14 · Cranial evidence of the evolution of intelligence in fossil apes

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INTRODUCTION

Fossil endocasts, natural or artificial casts of the inside of a cranial vault, provide the most direct evidence of the evolution of the brain. Among fossil hominoids, the vast majority of endocasts come from Plio-Pleistocene hominids, and these have been described in detail, (Conroy, Vannier & Tobias 1990; Dart 1925; Falk 1980a,b, 1983a,b, 1987, 1990; Falk & Conroy 1983; Holloway 1974a, 1982, 1983a, 1984, 1995; Holloway & De la Coste-Lareymondie 1982; Martin 1983, 1990; Martin & Harvey 1985; Schepers 1946, 1950; Tobias 1967, 1971a,b, 1975, 1978, 1983, 1991, 1995). Fossil great ape endocasts are extremely rare and are thus far undescribed. Therefore, beyond extrapolation from an outgroup, little is known of the primitive condition from which modern great ape and human brains could have evolved.

Six specimens of the primitive Oligocene catarrhine *Aegyptopithecus zeuxis* from about 33–33.5 Ma are described (Radinsky 1973, 1974, 1977; Rasmussen 2002; Simons 1993). Among hominoids, only four specimens are sufficiently complete to estimate brain size: one for *Proconsul nyanzae*, an early Miocene (*c.* 18 Ma) primitive or stem[1] hominoid that predates the emergence of the great ape and human clade, and three for the great apes *Dryopithecus brancoi* and *Oreopithecus bambolii* from between about 10 to 6 Ma (Begun 2002; Falk 1983a; Harrison 1989; Kordos 1990; Kordos & Begun 1997, 1998, 2001a; Walker *et al.* 1983).

The only fossil hominoid for which the endocast has yet been described is *Proconsul*. *Proconsul* is said to be more encephalized than monkeys of similar size, and close to living great apes (Walker *et al.* 1983), though this conclusion is revisited here. Most authorities have also concluded that the endocast of *Proconsul* is morphologically more primitive than that of any living hominoid (Falk 1983a; Radinsky 1974). Between the primitive endocast of the early catarrhine *Aegyptopithecus* and the stem hominoid *Proconsul* there is about a 15 Ma gap.

There is another 8 Ma gap from *Proconsul* to the late Miocene great ape *Dryopithecus brancoi* (Kordos & Begun 1997, 2001a). *Oreopithecus* and *Sahelanthropus*, a newly described hominid from Chad, both between 6 and 7 Ma in age, fill the gap between *Dryopithecus* and the earliest australopithecine for which brain and body size data are available, *Australopithecus afarensis* (Brunet *et al.* 2002; Harrison & Rook 1997). *Oreopithecus* appears unique in brain size (see below) while *Sahelanthropus*, like *Dryopithecus*, appears to have a great-ape-sized brain relative to its body mass (see below and Brunet *et al.* 2002). *A. afarensis*, from 3.6–2.9 Ma, shows a level of encephalization comparable to or slightly above that seen in living great apes and *Dryopithecus* and clearly above that seen in *Proconsul*, *Oreopithecus*, and most other anthropoids (see below and Jerison 1973, 1975; Kappelman 1996; Martin 1983, 1990; Pilbeam & Gould 1974; White 2002). In this chapter we review the available fossil evidence and assess its relevance to a reconstruction of the evolution of the brain in great apes.

APE ANCESTORS

Aegyptopithecus is a propliopithecoid, a primitive catarrhine (Harrison 1987; Rasmussen 2002), and its endocasts are informative as a precursor of the brain in hominoids. *Aegyptopithecus* lived before the divergence of the Old World monkeys and apes, and is known primarily from Oligocene deposits in the Fayum depression of Egypt (Fleagle 1983; Fleagle *et al.* 1986; Fleagle & Kay 1983; Harrison 1987; Kappelman, Simons & Swisher 1992; Kay, Fleagle & Simons 1981; Rasmussen 2002; Simons 1965, 1968, 1987, 1993).

Table 14.1. *Body mass and endocranial volume estimates in some fossil catarrhines*

Body mass (kg)[1]	*Proconsul* RU-7290[2]	*D. brancoi* RUD 77	*D. brancoi* RUD 200	*Aegyptopithecus*[3]
Log BM = 4.718 (log OHT) − 2.56	13.5	31.0	22.7	
Log BM = 4.445 (log OHT) − 2.155	14.3	31.2	23.2	5.3–6.0
Log BM = 4.420 (log OHT) − 2.12	14.0	30.4	22.6	
Log BM = 5.22 (log OB) − 3.35	18.5	28.7	20.3	
Ln BM = 1.62 (ln M[1]S.A.) + 2.72	16.2	22.8	21.6	
Ln BM = 1.37 (ln M[2]S.A.) + 3.49	17.9	19.7	19.0	
Endocranial volume[2]				
EV = 2.5 (CL) + 55.3	167 cc (155–181)	330 cc (302–350)	305 cc (280–330)	27–33 cc

Notes:

Abbreviations: BM = body mass; OHT = orbital height; OB = orbital breadth; M[#]S.A. = molar surface area; EV = endocranial volume; CL = cranial length. Ranges of endocranial volume estimates are 95% confidence intervals except for *Aegyptopithecus*. Ranges of body mass estimates for *Dryopithecus* are 95% confidence intervals. For *Proconsul*, see text.

[1] Body mass formulae from Aiello and Wood (1994), Kappelman (1996), Gingerich, Smith & Rosenberg (1982)

[2] Endocranial volume estimates formulae from Walker *et al*. (1983). Body mass estimates from this study (see text).

