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THE EVOLUTION OF THE HUMAN BRAIN
1979

THE FOSSIL RECORD OF PRIMATE BRAIN EVOLUTION

LEONARD RADINSKY

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THE FOSSIL RECORD OF PRIMATE BRAIN EVOLUTION

INTRODUCTION

The fossil record of primate brain evolution consists primarily of endocranial casts, or endocasts, which are casts of the inside of the braincase. Endocasts of most mammals reproduce the external morphology of the brain, because in life the inner surface of the braincase conforms closely to the configuration of the brain. Fossil endocasts are the only evidence we have of the brains of extinct mammals, and they can provide information on brain size, shape, and patterns of cerebral convolutions. In relatively large brained mammals, such as the living great apes and humans, impressions of cerebral convolutions are blurred or absent, and endocasts provide information only on brain size and shape. However, in smaller brained primates, such as prosimians and most monkeys, endocasts can reproduce all of the cerebral convolutions, and also some details of cerebellar morphology. (Bauchot and Stephan, 1967; Radinsky, 1968, 1972).

Endocasts can be prepared in two ways. If the matrix filling a fossil braincase is relatively hard, the bones of one side of the braincase can be stripped away to expose the natural stone endocast. If the matrix is soft, the braincase can be cleaned out and an artificial endocast prepared with liquid latex (see Radinsky, 1968, for the latter technique).

The external brain morphology revealed by fossil endocasts can be interpreted by extrapolating from the work of neurophysiologists on modern brains. Cortical mapping studies have shown that major functional areas are localized, and in brains with convolutions, functional areas may be delimited by sulci (grooves). Thus, by extrapolating from cortical maps of living primates (fig. 1), one may infer the functional significance of differential enlargement or reduction of parts of the brain seen on fossil endocasts. Such functional inferences are hypotheses that

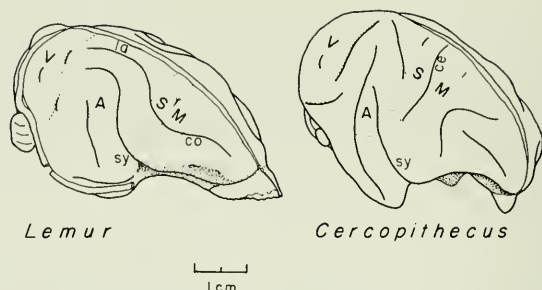
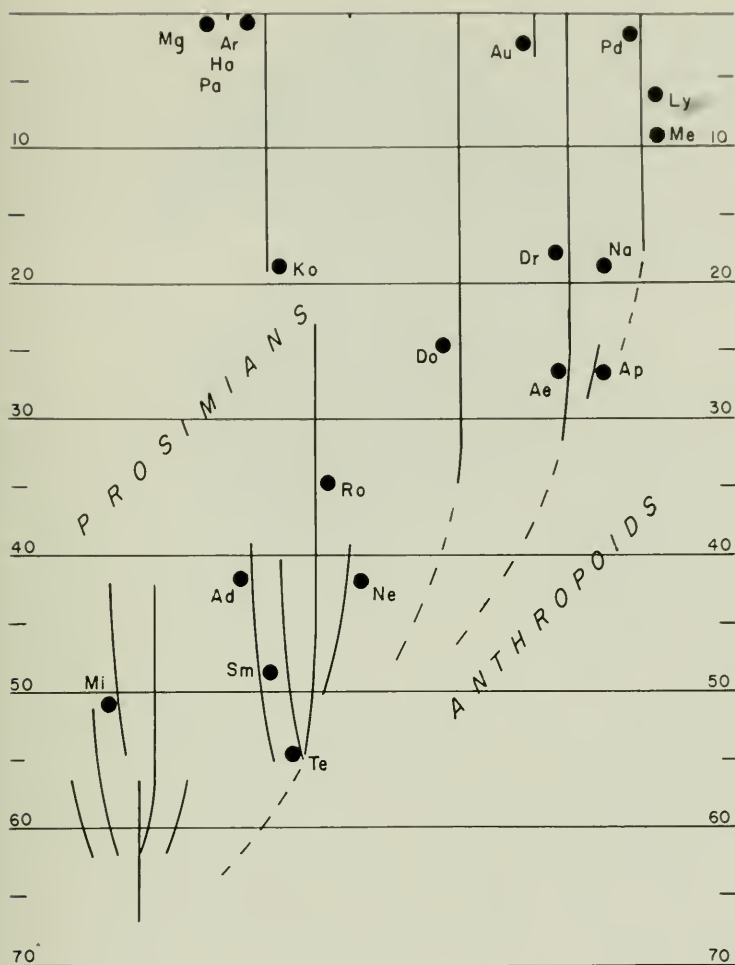


FIG. 1. Endocasts of a modern prosimian, *Lemur variegatus*, and a modern anthropoid, *Cercopithecus talapoin*, to show differences in cortical folding patterns and relationships of major sensory and motor cortical areas to sulci. Location of functional areas extrapolated from cortical mapping studies of a variety of modern primates. Abbreviations: A, auditory cortex; ce, central sulcus; co, coronal sulcus; la, lateral sulcus; M, primary motor cortex; S, primary somatic sensory cortex; sy, sylvian sulcus; V, primary visual cortex.

cannot be tested directly, but can be strengthened (or weakened) by correlations with other bits of evidence. For example, one would expect expanded visual cortex to be correlated with enlarged orbits, expanded auditory cortex with enlarged auditory bullae or modified auditory ossicles, and expanded facial somatic sensory (tactile) cortex with an enlarged infraorbital foramen (transmits nerves and blood supply to face).

Another source of information for interpreting fossil endocasts is comparative anatomical studies of the brains of living species. There are still only a few broad comparative studies of the neuroanatomy of living primates, and the most important of these for interpreting endocasts are the work of Bauchot, Stephan and colleagues (Stephan, Frahm and Bauchot, 1977, and references cited therein). They have provided a substantial amount of information on the gross anatomy and the relative sizes of major parts of the brain of a large number of primates and insectivorans, and those data provide a context against which various aspects of fossil endocasts can be compared.

