, 1982). EQ values for *P. cookei* fall instead within the range of living basal insectivores and contemporary early Paleogene archaic ungulate mammals (Fig. 4).

A partial endocast is known for one other plesiadapiform, the microsyopid *Megadelphus lundeliusi* (Gunnell, 1989). This endocast was described by Szalay (1969) and restudied by Radinsky (1977). It is similar to the endocast of *Plesiadapis* described here in having large olfactory bulbs, a single neocortical sulcus (marginal sulcus), and some exposed midbrain. The endocast of *Megadelphus* differs in being less elongate, and in having less midbrain exposure, without identifiable quadrigeminal colliculi. No one has attempted to determine the brain size or encephalization of *Megadelphus*.

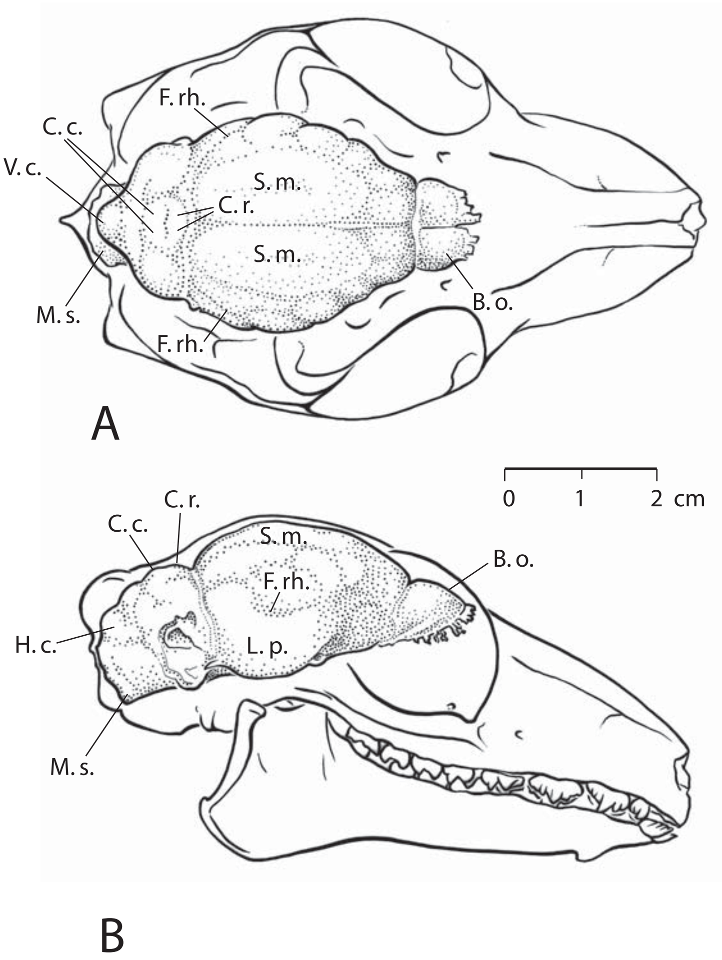

FIG. 5 – Brain and skull of extant male *Cynocephalus variegatus*, University of Michigan Museum of Zoology 117122, from Selangor, Kuala Lumpur, Malaysia. A, dorsal view. B, right lateral view. Condylobasal length of skull is 68.5 mm. Brain drawing is based on a latex endocast. Endocranial volume is 7 cc. Note globular shape of brain, with expanded neocortex above rhinal fissure, numerous sulci within neocortex, and midbrain exposure due to enlargement of corpora quadrigemina. Abbreviations as in Fig. 3.

The endocast of *Plesiadapis* indicates a basal olfactory brain very different in size and sensory development from that of any living or fossil primate, with no enlargement of visual, frontal, or temporal neocortex. These features also distinguish *Plesiadapis* from the living colugo *Cynocephalus*, which has a larger and more globular brain with numerous neocortical sulci (Fig. 5). Visual, frontal, and temporal areas of the neocortex are all enlarged to some degree. The midbrain is exposed in *Cynocephalus* (Gervais, 1872; Leche, 1886; Grassé, 1955), but this appears to be due at least in part to enlargement of the corpora quadrigemina (Starck, 1963; Edinger, 1964) (particularly the rostral pair concerned with visual reflexes; Gervais, 1872). *Cynocephalus* has an endocranial volume of 7 cc and an adult body weight of 1,300 gm (Davis, 1962; Walker, 1975), yielding EQ's of 0.49, 0.51, and 0.63 by Jerison's, Martin's, and Eisenberg's methods, and making it comparable to progressive insectivores (Stephan, 1967) in degree of encephalization.