[3] Body mass endocranial volume estimates for *Aegyptopithecus* from Simons (1993).

Radinsky originally interpreted the brain of *Aegyptopithecus* to be large compared with living prosimians, but later suggested that it is probably most similar in relative size to prosimians (Radinsky 1977; see also Jerison 1979 and Table 14.1). Simons (1993) estimated volumes of the most complete of the *Aegyptopithecus* endocasts at between about 27 and 33 cc and the body mass of *Aegyptopithecus* at between about 5300 to 6000 g, suggesting a very small brain size compared with living anthropoids. Radinsky (1973, 1974) stressed the more modern anthropoid-like qualities of the *Aegyptopithecus* endocast, including evidence of a larger visual cortex, reduced olfactory lobes, and a well-defined central sulcus between the primary somatic and motor cortices. He also listed a number of possibly primitive, more prosimian-like qualities, including smaller frontal lobes with fewer sulci and more rostral (anterior) olfactory lobes. He interpreted these primitive traits either as indications of the primitive nature of the brain of *Aegyptopithecus*, or due to allometric effects (Radinsky 1973, 1974). Radinsky noted that "primitive" aspects of the endocasts of *Aegyptopithecus* and *Alouatta*, the largest members of their respective clades, may be related to large body mass. Most recent analyses of *Aegyptopithecus*, however, have concluded that the primitive aspects of the endocranium are just that, primitive and prosimian-like (e.g., Simons 1993).

In summary, *Aegyptopithecus* was about as encephalized as many living prosimians and shares primitive characters with prosimians and derived characters with living anthropoids. However, in overall size, the brain of *Aegyptopithecus* was primitive anthropoid-like (see below). The exact behavioral implications of the brain of *Aegyptopithecus* are not clear. It is possible that increasing the amount of neurological tissue devoted to processing visual stimuli, decreasing that devoted to olfaction, and an emerging distinction between primary sensory and motor cortices reflect a greater dependence on vision over olfaction and more refined neurological control

over movement (Radinsky, 1973). These are conceivably precursors to more complex forms of cognitive processing that distinguish anthropoids from prosimians, and which are most elaborately developed in great apes and humans.

FOSSIL EARLY APES

The earliest direct evidence of hominoid brain evolution comes from the endocast of KNM RU-7290, a well-preserved skull of *Proconsul nyanzae*[1] from Rusinga Island, Kenya. Le Gros Clark & Leakey (1951) concluded that it had a relatively small frontal lobe and a simple, relatively primitive sulcal pattern. Radinsky (1974) concluded that it most closely resembles *Hylobates*. He noted that the only apparently primitive character of this endocast is the absence of a frontal sulcus, which is otherwise usually present in modern cercopithecoids and hominoids.

Falk (1983a) noted that the sulcal pattern of KNM RU-7290 (BMNH 32363)[1] is more complicated. She supported Radinsky's conclusion that the endocast is anthropoid-like, but did not see the hominoid affinities that Radinsky stressed. She noted that many of the sulci are also present in the brains of Old and New World Monkeys, suggesting that they are primitive for the anthropoids and not derived similarities shared with hominoids. However, the absence of sulci typical of apes in the *Proconsul* endocast is more ambiguous than, for example, the absence of skeletal attributes of the elbow joint or the face. Endocasts are trace fossils of brain surfaces. Even under the best circumstances, endocasts often do not reveal the sulci that are present on the surface of the cerebrum, due to the fact that the meninges, meningeal blood vessels, and cerebrospinal fluid intervene between the endocranial and brain surface. Sulci are notoriously difficult to identify on partial endocasts. The absence of specific sulci on an endocast is not especially strong evidence that they were not present on a cerebrum. In addition, at least one sulcus present on the *Proconsul* endocast is present only in great apes (Falk 1983a). The absence in hylobatids of various sulci present in *Proconsul*, great apes, and some cercopithecoids may simply reflect the absolutely small size of hylobatid brains, which is known to be correlated to sulcal complexity (Jerison 1973; MacLeod, Chapter 7, this volume). *Proconsul* endocast morphology represents a likely starting point for the evolution of all subsequent hominoid brains.

Radinsky (1974) estimated the volume of the *Proconsul* endocast at about 150 cc, but he later decided that the specimen was too damaged to estimate its volume accurately (Radinsky 1979). Falk (1983a) agreed with Radinsky's "ball park" estimate of the brain size being close to that of *Papio*. Walker *et al.* (1983) used a regression analysis to predict the brain size of KNM RU-7290 from a new reconstruction of the skull with additional conjoining fragments. They estimated the cranial capacity of this *Proconsul* individual to be 167 cc (95% CI=155–181). With this and an estimate of body mass, they calculated an encephalization quotient or EQ for *Proconsul*, which they characterized as larger than in monkeys of similar size. They suggest that this may be a great ape trait, but express uncertainty given the fact that all living great apes are much larger than this individual of *Proconsul*. Manser and Harrison (1999) estimated the cranial capacity of the same specimen at 130.3 cc based on foramen magnum size. Based on the overall size of the cranium and damage to the foramen magnum, we place more confidence in the estimates of Walker *et al.* (1983), which are used here.