Endocasts are known from only a small number of fossil primates (fig. 2). This is because primates are, with a few exceptions, relatively rare in the fossil record, and uncrushed



braincases, from which endocasts can be prepared, are even rarer. I have reviewed much of the fossil record of non-hominid primate endocasts (Radinsky, 1970, 1974, 1977), and fossil hominid endocasts have been discussed recently by Holloway (1975, 1976) and Kochetkova (1978). Some new evidence, plus the desire to reassess some of the old evidence, provided the impetus for this review.

EARLY PROSIMIAN ENDOCASTS

The oldest good evidence of early primate brains is an endocast of *Tetonius*, an omomyoid prosimian from the early Eocene (about 55 my) of Wyoming. The brain of *Tetonius* was advanced over the primitive condition (seen in most insectivorans) in having a more expanded neocortex (rhinal fissure not visible in dorsal view), with the expansion most apparent in occipital and temporal regions (fig. 3). The brain of *Tetonius* was primitive compared with those of modern prosimians in having a relatively small frontal lobe (here taken as the neocortex rostral to the sylvian fissure). The olfactory bulbs appear relatively small in *Tetonius* compared with the primitive condition, but that may reflect either expansion of the neocortex or reduction in size of olfactory bulbs, or both (see discussion below). Except for the faint impression of the sylvian fissure, the neocortex of *Tetonius* was unconvoluted. That lack of sulci should not be considered a primitive feature relative to later primates, since small modern primate brains show a similar condition.

Endocasts are known for two other early omomyoid prosimians: *Necrolemur*, from the late Eocene of Europe (about 40 to 45 my), and *Rooneyia*, from the early Oligocene (about 35 my) of Texas. The endocast of *Necrolemur* (fig. 4) was larger than that of *Tetonius* but otherwise apparently similar in proportions and preserved morphology. The *Rooneyia* endocast (fig. 4) suggests a brain more advanced than that of the older omomyoids in having a relatively larger frontal lobe and relatively smaller olfactory bulbs. However, the frontal lobes appear to have been

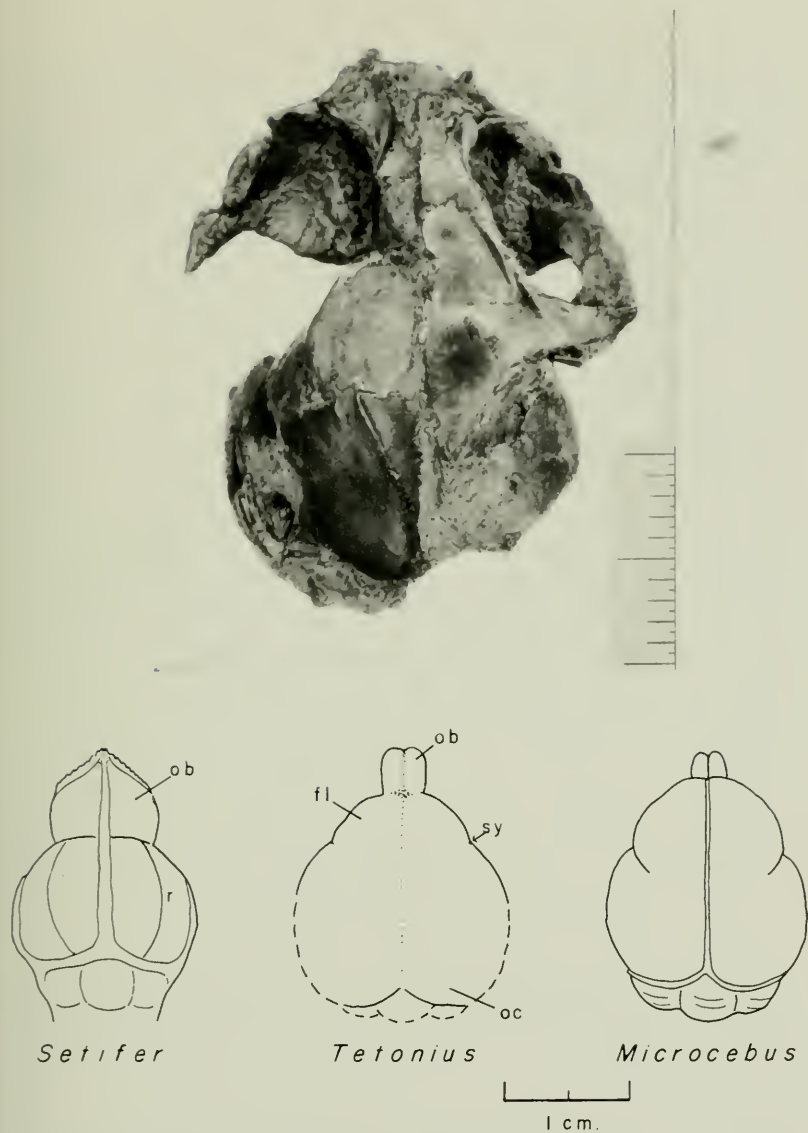


FIG. 3. Top, skull of *Tetonius homunculus*, showing natural endocranium. Scale on right is 1 cm. long. Bottom, restoration of *Tetonius* endocranium, compared with endocrania of a modern insectivoran, *Setifer setosus*, and a modern prosimian, *Microcebus murinus*. Abbreviations: fl, frontal lobe; ob, olfactory bulb; oc, occipital lobe; r, rhinal fissure (=lateral boundary of neocortex); sy, sylvian sulcus. All three drawn to same scale (from Radinsky, 1975).