DISCUSSION

Plesiadapis and its allies are interesting as representatives of an important Paleocene diversification of mammals. Plesiadapiform Proprimates share some specializations with Primates and some with Dermoptera, but it is difficult to determine which if any may represent synapomorphies. When the full scope of plesiadapiform Proprimates is considered, unusual specialization (e.g. enlarged anterior teeth) and a host of primitive features (claws on digits, absence of a postorbital bar, small brain, smooth neocortex, midbrain exposure) characterize them in comparison with most Eocene-Recent representatives of modern orders of mammals. The brain of *Plesiadapis* is much more primitive than that of any true primate.

ACKNOWLEDGMENTS

William Ryan prepared the new *Plesiadapis* skull, and Bonnie Miljour drew figures 3 and 5. We thank R. McN. Alexander for providing the data set used to regress body weight on long bone lengths and diameters. Philip Myers provided access to University of Michigan Museum of Zoology specimens of *Cynocephalus*. We thank anonymous reviewers for comments improving the manuscript when an earlier version of this study was submitted to Nature in 1990. Field research was supported by a series of grants from the U. S. National Science Foundation, including EAR 84-08647 active when UM 87990 was found, and EAR-0125502 active now (PDG). Study of plesiadapiform primates was carried out with support from BCS-0129601 (GFG and PDG).

LITERATURE CITED

ALEXANDER, R. M., A. S. JAYES, G. M. O. MALOIY, and E. M. WATHUTA. 1979. Allometry of the limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). Journal of Zoology, London, 189: 305-314.

BEARD, K. C. 1990. Gliding behavior and palaeoecology of the alleged primate family Paromomyidae (Mammalia, Dermoptera). Nature, 345: 340-341.

——— and J. WANG. 1995. The first Asian plesiadapoids (Mammalia: Primatomorpha). Annals of Carnegie Museum, 64: 1-33.

BLOCH, J. I. and D. M. BOYER. 2002. Grasping primate origins. Science, 298: 1606-1610.

BLOCH, J. I. and M. T. SILCOX. 2001. New basicrania of Paleocene-Eocene *Ignacius*: re-evaluation of the plesiadapiform-dermopteran link. American Journal of Physical Anthropology, 116: 184-198.

BUTLER, P. M. 1956. The skull of *Ictops* and the classification of the Insectivora. Proceedings of the Zoological Society of London, 126: 453-481.

CARTMILL, M. 1972. Arboreal adaptations and the origin of the order Primates. In R. H. Tuttle (ed.), The Functional and Evolutionary Biology of Primates, Aldine-Atherton, Chicago, pp. 97-122.

———. 1974. Rethinking primate origins. Science, 184: 436-443.

CONROY, G. C. 1987. Problems of body-weight estimation in fossil primates. International Journal of Primatology, 8: 115-137.

DAVIS, D. D. 1962. Mammals of the lowland rain-forest of North Borneo. Bulletin of the Singapore National Museum, 31: 1-129.

EDINGER, T. 1964. Midbrain exposure and overlap in mammals. American Zoologist, 4: 5-19.

EISENBERG, J. F. 1981. The Mammalian Radiations: an Analysis of Trends in Evolution, Adaptation, and Behavior. University of Chicago Press, Chicago, 610 pp.

GERVAIS, P. 1872. Mémoire sur les formes cérébrales propres à différents groupes de mammifères. Journal de Zoologie, Paris, 1: 425-469.

GINGERICH, P. D. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). University of Michigan Papers on Paleontology, 15: 1-140.

———. 1990a. Mammalian order Proprimates. Journal of Human Evolution, 19: 821-822.

———. 1990b. Prediction of body mass in mammalian species from long bone lengths and diameters. Contributions from the Museum of Paleontology, University of Michigan, 28: 79-92.

———. 2001. Biostratigraphy of the continental Paleocene-Eocene boundary interval on Polecat Bench in the northern Bighorn Basin. In P. D. Gingerich (ed.), Paleocene-Eocene Stratigraphy and Biotic Change in the Bighorn and Clarks Fork Basins, Wyoming, University of Michigan Papers on Paleontology, 33: 37-71.

——— and G. F. GUNNELL. 1992. A new skeleton of *Plesiadapis cookei*. Display Case, A Quarterly Newsletter of the Exhibit Museum, University of Michigan, 6: 1-3.

GRASSÉ, P.-P. 1955 . Ordre des Dermopteres. In P.-P. Grassé (ed.), Traité De Zoologie: Anatomie, Systematique, Biologie, Masson, Paris, 17: 1713-1728.

GUNNELL, G. F. 1989. Evolutionary history of Microsyopoidea (Mammalia, ?Primates) and the relationship between Plesiadapiformes and Primates. University of Michigan Papers on Paleontology, 27: 1-157.

——— and P. D. GINGERICH. 1987. Skull and partial skeleton of *Plesiadapis cookei* from the Clarks Fork Basin. American Journal of Physical Anthropology, 72: 206.

GURCHE, J. A. 1982. Early primate brain evolution. In E. Armstrong and D. Falk (eds.), Primate Brain Evolution Methods and Concepts, Plenum Press, New York, pp. 227-246.