Walker *et al.*'s (1983) estimate of body mass (11 kg) is based on a second individual, R114 or KNM RU-2036, a partial skeleton of a subadult *Proconsul* and the type specimen of *Proconsul heseloni* (Walker *et al.* 1993). Only small fragments are known of the cranium of KNM RU-2036. Comparable portions are smaller overall than in KNM RU-7290, and there are a number of morphological differences as well (Walker *et al.* 1993; Begun & Kordos pers. obs.). These specimens may not represent the same species of *Proconsul*, and even if they do, the evidence suggests that KNM RU-7290 represents a larger individual than KNM RU-2036. While KNM RU-2036 is about the skeletal size of an average adult male *Colobus polykomos*, KNM RU-7290 is larger than this monkey and *Hylobates symphalangus*, as well as larger than male *Macaca fuscata* and *Alouatta pigra* (11–13 kg) in almost all cranial measurements (Delson *et al.* 2000; Smith & Jungers 1997). It is closer to male *Semnopithecus entellus* and female *Papio anubis* and *Mandrillus sphinx* (Begun pers. obs.), which are all about 13–18 kg in mean body mass.

KNM RU-7290 preserves a complete dentition and orbits, which have been shown to have a close relationship to body mass (Aiello & Wood 1994; Conroy 1987; Dagasto & Terranova 1992; Gingerich 1979; Kappelman 1996). Following methods described by these authors we estimated the body mass of this

individual at between 13.5 and 18.5 kg (Table 14.1). At this body mass, the EQ of the species of *Proconsul* represented by KNM RU-7290 is within the range of values for similarly sized Old World monkeys. There is no strong evidence that *Proconsul* shares any degree of increased encephalization with living great apes. The significance of EQ measures of relative brain size is discussed in more detail below.

FOSSIL GREAT APES

Following Walker *et al.*'s lead, we focus in this section on the bases for estimating body size, brain size, and EQ in fossil great apes. Comparative evolutionary implications of these EQ estimates are discussed in the following section.

Dryopithecus

Two cranial specimens of *Dryopithecus* provide the earliest direct evidence of brain size and morphology in a fossil great ape. RUD 77 is a partial cranium from the late Miocene locality of Rudabánya attributable to *Dryopithecus brancoi* (Begun & Kordos 1993; Kordos & Begun 1997). It preserves much of the cranial vault of an adult female, which allows for a relatively confident estimate of cranial capacity, using techniques similar to those described above for *Proconsul* (Kordos & Begun 1997, 1998, 2001a; Walker *et al.* 1983). RUD 200 is a more recently discovered and more completely preserved cranium, which makes the estimate of cranial capacity in this specimen even more certain than in RUD 77 (Kordos & Begun 2001a). Both specimens of *Dryopithecus* preserve a few details of endocranial surface morphology and general features of relative cerebral lobe size.

Both endocasts of *Dryopithecus* preserve portions of the frontal and parietal lobes, but very little of the temporal and occipital lobes, and none of the cerebellum, olfactory lobes, or any structure of the ventral surface of the brain. The frontal lobes are preserved anteriorly and superiorly but not inferiorly. They are broader relative to length than in *Proconsul* and *Hylobates* but narrower rostrally compared with living great apes. The parietal lobes are also broad transversely compared with *Proconsul* and *Hylobates*. The endocast is asymmetric, with subtle right frontal and more pronounced left occipital petalia (for comparison, see MacLeod, Chapter 7, this volume).

The sulci of the frontal lobes are more discernable than on the parietal and occipital lobes. They are clearly more complex than in *Proconsul* or the typical pattern in *Hylobates*. The rectus sulcus is short and immediately superior to the superior orbital surface, and it is surrounded caudally by a clear arcuate sulcus, which does not occur in *Proconsul* or *Hylobates* (Falk 1983a). Between the arcuate and central sulci on both endocasts, two additional sulci are apparent, which probably correspond to the precentral and the superior frontal sulcus. Only hominids have such complexity to their lateral frontal endocasts, reinforcing the view that *Dryopithecus* shares brain morphology with living hominids.

We took three neurocranial measurements on *Dryopithecus* and a sample of great ape specimens of known cranial capacity to estimate brain size in the fossils. Based on these measurements we calculated least squares (LS) and reduced major axis (RMA) regressions, and used the resulting regression formulae (shown in Table 14.1) to estimate cranial capacity. The six formulae produce consistent results; one is reproduced in Table 14.1 and Figure 14.1. Our best estimates of brain size in these two specimens are 305 and 330 cc.

The mean percentage predictor errors (MPE) for all equations were well under 10%, which is quite low (Dagasto & Terranova 1992). The frequency with which predicted endocranial volumes were within 20% of the observed cranial capacities (% ± 20%) was over 99%. The MPE and % ± 20% analysis of these regressions suggest that the predictions are reasonable, despite relatively modest correlation coefficients.

A separate sample of four bonobo (*Pan paniscus*) crania of similar size to *Dryopithecus* was also used to assess the reliability of the predictions. For all these bonobos, the regression predicts a cranial capacity within 10% of the known values for each cranium. Finally, the predicted size of the endocranial volumes of RUD 77 and RUD 200 was compared to actual volumes of great ape endocasts of similar linear dimensions. The overall sizes of the endocasts are close to small endocasts of *Pan* and *Pongo*, in the range of 300 to 350 cc.