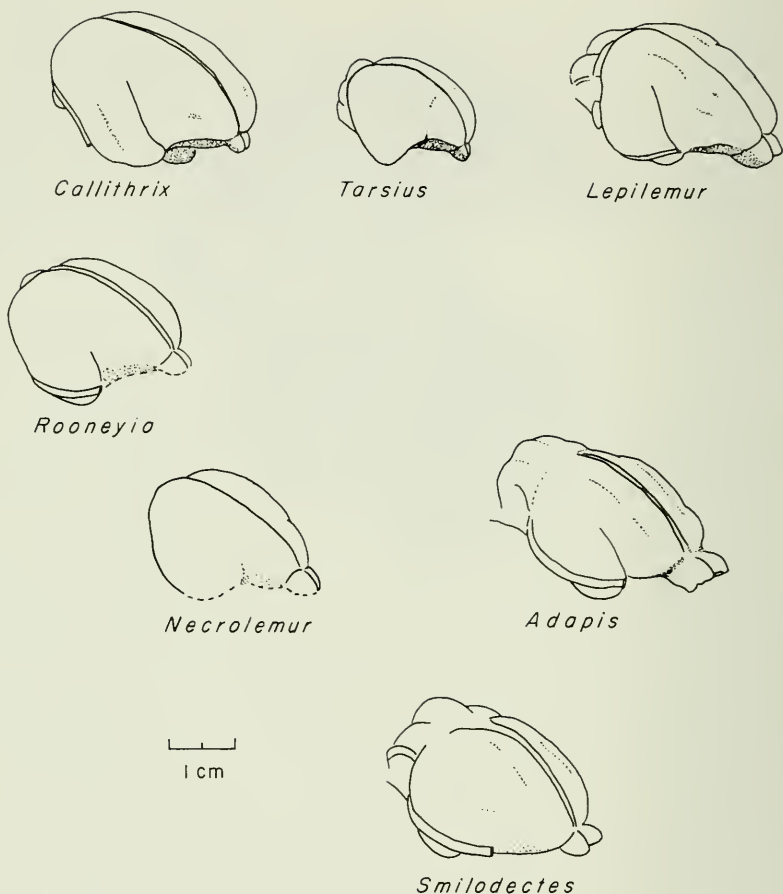


FIG. 4. Fossil prosimian endocasts compared with those of modern prosimians (*Tarsius* and *Lepilemur*) and a modern anthropoid (*Callithrix*). See text for discussion, and Radinsky (1970), for dorsal and lateral views of the fossil endocasts. All drawn to same scale.

relatively smaller in *Rooneyia* than in modern prosimians, and a modern prosimian brain the size of that of *Rooneyia* would have other sulci in addition to the sylvian fissure.

The other main branch of Eocene prosimians, the adapoids, is represented by endocasts of three genera: the closely related *Smilodectes* and *Notharctus*, from the middle Eocene (about 48

my) of Wyoming, and *Adapis*, from the late Eocene (about 40 to 45 my) of Europe. The brain of *Smilodectes* (fig. 4) lacked a sylvian fissure, and the cerebrum did not overlap the cerebellum. However, there was a longitudinally oriented neocortical sulcus that paralleled the dorsal midline, and, in one of the two known endocasts, a rostromedially oriented sulcus situated more laterally. The cerebrum of *Smilodectes* was relatively short, broad and shallow compared with that of the omomyoids, and the olfactory bulbs appear to have been relatively smaller than in *Tetonius* and *Necrolemur*. One partial endocast of *Notharctus* suggests a brain similar to that of *Smilodectes*.

The brain of *Adapis* (fig. 4) was similar to that of *Smilodectes* and *Notharctus* in being relatively broad across the temporal region, and in having a longitudinal sulcus near the dorsal midline and a dorsally exposed cerebellum. However, *Adapis* was advanced over the middle Eocene genera in having a well-developed sylvian fissure and a more expanded frontal lobe. The frontal lobe appears to have been relatively smaller in *Adapis* than in modern prosimians (compare with *Lepilemur* in fig. 4).

Accurate estimates of relative brain size in the early prosimians just discussed are not possible because we have as yet no good estimates of body weight for these genera. In my early studies of fossil prosimian endocasts (e.g., Radinsky, 1970), I estimated relative brain size using foramen magnum area as a substitute for body weight. However, partial correlation analysis shows that while foramen magnum area is a reasonable estimator of body weight in some groups of mammals, it is not a good estimator of body weight for relative brain size comparisons in prosimians (Radinsky, unpublished data). Fleagle (1978) inferred body size of fossil primates from lower molar lengths, based on Kay's (1975) analysis of this relationship in modern primates. However, as Kay noted, molar size-body weight relationships in modern primates vary significantly between the major dietary types. Thus consideration of dietary specialization is necessary for estimating body weight from tooth size in primates. Jerison (1973) and I (1977) have estimated relative brain size in fossil prosimians with body weights estimated very approximately from skull size. My

estimates, which are lower than those of Jerison, place *Tetonius*, *Smilodectes*, and *Adapis* within the insectivoran range, below the modern prosimian range, and *Necrolemur* and *Rooneyia* within the lower half of the modern prosimian range. In view of the uncertainties involved in the body weight estimates, I would not place much significance on those relative brain size estimates.

INFERENCES

The early prosimian endocasts described above indicate that by the beginning of the Eocene the neocortex had expanded beyond the primitive condition still seen today in most insectivorans. In the omomyoids, neocortical expansion is most apparent in occipital and temporal regions, which suggests expansion of visual and possibly also auditory cortical areas. The skulls of *Tetonius*, *Necrolemur*, and *Rooneyia* (see Szalay, 1976) have relatively large orbits and large, ossified auditory bullae, compared with the primitive condition seen in most insectivorans. Thus, the peripheral anatomy supports inferences from the endocasts of increased importance of vision and auditory abilities. Since those specializations appeared 55 million years ago, at the base of the great Eocene omomyoid radiation, it is possible that they were among the adaptations responsible for that radiation.

In the adapoids, the occipital pole had not expanded back to overlap the cerebellum, as in the omomyoids, and neocortical expansion is most evident in the temporal region. Extrapolating from cortical maps of modern mammals, this also suggests visual and possibly auditory specialization. The skulls of *Smilodectes*, *Notharctus*, and *Adapis* have inflated, ossified auditory bullae, supporting the inference of auditory specialization over the primitive condition, but the orbits do not appear to be relatively large. Relatively smaller orbits than in omomyoids may be a reflection of the larger size of the adapoids, since eyes scale with negative allometry (i.e., are relatively smaller in larger forms), and without better comparative series, it is not obvious if orbits are enlarged over the primitive condition in the adapoids.

The olfactory bulbs appear relatively small (compared to brain size) in the early prosimians, and in previous papers (Radinsky, 1970, 1975) I inferred from that condition reduction in importance of olfaction. However, relative size of olfactory bulbs can be deceptive, since expansion of neocortex with no reduction in size of olfactory bulbs can give the appearance of reduced olfactory bulbs (as noted by Martin, 1973, p. 327). The analysis of olfactory bulb size compared with body weight in modern insectivorans and primates (Stephan and Andy, 1969) reveals several species of modern prosimians with olfactory bulbs that appear small relative to the rest of the brain but which fall within the insectivoran range when compared with body weight. If the relative brain size estimate for *Tetonius* is correct, and it fell within the insectivoran (=primitive) range, then its small olfactory bulbs (relative to brain size) would indeed indicate reduction of olfactory bulb size from the insectivoran condition. However, until we have better body weight estimates for the early prosimians, we have no good basis for inferences on the relative importance of olfaction.