JERISON, H. J. 1973. Evolution of the Brain and Intelligence. Academic Press, New York, 482 pp,

KAY, R. F., J. G. M. THEWISSEN, and A. D. YODER. 1992. Cranial anatomy of *Ignacius graybullianus* and the affinities of the Plesiadapiformes. American Journal of Physical Anthropology, 89: 477-498.

KIRK, E. C., M. CARTMILL, R. F. KAY, and P. LEMELIN. 2003. Comment on ‘Grasping primate origins’. Science, 300: 741.

LE GROS CLARK, W. E. 1932. The brain of the Insectivora. Proceedings of the Zoological Society of London, 1932: 975-1013.

LECHE, W. 1886. Über die Säugethiergattung *Galeopithecus*: eine morphologische untersuchung. Kongliga Svenska Vetenskaps-akademiens Handlingar, Stockholm, 21: 3-92.

LOFGREN, D. L., J. A. LILLEGRAVEN, W. A. CLEMENS, P. D. GINGERICH, and T. E. WILLIAMSON. 2004. Paleocene biochronology of North America: the Puercan through Clarkforkian land-mammal ages. In M. O. Woodburne (ed.), Late Cretaceous and Cenozoic Mammals of North America, Columbia University Press, New York, pp. 43-105.

MARTIN, R. D. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature, London, 293: 57-60.

———. 1986. Primates: a definition. In B. A. Wood, L. B. Martin, and P. J. Andrews (eds.), Major Topics in Primate and Human Evolution, Cambridge University Press, Cambridge, pp. 1-31.

RADINSKY, L. B. 1977. Early primate brains: facts and fiction. Journal of Human Evolution, 6: 79-86.

———. 1978. Evolution of brain size in carnivores and ungulates. American Naturalist, 112: 815-831.

ROSE, K. D. 1981. The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene-Eocene boundary. University of Michigan Papers on Paleontology, 26: 1-197.

RUSSELL, D. E. 1959. Le crâne de *Plesiadapis*. Bulletin de la Société Géologique de France , 1: 312-315.

———. 1964. Les mammifères Paléocènes d’Europe. Mémoires du Muséum National d’Histoire Naturelle, Paris, Série C, 13: 1-324.

SILCOX, M. T., D. W. KRAUSE, M. C. MAAS, and R. C. FOX. 2001. New specimens of *Elphidotarsius russelli* (Mammalia, ?Primates, Carpolestidae) and a revision of plesiadapoid relationships. Journal of Vertebrate Paleontology, 21: 132-152.

SIMPSON, G. G. 1935. The Tiffany Fauna, Upper Paleocene. III. Primates, Carnivora, Condylarthra, and Amblypoda. American Museum Novitates, 817: 1-28.

SMITH, T., J. V. ITTERBEECK, and P. MISSIAEN. 2004. Oldest Plesiadapiform (Mammalia, Proprimates) from Asia and its palaeobiogeographical implications for faunal interchange with North America . Comptes Rendus Palevol, 3: 43-52.

STARCK, D. 1963. ‘Freiliegendes Tectum mesencephali,’ ein Kennzeichen des primitiven Säugetiergehirns? Zoologischer Anzeiger, Jena, 171: 350-359.

STEPHAN, H. 1967. Zur Entwicklungshöhe der Insektivoren nach Merkmalen des Gehirns und die Definition der ‘Basalen Insektivoren’. Zoologischer Anzeiger, Jena, 179: 177-199.

———, R. BAUCHOT, and O. J. ANDY. 1970. Data on the size of the brain and of various brain parts in insectivores and primates. In C. R. Noback and W. Montagna (eds.), The Primate Brain, Appleton-Century-Crofts 320, New York, pp. 289-297.

SZALAY, F. S. 1969. Mixodectidae, Microsyopidae, and the insectivore-primate transition . Bulletin of the American Museum of Natural History, 140: 193-330.

———, I. TATTERSALL, and R. L. DECKER. 1975. Phylogenetic relationships of *Plesiadapis*-- postcranial evidence. In F. S. Szalay (ed.), Approaches to Primate Paleobiology, Karger, Basel, Contributions to Primate Biology, 5: 136-166.

TABUCE, R., M. MAHBOUBI, P. TAFFOREAU, and J. SUDRE. 2004. Discovery of a highly-specialized plesiadapiform primate in the early-middle Eocene of northwestern Africa. Journal of Human Evolution, 47: 305-321.

THEWISSEN, J. G. M. and P. D. GINGERICH. 1989. Skull and endocranial cast of *Eoryctes melanus*, a new palaeoryctid (Mammalia: Insectivora) from the early Eocene of western North America. Journal of Vertebrate Paleontology, 9: 459-470.

WALKER, E. P. 1975. Mammals of the World. Johns Hopkins Press, Baltimore, 1500 pp.