RUD 77 and RUD 200 have the orbits and dentition sufficiently well preserved to make reasonable estimates of body mass. Based on orbital dimensions, the estimates range from 28.7 to 31.2 kg for RUD 77 and 20.3 to 23.2 kg for RUD 200 (Table 14.1). These estimates are consistent with overall cranial and postcranial dimensions in extant catarrhines of known body mass. RUD 77 and RUD 200 are larger than monkeys in most
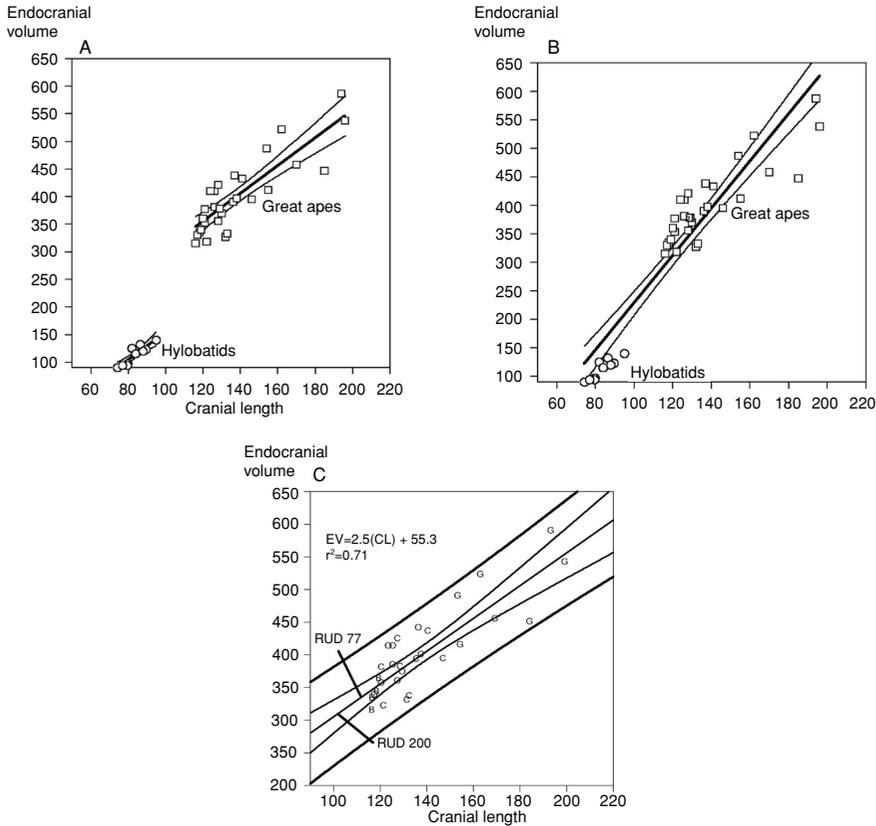
Figure 14.1. (A) Least squares regressions and 95% confidence intervals of endocranial volume against cranial length in hylobatids and great apes. Note the downward displacement of the hylobatid line, which has statistically the same slope but a different *y*-intercept from the great ape line. (B) Combining these data sets produces a regression with a tighter fit, but this is an artifact of the large size range and results in a slope that is not meaningful for either group. (C) Although the *Dryopithecus* specimens are slightly smaller than the smallest specimens of the comparative sample, the morphological similarities and close evolutionary relationship with these taxa (extant great apes) make this regression more informative for predicting brain mass in *Dryopithecus*. See text for discussion.

dimensions and smaller overall than the smallest great apes (*Pan troglodytes schweinfurthii* and *Pan paniscus*) (Smith & Jungers 1997). Female *Dryopithecus* postcrania are much smaller than their homologues in *Pan* and larger than in most monkeys (Begun 1992b, 1993, 1994; Jungers 1982; Kordos & Begun 2001b; Morbeck 1983). Most monkeys are smaller than 20 kg and great apes are larger than 27 kg (Smith & Jungers 1997).

Oreopithecus

The only other fossil ape for which an estimate of cranial capacity has been made directly from the cranial evidence is *Oreopithecus*. Straus (1963) and Straus and Schön (1960) estimated the cranial capacity of a very severely crushed adult male specimen of *Oreopithecus* to have been between about 276–529 cc, with a best guess estimate of about 400 cc, which they said compares favorably with australopithecines as well as great apes. This estimate is based on external dimensions of a reconstruction and is much too high. Harrison (1989) estimated cranial capacity from another individual of unknown sex with a well-preserved foramen magnum, using a regression of foramen magnum area on brain size in a sample of modern anthropoids. His estimate was 128 cc, with a range between 83 and 173 cc. Using an estimated species mean body mass of 22.5 kg, Harrison (1989) calculated that the relative brain size of *Oreopithecus* as quite low by modern anthropoid standards. A male *Oreopithecus* has a body mass estimated at about 30 kg (Jungers 1987) and females, which are thought

Table 14.2. *Brain mass, body mass and relative brain size in fossil (bold) and extant primates. Taxa are listed in increasing order of brain mass*

Taxon	Brain mass (g)	Body mass (kg)	Encephalization EQ
Callitrichids	9.5–17.6	0.35–0.67	1.43–1.92
Aegyptopithecus **female**	**29**	**6**	**0.78**
Cebids	24.8–118.4	0.63–8.89	1.38–4.79
Old World Monkeys[1]	41.1–119.4	1.38–21.32	1.05–2.76
Hylobatids	87.5–133	5.70–12.74	1.93–2.74
Gibbons	87.5–105	5.70–7.37	1.93–2.74
Oreopithecus **female**	**112**	**15**	**1.49**
Most papionins[2]	116–179	8.68–32	1.48–2.76
Siamang	133	12.74	2.03
Proconsul **female**	**146**	**15**	**1.94**
Papio	179–222	16–35	1.73–2.35
Pongo female	288	44.45	1.63
Dryopithecus **female**	**289**	**31**	**2.35**
Pan troglodytes female	325	43.90	2.17
Pan paniscus female	314	38	2.24
Pan paniscus male	334	61	1.73
Pongo male	395	90.72	1.91
Gorilla female	426	90.72	1.76
Pan troglodytes male	440	56.69	2.48
Gorilla male	570	172.37	1.53

Notes:

Data on most extant primates are from Jerison (1973). They are the largest brain and body mass data, taken from Bauchot and Stephan (1969) from the same individuals. These body masses should not be considered accurate species means, as provided more reliably by Smith and Jungers (1997). Values for fossil catarrhines are from Harrison (1989), Radinsky (1977), Walker *et al.* (1983) and this chapter. Values for cranial capacity were divided by 1.14 to convert brain volume into brain mass in grams (Hartwig-Scherer 1993; Kappleman 1996). EQ for fossil taxa and *Pan paniscus* were calculated using formulae from Jerison (1973) for comparability. It is noteworthy that data from Jungers and Susman (1984) and Tobias (1971b) are generally higher than those from Bauchot and Stephan (1969) that are reproduced in Jerison (1973).