There appears to be an increase in relative frontal lobe size (here taken as the cortex rostral to the sylvian fissure relative to the rest of the brain), in *Rooneyia* compared with the earlier omomyoids, and in *Adapis* compared with *Smilodectes*. However, even in *Rooneyia* and *Adapis*, the frontal lobe appears smaller compared with the rest of the brain than is the condition in modern prosimians (excluding *Tarsius*). The frontal lobe (as here defined) contains the primary somatic sensory (tactile) and motor areas, as well as "association" cortex, and I see no way to infer significance of changes in its relative size.

The early prosimians discussed above evolved in the second adaptive radiation of primates. The earliest primates appeared around 70 million years ago, and underwent a first evolutionary radiation between about 65 to 55 million years ago (see fig. 2). An obvious question is whether the brain specializations noted for the Eocene prosimians (expanded neocortex, apparent expansion of visual and possibly also auditory areas, possible reduction in size of olfactory bulbs) also characterized their Paleocene prede-

cessors. Unfortunately, there is almost no direct evidence of the brain in the Paleocene primates (see discussion in Radinsky, 1977). The most significant information comes from the analysis by Kay and Cartmill (1977) of a partial skull of *Palaechthon*, a middle Paleocene (60 my) paromomyid primate. Relatively small orbits, a large olfactory fossa, and a large infraorbital foramen suggest the primitive insectivoran condition of emphasis on olfaction and tactile vibrissae (blood and nerve supply *via* the infraorbital foramen), and relative unimportance of vision in this 60-million-year-old primate. Thus it appears that the emphasis on vision that characterizes later primates was not involved in the origin of primates but rather evolved in connection with their second evolutionary radiation at the beginning of the Eocene.

LATER PROSIMIAN ENDOCASTS

The fossil record of later prosimian endocasts is poor, making it difficult to pinpoint when modern proportions and relative size of brain were attained. An endocast from the Miocene of East Africa, (probably 15 to 20 million years old), referred to the lorisoid *Komba*, is the only other Tertiary prosimian endocast known. It reveals that modern frontal lobe size and modern sulcal pattern were attained by that time (Radinsky, 1970). The only other fossil prosimian endocasts known are from several large to gigantic extinct Malagasy lemuroids from the latest Pleistocene or subrecent. While they shed no light on the evolution of modern prosimian brains, they are of interest for extending our knowledge of how allometry can affect gross brain morphology.

The long-faced giant lemuroids, like *Palaeopropithecus* and *Megaladapis*, show two unusual features of external brain morphology: the olfactory bulbs are located on stalks (the olfactory peduncles), rostral to the rest of the brain, and the sylvian fissure appears to be open (fig. 5). The pedunculate olfactory bulbs are the expected result of extremely large body size, an extension of the trend seen in modern prosimians where olfactory bulbs are more tucked under the frontal lobes in smaller species and extend

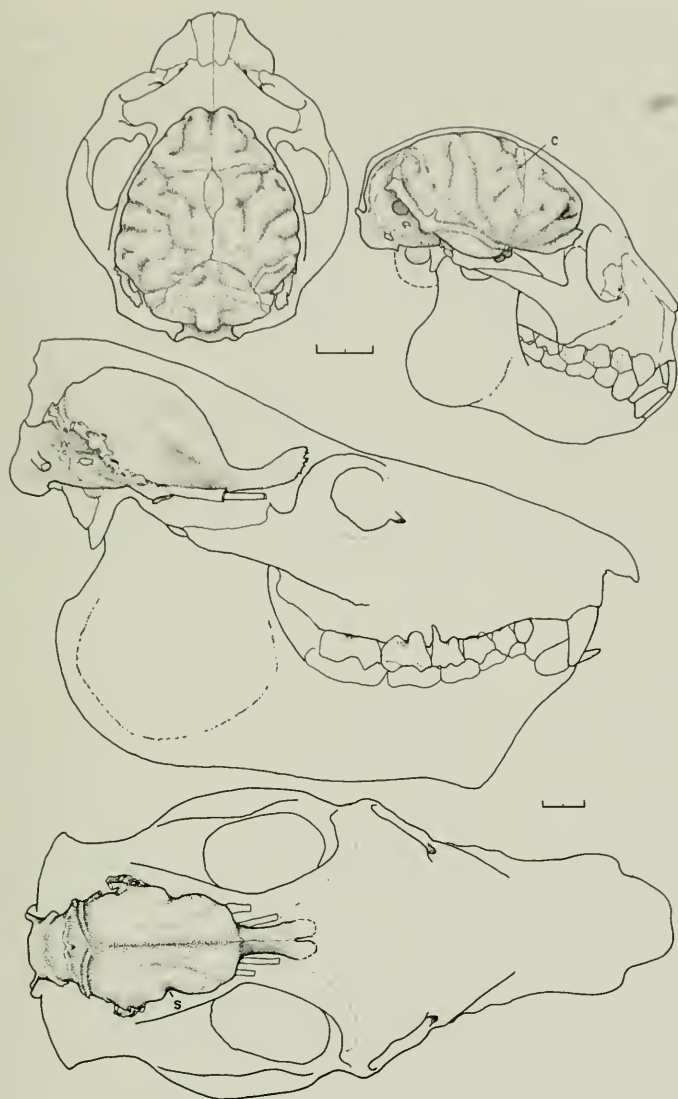


FIG. 5. Endocasts and skulls of short and long-faced extinct giant lemuroids, to show differences in brain shape. Above, *Archaeolemur majori* (c = central sulcus); below, *Megaladapis edwardsi* (s = open sylvian sulcus). See text for discussion. Scales = 2 cm. (from Radinsky, 1970).

out more rostrally in their larger relatives (cf. figures in Radinsky, 1968). The main reason for this trend is the negative allometry of brains (i.e., brains are relatively smaller in larger species), which results in the brain occupying less of the space between face and occipital condyles in large forms. The olfactory bulbs must remain immediately behind the cribriform plate, which is at the back of the facial portion of the skull, and therefore they come to lie rostral to the frontal pole of the cerebrum. The open sylvian fissure may reflect the relatively small size of the brain compared with the skull and the lack of large orbits impinging on the brain rostrally. The only modern primate in which the orbits do not impinge on the frontal lobes is *Daubentonia*, and it also has an open sylvian fissure (Radinsky, 1968). Extrapolating from trunk length/body weight relationships in modern prosimians, Jungers (1978) estimated body weights of *Megaladapis grandidieri* and *M. edwardsi* to be 40 and 52 kg., respectively, with endocranial volumes of 85 and 138 cc., that yields relative brain sizes within the lower quarter of the modern prosimian range.

The short-faced giant lemuroids, like *Archaeolemur* and *Hadropithecus*, had relatively shorter and wider brains than did their long-faced contemporaries, with the olfactory bulbs tucked up against the front of relatively voluminous frontal lobes (fig. 5). The sulcal pattern differs from that of their small modern relatives (indriids) in being more wavy, and with more secondary sulci. The relatively globose shape is not what one would predict from simple allometric extrapolation from modern indriid brain shape. Rather, it suggests increased relative brain size in the extinct species over what exists in the modern indriids, with the more spherical shape reflecting having a larger brain relative to skull size (cf. modern anthropoids vs. similar-sized modern prosimians). The more wavy sulcal pattern, with more secondary sulci, in the giant extinct forms is expected, and conforms to trends seen in modern primates and ungulates, where larger forms have a more folded neocortex than their smaller relatives. This presumably reflects the fact that the neocortex increases in volume approximately isometrically with the rest of the brain, but is

organized as a thin sheet, and therefore must fold to be accommodated on the relatively decreasing amount of surface area/volume of the rest of the brain as brain size increases (Clark, 1947; Radinsky, 1975).

EARLY ANTHROPOID ENDOCASTS

The oldest known anthropoid endocasts are from the late Oligocene (about 27 my) of the Fayum region, Egypt. Incomplete endocasts of *Aegyptopithecus*, an early ape and a suitable ancestor for later apes and humans, reveal a lunate sulcus located more rostrally than in modern prosimians, and three additional transverse sulci, the most rostral of which is probably the central sulcus (fig. 6). The dorsal imprint of the olfactory bulbs suggest that they were relatively small. The brain appears to have been

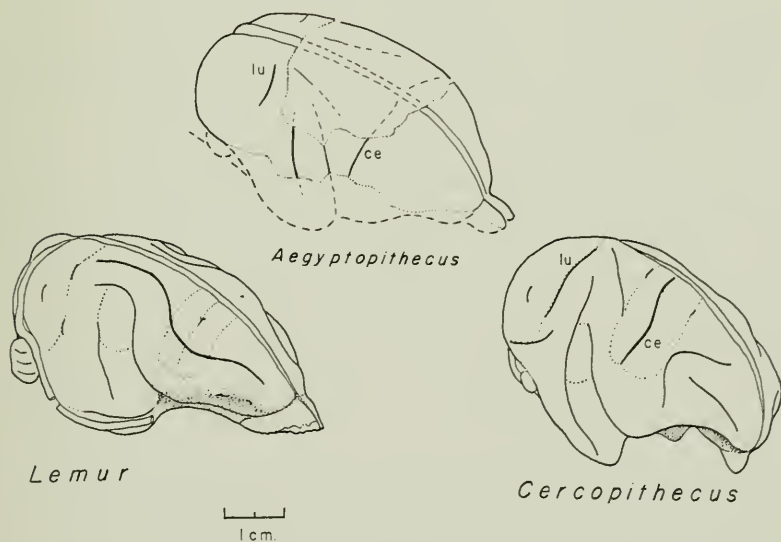


FIG. 6. Restoration of endocast of *Aegyptopithecus zeuxis*, compared with *Lemur variegatus* and *Cercopithecus talapoin* endocasts. Abbreviations: ce, central sulcus; lu, lunate sulcus. Dotted lines on modern endocasts delimit major functional areas (see fig. 1). All drawn to same scale.

relatively low and flat compared with the more spherical brains of most modern anthropoids, and the frontal lobe appears to have been relatively small.

The lunate sulcus bounds primary visual cortex in modern primates, and its relatively rostral position in *Aegyptopithecus* suggests expansion of that cortical area over the condition seen in most prosimians. The orbits of *Aegyptopithecus* do not appear to be relatively large, but comparative analysis, taking into account the affects of allometry, would be necessary to determine if they were larger than one would expect in a prosimian skull of that size.

A central sulcus is present in modern anthropoids but is absent in most prosimians (pottos are the main exception). It separates primary somatic sensory from primary motor cortex, and the significance of its presence vs. absence is not obvious. The apparently relatively small olfactory bulbs may be deceptive (if the rest of the brain has enlarged). If the brain is not relatively larger in *Aegyptopithecus* than in modern prosimians (see discussion below), then it is likely that the olfactory bulbs were reduced in size compared with what is seen in modern prosimians and in insectivorans.

Expanded visual cortex, development of a central sulcus, and possible reduction in size of olfactory bulbs are features in which the brain of *Aegyptopithecus* was advanced over the condition seen in most prosimians. A primitive feature of the brain of *Aegyptopithecus* was the relatively small frontal lobe (measured either from the sylvian fissure or the central sulcus, and compared with the rest of the brain), which lacks sulci (at least the sulcus rectus) that would be seen on frontal lobes of modern anthropoid brains of that size. The relatively low and flat brain shape is like that of large modern prosimians, and unlike the more spherical brain shape of most anthropoids. That difference probably is a reflection of brain size compared with skull size. Relatively large brains are more spherical in shape, presumably a packaging phenomenon as seen in miniature vs. large dogs (Radinsky, 1973a), small monkeys vs. comparably sized prosimians (Radinsky, 1975), small vs. large prosimians (allometric

effect) (Radinsky, 1968). If that interpretation is correct, it suggests that *Aegyptopithecus* had a relatively small brain compared to that of modern anthropoids (*contra* Radinsky, 1973b, 1974, based on foramen magnum comparisons). The only modern anthropoid with a brain shape like that of *Aegyptopithecus* is *Alouatta*, the howler monkey, which has the lowest relative brain size of any living anthropoid. From molar tooth size, Gingerich (1977) estimated body weight of *Aegyptopithecus* to be between 4.5 and 7.5 kg. The restored endocast suggests a brain volume of 27 to 32 cc., which results in a relative brain size falling below the modern anthropoid range, and within the lower half of the modern prosimian range.