[1] Includes only *Cercopithecus*, *Miopithecus*, *Macaca*, and *Semnopithecus*.

[2] Includes *Cercocebus*, *Lophocebus*, and *Mandrillus* and excludes *Papio*.

to have been about half the size of males, have an estimated mean body mass of about 15 kg (hence Harrison's 22.5 kg species mean). Using any of these body mass estimates, the low degree of encephalization in *Oreopithecus* found by Harrison is confirmed (see Table 14.2). Our examination of the specimen used by Straus and Schön supports Harrison's conclusions. The cranium appears large due to the presence of massive ectocranial crests, but the neurocranial cavity itself was clearly short and quite small transversely. If *Oreopithecus* is a great ape, which is likely based on the preponderance of fossil evidence (Begun 2002; Begun, Ward & Rose 1997; Harrison 1986; Harrison & Rook 1997; Hürzeler 1949, 1951, 1958, 1960; Straus 1961, 1963), then it represents a relatively unusual case of "de-encephalization," which is discussed briefly below. Nothing has been published to date on the morphology of the brain of *Oreopithecus*, for which no endocast is currently described.

Other fossil great apes

Kelley (1997, Chapter 15, this volume) carried out a detailed analysis of the pattern and timing of dental

maturation in *Sivapithecus parvada*, a fossil great ape from South Asia widely believed to be closely related to *Pongo* (Andrews 1992; Andrews & Cronin 1982; Andrews & Martin 1987; Begun & Güleç 1998; Begun *et al.* 1997; Kelley 2002; Kelley & Pilbeam 1986; McCollum & Ward 1997; Pilbeam 1982; Ward 1997b; Ward & Brown 1986; Ward & Kimbel 1983; Ward & Pilbeam 1983; but see Pilbeam 1997; Pilbeam & Young 2001). Kelley's analysis indicates that *Sivapithecus* matured dentally in a manner essentially identical to living great apes. He used a well-known correlation between the rate of dental maturation in primates, particularly the age at which the first molar M1 erupts, and brain size, to estimate an older-than-expected (i.e., hominoid-like) age of M1 emergence for *Proconsul* (Smith 1989, 1991). Applying the same logic to the finding of a great-ape-like age of M1 emergence for *Sivapithecus* suggests that this taxon had a brain size in the modern great ape range (Kelley, Chapter 15, this volume). Unfortunately, the neurocranium of *Sivapithecus* is not known, so this prediction cannot be tested directly at present.

A male and female cranium of the Chinese fossil great ape *Lufengpithecus lufengensis* are described in Kordos (1988), Schwartz (1984a, b, 1990), and Wu, Qinghua & Quingwu 1983. They are very badly crushed, but, as is the case with *Oreopithecus*, careful scrutiny can reveal some important anatomical details. It is clear from our examination of these specimens that the crania are very close in overall size to those of small- to medium-sized living great apes (female *Pongo* to male/female *Pan*) and that they lacked the ectocranial cresting of *Oreopithecus*. The neurocrania, though crushed to the thickness of a thick pancake, were large in relation to the face, and the brains were probably in the range of modern great apes. No numerical estimate of cranial capacity is possible, but the conclusion that *Lufengpithecus* probably had a great-ape-sized brain is consistent with its phylogenetic position as closely related to *Sivapithecus* and *Pongo* (Kordos 1988; Schwartz 1984a, b, 1990; Wu *et al.* 1983). As with *Sivapithecus*, the morphology of the brain of *Lufengpithecus* is not currently known.

RELATIVE BRAIN SIZE

Encephalization quotient

With body mass and cranial capacity estimates from the same individuals of *Dryopithecus* it is possible for the first time to quantify relative brain size in a fossil great ape. New data also allow for a proposed revision of the relative brain size calculation of *Proconsul*. There are many methods of normalizing brain size, most of which give equivalent results (Bauchot & Stephan 1969; Begun & Walker 1993; Hartwig-Scherer 1993; Harvey 1988; Jerison 1973, 1979; Kappelman 1996; Martin 1983, 1990; Martin & Harvey 1985; Pagel & Harvey 1988; Radinsky 1974, 1977, 1979, 1982; Tobias 1971a, 1975). The most widely used techniques employ regression analysis to compare predicted brain sizes at a given body mass with observed brain sizes in animals of known or estimated (in the case of fossils) body mass. Primates with brains that are larger than expected for mammals of the same body mass are considered "encephalized," which is generally the case for hominoids. The techniques basically vary in the assumptions made with regard to the expected relationship of brain mass to body mass and depend in large part on the animals included in the comparison. Here we calculate EQ, probably the most widely used brain size normalizing statistic, using the formula from Jerison (1973) to facilitate comparisons across the large number of primates included in his analysis and widely reproduced elsewhere. However, EQ is not without its problems (see below).

Estimates of EQ are shown in Table 14.2. With a revised estimate of the body mass of *Proconsul* (KNM RU-7290), a revised EQ is reported. The EQ estimate for *Dryopithecus* is based on the maximum body mass estimate and the larger of endocranial volume estimates, following the methods outlined by Jerison (1973). The EQ estimates for *Aegyptopithecus* are also based on maxima and for *Oreopithecus*, on the only available values.