The only other Fayum primate for which endocranial anatomy is known is *Apidium*, also about 27 my, and possibly close to the ancestry of Old World monkeys. Unfortunately, only the frontal lobe and olfactory fossa are preserved (see Radinsky, 1974), and they provide no significant information.

The oldest New World record of anthropoid brains is an endocast of *Dolichocebus*, a late Oligocene (25-30 my) form from Argentina, and an approximate contemporary of *Aegyptopithecus* and *Apidium* (fig. 7). The apparent lack of sulci other than the sylvian fissure may be an artifact of poor preservation. The significant feature revealed by the *Dolichocebus* endocast is that the occipital lobe was expanded beyond the condition seen in modern prosimians, and similar to the condition seen in modern anthropoids (compare lateral profiles in fig. 7). This suggests expansion of visual cortex to the modern anthropoid condition in ceboids as well as in hominoids back between 25 to 30 million years ago, not long after their first appearance in the fossil record.

Returning to the Old World, an isolated primate frontal bone from the early Miocene of Napak, Uganda (approximately 19 my) has yielded an impression of a frontal lobe with a sulcus rectus and a superior precentral sulcus (fig. 8). Judging from its size and morphology, it is most likely that the frontal bone is from the tiny ape *Micropithecus clarki* (Fleagle and Simons, 1978). It indicates considerable expansion of the frontal lobe over the

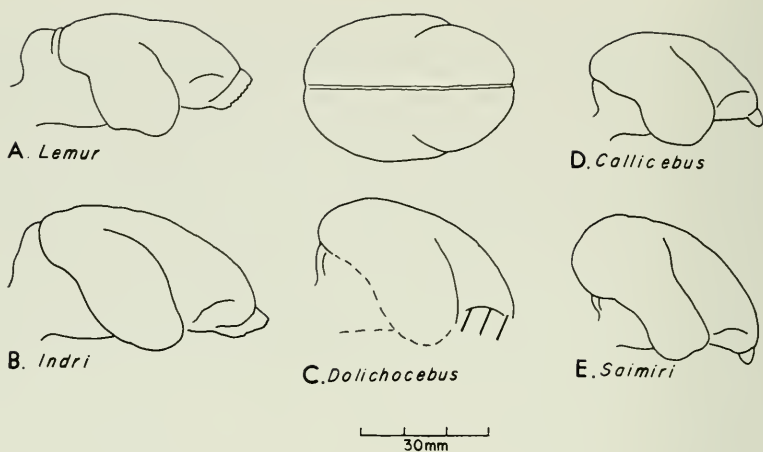


FIG. 7. Endocast of *Dolichocebus gaimanensis*, in dorsal and lateral views, compared with lateral views of endocasts of similar sized modern prosimians (left) and anthropoids (right), to show relative size of occipital lobe. Only the sylvian sulcus is indicated. All drawn to same scale (from Radinsky, 1974).

condition that existed 8 million years earlier in the larger ape *Aegyptopithecus* (cf. fig. 6). In fact, owing to the allometry of neocortical folding, one would not expect to see any more folding in the frontal lobe of a modern ape the size of *Micropithecus*. The frontal lobe of a modern cercopithecoid monkey the size of *Micropithecus* would have an arcuate sulcus caudal to the sulcus rectus (cf. *Cercopithecus*, fig. 8).

A partial endocast is known for another ape of approximately the same age as *Micropithecus*, but considerably larger in size: *Dryopithecus* (*Proconsul*) *africanus*, from 18-million-year-old (early Miocene) deposits in Kenya (fig. 9). The imprint of most of one cerebral hemisphere is preserved, and it reveals a sulcal pattern similar to that of the Napak specimen, with a superior precentral sulcus and a sulcus rectus (here with a short secondary spur) on the frontal lobe. The *Dryopithecus* sulcal pattern is similar to that seen in modern gibbons, except for the lack of a frontal lobe sulcus medial to the sulcus rectus. Since *D. africanus* was larger than a modern gibbon, that indicates less expansion of the frontal lobe in the Miocene form. The sulcal pattern of

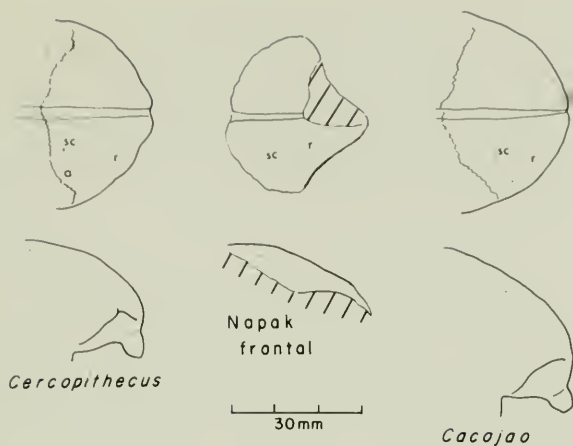


FIG. 8. Endocast from the Napak frontal, in dorsal and lateral views, compared with modern cercopithecoid (left) and ceboid (right) endocasts. The jagged line on the modern endocasts indicates the position of the frontoparietal suture. Abbreviations: a, arcuate sulcus; r, sulcus rectus; sc, superior precentral sulcus. All drawn to same scale (from Radinsky, 1974).

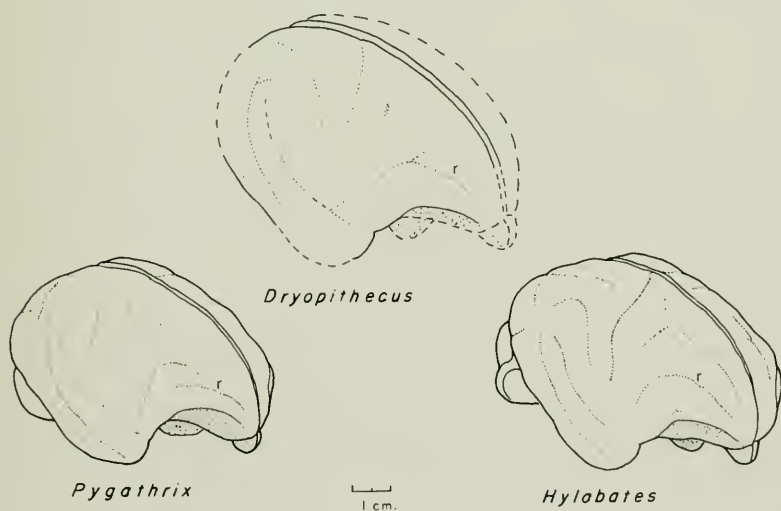


FIG. 9. Restoration of endocast of *Dryopithecus* (*Proconsul*) *africanus*, compared with endocasts of a modern cercopithecoid (left) and a modern hominoid (right). Abbreviation: r, sulcus rectus. All drawn to same scale.

Dryopithecus differs from that of modern Old World monkeys in lacking the arcuate sulcus. In 1974 I estimated the endocranial volume of *Dryopithecus africanus* at 150 cc. However, after reconsidering the crushed and incomplete nature of the endocast, I now believe that no reasonably accurate estimate of endocranial volume can be made from the specimen.

LATER ANTHROPOID ENDOCASTS

After *Dryopithecus*, only cercopithecids (Old World monkeys) and hominids are represented in the fossil record of anthropoid brain evolution. Although cercopithecids appear in the fossil record about 19 my, the oldest known endocast of this group is only 9 my, from the colobine *Mesopithecus*, from Pikermi, Greece. The *Mesopithecus* endocast (fig. 10) preserves the imprint of most of the cerebrum, and reveals a sulcal pattern indistinguishable from those seen on modern colobine endocasts. (Note in particular the arcuate-rectus sulcal complex, and compare with the condition seen in *Dryopithecus*). Among modern cercopithecids, brains of cercopithecines appear to be more advanced than those of colobines in several features (Falk, 1978), and it would be interesting to know when the cercopithecine condition was attained. Unfortunately, the oldest cercopithecine endocast is only 2 my. It is from *Paradolichopithecus arvernensis*, from the Villafranchian early Pleistocene of France, and as expected for such a late specimen, it shows in preserved portions the modern cercopithecine condition (Radinsky, 1974).

The fossil record of hominid endocasts consists of several specimens of small and large *Australopithecus* species (between 1 to 3 my), and of extinct *Homo* species. Unfortunately, they preserve little or no impressions of the cerebral convolutions, and we are left with information primarily on size and gross shape. Holloway (1975, 1976) concluded that *Australopithecus* endocasts (fig. 11) resemble those of modern humans and differ from those of chimps and gorillas in having greater relative height, more voluminous temporal lobes, a more horizontal orbital surface of

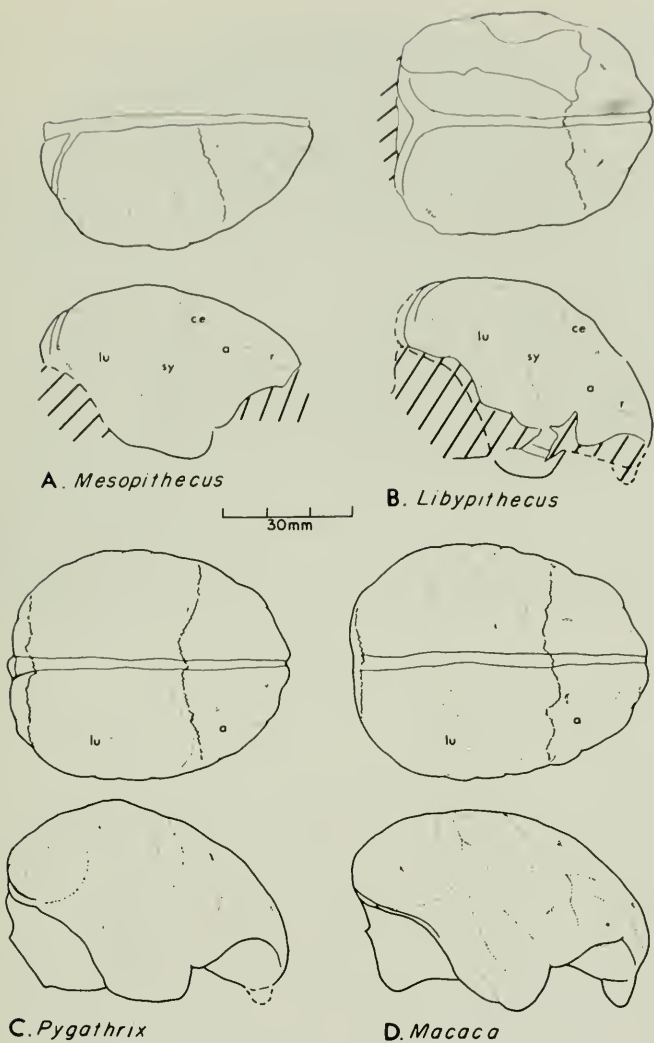


FIG. 10. Endocasts of extinct (above) and modern (below) Old World monkeys, in dorsal and lateral views. A, *Mesopithecus pentelici*; B, *Libypithecus markgrafi*; C, *Pygathrix nemaeus*, a modern colobine; D, *Macaca mulatta*, a modern cercopithecine. Abbreviations: a, arcuate sulcus; ce, central sulcus; lu, lunate sulcus; r, sulcus rectus; sy, sylvian sulcus. All drawn to same scale (from Radinsky 1974).



FIG. 11. Right lateral view of the Taung infant endocranium and face. Courtesy of Ralph L. Holloway.

the frontal lobe, and an apparently more caudally located lunate sulcus. Relative brain size in *Australopithecus* is difficult to estimate, owing to insufficient evidence of body weight. Endocranial volumes of *A. robustus* and *A. africanus* average about 530 cc. and 440 cc., respectively (Holloway, 1975), and body weight estimates generally average around 40 to 50 kg. for the larger species and 30 to 35 kg. for the smaller (e.g., Pilbeam and Gould, 1974; McHenry, 1975). Those data suggest that relative brain size in *Australopithecus* was above the observed range of modern apes and monkeys, but considerably below that of modern humans.