The EQ of *Aegyptopithecus* is low by anthropoid standards, which is consistent with many previous assessments of encephalization in this taxon. In *Oreopithecus*, EQ is also quite low, toward the low end of the range of variation in monkeys and below all hominoid ranges. The revised EQ for *Proconsul* is not especially hominoid-like, which is consistent with the analysis of Falk (1983a) concerning endocranial morphology. The EQ estimate for *Dryopithecus* is among the highest values for living apes. However, the significance of these EQ values with regard to an understanding of intelligence in these taxa is not immediately clear. For example, *Gorilla* and male *Pongo* EQ values are equal to or lower than EQs for hylobatids and many monkeys, though most agree that they are cognitively superior to hylobatids and
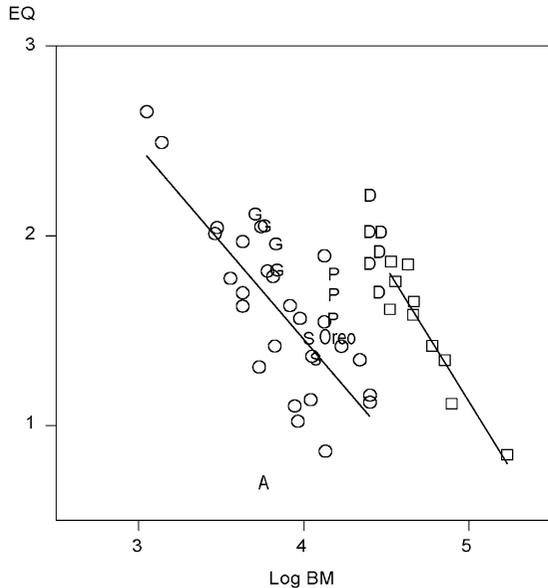
Figure 14.2. The relationship between EQ and body mass (BM). Open circles represent living cercopithecoids and open squares represent living great apes. G = gibbons, S = siamangs, A = *Aegyptopithecus*, P = *Proconsul*, Oreo = *Oreopithecus*, D = *Dryopithecus*. Multiple points for *Proconsul* and *Dryopithecus* represent different possible brain mass and body mass estimates. Note that *Dryopithecus* clusters with great apes while the other hominoids cluster with cercopithecoids. *Aegyptopithecus* has a much smaller EQ relative to body mass. Note also that the largest cercopithecoids that approach hominids in body mass have much lower EQ values. See text.

monkeys and certainly equivalent to other great apes of smaller body mass (*Pan* and female *Pongo*) (see other contributions in this volume).

The EQ allows for a comparison of brain size among animals of differing body sizes but retains a body size artifact. Jerison (1973) recognized this uncertainty and noted that the EQ is most useful in comparisons at higher taxonomic levels. Many statistical or sampling factors have been proposed to account for the residual effects of body mass on EQ (Harvey 1988; Martin 1983, 1990; Pagel & Harvey 1988). Other biological or behavioral causes of EQ diversity have also been suggested, which are indirectly related or even unrelated to intelligence (Barton & Dunbar 1997; Clutton-Brock & Harvey 1980; Gibson, Rumbaugh & Beran 2001; Harvey 1988; Jerison 1973; Kappelman 1996; Martin 1983, 1990; Milton 1988; Radinsky 1977). While reviewing these is beyond

the scope of this chapter, Figure 14.2 illustrates that EQ declines with increasing body mass at similar rates in Old World monkeys and great apes, but along displaced trajectories.

Despite the effects of body mass, a few facts about EQ diversity remain clear. Figure 14.2 shows that no non great ape of body mass close to that of any great ape approaches EQ values for great apes. Monkeys that over-lap in body mass with the smallest great apes, the largest papionins, have much lower EQ values than the smallest great apes, even though they are the largest-brained cercopithecoids. In Table 14.2, the papionins that have EQ values exceeding those of great apes are all at the low end of the range of variation in body mass in this group, much smaller than any great ape (Figure 14.2). Hylobatids follow the trend line for monkeys and have EQ values that are consistent with Old World monkeys of similar body mass. *Dryopithecus* follows the trend set by living non-*Homo* hominids, cluster-ing around living great apes with the smallest body masses. *Proconsul* is intermediate though somewhat more monkey/hylobatid-like than great-ape-like. *Oreo-pithecus* is more clearly cercopithecoid-like. *Aegypto-pithecus* is well below both trends, with a much lower EQ than other catarrhines of similar body mass.

In sum, although issues of body mass and analytical artifacts make EQ difficult to interpret, the analysis pre-sented here addresses some of the body mass issues and suggests that the EQ of *Dryopithecus* indicates a level of encephalization equivalent to that of living great apes. This level of encephalization in a fossil great ape that is both closely related to living great apes, and of similar body mass, is most probably a shared derived trait of the great ape clade.

Absolute brain size

Jerison (1973) noted that while EQ effectively mea-sures relative brain size and intelligence across broad taxonomic levels, a second measurement that quantifies the amount of brain mass beyond that determined exclu-sively by body mass was needed at finer taxonomic levels. His "theory of brain size" or "extra neurons" attempts to calculate the number of neurons required for normal metabolism and basic or "primitive" patterns of behav-ior at a given body mass in mammals, and the number of "extra neurons" represented by larger than expected brain masses. This idea is dependent on a number of

definitions and assumptions, most of which are highly debatable (Holloway, 1969; 1974a). However, Jerison's theory of brain size resembles current theories of intelligence that emphasize absolute size and is consistent with observations of intelligence differences among primates (Dunbar 1993; Gibson *et al.* 2001).