Holloway (1975, 1976) has hypothesized that the resemblances between endocranial casts of *Australopithecus* and *Homo*, and in particular the inferred relatively caudal position of the lunate sulcus, indicate cortical reorganization to a human pattern in *Aus-*

tralopithecus. However, the caudal displacement of the lunate sulcus, presumed to reflect expansion of the parietal association cortex, is suggested only by blurred gyral impressions on one specimen (the Taungs endocast). From that evidence, I see a relatively caudal position of the lunate sulcus as possible but not necessarily probable (it may have been more rostrally located). The differences in shape of *Australopithecus* vs. chimp and gorilla endocasts may be a packaging phenomenon, reflecting the greater relative brain size of *Australopithecus*. In any event, even if new material confirms the suggestion of a caudally displaced lunate sulcus in *Australopithecus*, I do not see that feature, plus the shape differences, as sufficient evidence for the conclusion that the brain of *Australopithecus* was reorganized to a human pattern, or was significantly more human-like than ape-like in terms of functional capabilities. The only concrete evidence we have of significant divergence from the modern anthropoid brain condition in *Australopithecus* is the increased relative brain size, and in that feature *Australopithecus* is about one-half of what one would expect in a modern human brain.

Endocasts of extinct species of *Homo* have been analyzed primarily with respect to gross size (e.g., Lestrel, 1975), although attempts have been made to define and infer significance of apparent changes in size and shape of various parts of the endocast (e.g., LeMay, 1976; Kochetkova, 1978; Holloway, in prep.). Owing to the lack of impressions of cerebral convolutions on fossil hominid endocasts, I see brain size as the only data we can be sure of. Endocasts of *Homo erectus*, from between 0.5 to 1.0 my, average about 930 cc. in volume (Holloway, 1975), which is about 70 percent the size of modern human brains. Unfortunately, lack of information on body weights precludes refined analysis of changes in relative brain size.

EVOLUTIONARY TRENDS

Quantitative studies show that the brains of modern primates differ from those of insectivorans (representative of the primitive

placental condition) in being relatively larger compared with body size, and in having relatively more neocortex (beyond what one would expect from the increased brain size), an expanded visual system, and a reduced olfactory system (Stephan, 1969; Stephan, Bauchot and Andy, 1970). Brains of modern anthropoids differ from those of modern prosimians in being more derived (i.e., further removed from the primitive condition) in those features, and also in having the primary motor and somatic sensory cortices divided by a transverse central sulcus instead of having head and postcranial body representations in those areas separated by a longitudinal coronal sulcus (see fig. 1). There may be major differences indicative of evolutionary trends in other systems, such as auditory, somatic sensory, or motor, and we await the quantitative comparative studies needed to investigate those possibilities.

The fossil record of primate endocasts suggests that expansion of neocortex in general, expansion of visual cortex, and possibly also reduction of olfactory bulbs had begun by 55 million years ago, at the beginning of the second evolutionary radiation of primates. Endocasts of some of the oldest known anthropoids suggest that by 25 to 30 million years ago, expansion of visual cortex and reduction in olfactory bulb size had progressed further, and was within the modern anthropoid range. Further, the *Aegyptopithecus* endocast reveals that the central sulcus had appeared by that time, at least in Old World anthropoids. In both anthropoids and prosimians, expansion of frontal lobes lagged behind that of the rest of the brain.

Reliable estimates of relative brain size are not available for most fossil primate endocasts. It is likely that in the early (55 to 35 million years old) prosimians, relative brain size was below the modern prosimian average, and in some of the early forms (*Tetionius*, *Smilodectes*, *Adapis*), may have fallen below the range of modern prosimians. It also is likely that relative brain size in *Aegyptopithecus*, one of the oldest known anthropoids, fell below the range of modern anthropoids, and was within the lower half of the modern prosimian range. We do not know when modern relative brain sizes were attained by prosimians and anthropoids,

but endocasts that are modern in general appearance are known for both groups by about 18 million years ago (*Komba* and *Dryopithecus*).

Brains of modern humans average about 3 to 3.5 times as large as one would expect in a modern anthropoid of our body size, and many of the unusual features of our brain (extraordinarily expanded and highly folded neocortex, large neocortical association areas, large cerebellum) may be results of our unusually large brain [Radinsky, 1975]. The fossil record of hominid endocasts suggests that the increase in relative brain size above the normal anthropoid range had begun by 2 to 3 million years ago (seen in *Australopithecus*), and that the modern condition was attained only within the past half-million years (after *Homo erectus*).

OUTSTANDING QUESTIONS

Some of the trends seen in the fossil record of primate brain evolution can be interpreted functionally, at least in a very general way. Expansion of visual cortex and reduction in size of olfactory bulbs suggests increased importance of vision and decreased importance of olfaction in the way of life of the animals under consideration. However, what that means more specifically cannot be inferred at this time. We need more information of two kinds: experimental evidence of the functional significance of major differences in size of visual and olfactory systems, and more extensive behavioral observations of species in the wild, comparing those with relatively small vs. relatively large visual and olfactory systems.

Other trends in primate brain evolution cannot be interpreted at this time, even in a general way. These include development of a central sulcus in anthropoids (and a few prosimians), expansion of frontal lobes, and increase in relative brain size. Insights into the first two might be obtained from comparative quantitative analyses (does frontal lobe size scale allometrically? are the primary motor and somatic sensory strips broader [rostrocaudally]

in primates with a central sulcus?). The last, increase in relative brain size, is an evolutionary trend of particular interest, for it occurred in many other groups of mammals (see e.g., Jerison, 1973; Radinsky, 1978), and was carried to a unique extreme relatively recently in humans. It is commonly believed that relative brain size is correlated with intelligence, and that intelligence has important survival value. However, there is surprisingly little scientific evidence demonstrating a relationship between brain size and intelligence. It is difficult to devise experiments that compare intelligence in different species, with brain size isolated as the critical variable, and it is not clear how abilities tested in the lab relate to abilities used in the wild. Further, and related to the last point, I know of no evidence that shows a relationship between intelligence, however one defines it, and fitness (increased reproductive probability). Elucidation of the factors responsible for the widespread evolutionary trend of increase in relative brain size in mammals, and for the extreme to which that trend was carried in humans, remains a fascinating unsolved problem.

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