While Jerison's calculations do attempt to account for differences in body mass in assessing the significance of brain mass, too many uncertainties remain to be confident in the accuracy of his neuron counts (Holloway 1969; 1974a). Although his measurements of extra neurons (N_c) have recently been used in an analysis of brain mass and intelligence in primates (Gibson *et al.* 2001), we agree in part with Holloway that the precise numbers are controversial and so they are not reproduced here. However, in Table 14.2 we list values for brain mass, body mass and EQ in a diversity of primates, mainly from data taken from Jerison (1973). Taxa in Table 14.2 are listed in order of brain mass, exactly the same as the order in which they would have been if listed in order of N_c (Jerison, 1973).

Jerison (1973) reported EQ, brain, and body mass values for a large number of primates from the largest specimens in each taxon. To make comparisons to fossil taxa more directly comparable to the values for extant taxa, the largest reasonable estimates of body and brain mass in *Aegyptopithecus*, *Proconsul*, *Oreopithecus*, and *Dryopithecus* are also used here. Table 14.2 updates and reinforces the conclusions reached by Gibson *et al.* (2001) and Jerison (1973) that absolute brain size appears to track broadly accepted categories of cognitive capabilities better than EQ. Brain mass is lowest in the most primitive anthropoids, higher in cebids and Old World monkeys excluding papionins, and highest in great apes, with no overlap among these groups. Hylobatids have great-ape-like EQ values, but Old-World-monkey-like brain sizes, with gibbons clustering with non-papionins and siamangs with papionins. This is consistent with the conclusions presented earlier regarding the effects of body mass on EQ. Interestingly, siamangs fall within the range of papionins other than *Papio*, i.e., *Cercocebus, Lophocebus,* and *Mandrillus*. *Papio* has a larger brain that does not overlap with the ranges in other catarrhines. These results are generally similar to those obtained by Gibson *et al.* (2001), with finer categories discriminated here. It is beyond the scope of this chapter to interpret the significance of these differences, though tempting to suggest that it may be related to the unique aspects of baboon adaptation (social, dietary, ecological, or all of the above) (Parker, Chapter 4, this volume).

Not only are the brain mass values for great apes above those of all other living nonhuman primates, the range of great ape values is essentially the same as within the papionins, the minimum value being about 50% of the maximum in each set. When male gorillas and *Papio* are excluded, the minimums of papionin and great ape values both climb to about 65% of the maximum, which is about the same as the minimum/maximum ratio in hylobatids (Table 14.2). This pattern provides a context to interpret the significance of differences in brain size among great apes. They appear to be no more important or extensive than are brain size differences among papionins or even within the single genus *Hylobates* when outliers are removed. Finally, it is noteworthy that the order in which the taxa in Table 14.2 are listed would be nearly the same if they were listed in increasing order of body mass. While this may be taken to imply that body mass alone is sufficient to estimate relative brain size, the interesting exceptions represented by *Papio* and the positions of some of the fossil taxa would be difficult to interpret using body mass alone (see below).

Brain mass for *Aegyptopithecus* is above the range of variation for the anthropoids with the smallest brains, callitrichids, while its EQ is unusually low. This is consistent with Radinsky (1973), who noted that the appearance of a low relative brain size in *Aegyptopithecus*, reflected here in its low EQ, may be an artifact of its large body mass compared with other paleogene primates. In contrast, brain mass in *Aegyptopithecus* is at the low end of the range of variation for cebids, while its body mass is toward the upper end of the range of variation in cebids. *Aegyptopithecus* is probably anthropoid-like in brain mass, i.e., intermediate between callitrichids and cebids, and represents a reasonable ancestral morphotype for catarrhines.

Proconsul has a brain mass in the range of papionins other than *Papio*, but above those of other Old World monkeys and hylobatids. *Proconsul* EQ is low in comparison with hylobatids, which are considerably smaller in body mass, and within the range of all Old World monkeys (papionins are not distinguished from other Old World monkeys by EQ). This pattern is difficult to interpret in isolation. One explanation suggests itself, given observations of behavioral complexity in papionins (Parker, Chapter 4, this volume and references

therein), and the consensus view is that *Proconsul* is a basal hominoid. It may be that *Proconsul* shows the ancestral brain mass pattern for hominoids. Hylobatids have artificially high EQ values, in part due to phyletic dwarfing resulting in their unusually low body mass (Begun, Chapter 2, this volume). They also have smaller brains, probably mostly the direct effect of body mass decrease, which may imply a lowering of cognitive capabilities if smaller body masses led to some reduction in selection for or ability to support large brains in hominoids. Papionins, especially *Papio*, have converged on the relative brain mass increases shown by hominids, though not to the same degree. This last observation has intriguing implications for interpreting the significance of brain size increase in the separate lineages of hominins ("robust australopithecines" and *Homo*), but this too is beyond the scope of this chapter (Elton, Bishop & Wood 2001; Falk *et al.* 2000).

Dryopithecus has EQ, body mass, and brain mass values within the range of variation of living great apes. This is consistent with the view that *Dryopithecus* is phyletically a great ape (Begun 1992a, 1994; Begun, Ward & Rose 1997; Kordos 1990; Kordos & Begun 1997, 2001a). It is also consistent with the observation of probable great ape levels of encephalization in other fossil great apes of similar age, *Sivapithecus* and *Lufengpithecus* (see above). These three fossil great apes belong to the two main clades of living great apes, pongines (*Sivapithecus*, *Lufengpithecus*, and *Pongo*) and hominines (*Dryopithecus* and the African apes and humans) (Andrews & Cronin 1982; Andrews & Martin 1987; Begun 1994; Begun & Kordos 1997; Kelley 2002; Kelley & Pilbeam 1986; Pilbeam 1982; Schwartz 1990, 1997; Ward, 1997b). That levels of encephalization are indistinguishable in the ancestors of both clades of living hominids suggests that this level of encephalization was probably inherited from the common ancestor of all hominids (Begun, Chapter 2, this volume; but see Potts, Chapter 13, this volume for suggestions of parallelism). Brain size increase beyond that seen both in more primitive hominoids such as *Proconsul* and *Hylobates*, and in the most encephalized monkey, *Papio*, may be part of a suite of characters that define the Hominidae and distinguish them from all other primates.

What about *Oreopithecus*? Typically for this taxon, its body mass–brain mass relationship does not follow the same pattern in other anthropoids. The *Oreopithecus* female brain mass reported in Table 14.2 is slightly larger

than the largest gibbon brain cited by Jerison (1973), but its body mass is over twice that of the same gibbon individual. Its brain mass is also below that in siamangs of somewhat smaller body mass. In body mass this *Oreopithecus* female falls in the middle of the range of variation in papionins excluding *Papio*, while its brain mass is lower than in papionins. The smallest *Papio* is very close in body mass to this *Oreopithecus* female but has a 60% larger brain (Table 14.2). Finally, the *Oreopithecus* female has a considerably smaller brain than a similarly sized *Proconsul* female (Table 14.2). *Oreopithecus* appears to cluster more closely with non-papionin Old World monkeys than with hominoids (Table 14.2).

Oreopithecus is generally considered to be a basal great ape (Begun *et al.* 1997; Harrison & Rook 1997) and as such probably has experienced a reduction in relative brain mass given its considerably smaller brain compared with the basal hominoid *Proconsul*. This may well be convergent on brain mass reduction in hylobatids since it is not accompanied by (or caused by) body mass reduction, as appears to be the case in hylobatids. Both of these cases reveal a surprising diversity in hominoid brain evolution, with lineages appearing to be as likely to lose brain mass as to gain it. However, hominids have maintained relatively stable levels of encephalization. Early humans ("australopithecines") are marginally encephalized, if at all, compared with living great apes, *Dryopithecus*, and probably other fossil great apes (Hartwig-Scherer 1993; Kappelman 1996). The first clear evidence of substantial increases in absolute and relative brain mass in hominids comes with the origin of the genus *Homo* (Begun & Walker 1993; Falk 1980a, 1987; Falk *et al.* 2000; Kappelman 1996; Martin 1983; Tobias 1971a). The brain size–body mass relations among the taxa reviewed here are summarized in Figure 14.3.

Reorganization

One constant feature in the evolution of catarrhine brains is the partial de-coupling of size and morphology. *Aegyptopithecus*, *Proconsul*, and *Dryopithecus* endocasts all have more primitive features of cerebral morphology than living catarrhines of similar brain size. *Aegyptopithecus* appears to retain smaller frontal lobes, fewer sulci, and more rostral olfactory lobes compared with most living catarrhines. *Proconsul* brain size is small for a hominoid of its size, with possibly fewer sulci.
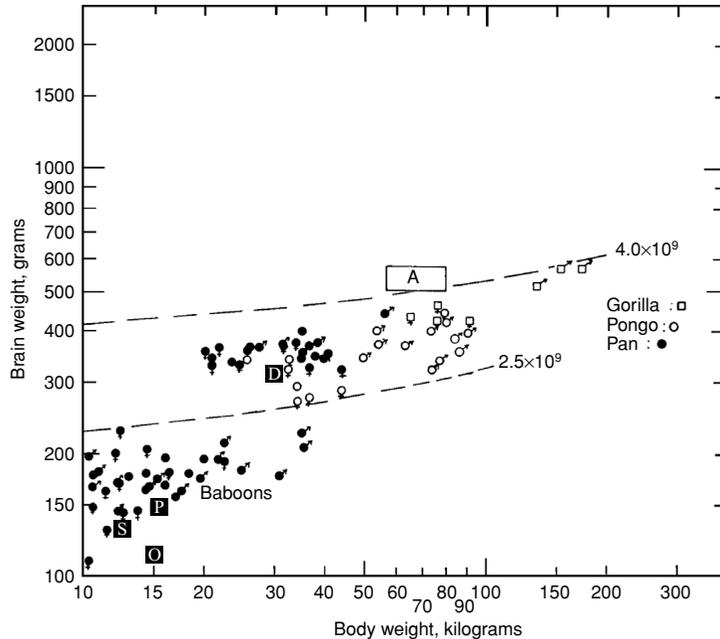
Figure 14.3. Brain weight and body mass in selected catarrhines. D = *Dryopithecus*, P = *Proconsul*, S = Siamang, O = *Oreopithecus*. A = *Australopithecus afarensis*. The position of fossil apes is based on the largest values (see text). *Australopithecus afarensis* is also based on the largest published specimens for this species, the AL 444–2 skull (*c*. 550 cc) and the AL 333–3 femur (67 kg, the mean of eight estimates ranging from 50 to 91 kg) (Lockwood, Kimbel & Johanson 2000; Jungers 1988; McHenry 1988, 1992; McHenry & Berger 1998). Modified from Jerison (1973:398).

Dryopithecus has the brain size and sulcal complexity (at least on the frontal lobes) of a great ape of its size, but may retain comparatively narrower frontal lobes rostrally. This result supports recent research challenging the idea of Finlay and Darlington (1995) that most if not all cerebral evolution is a direct result of overall size increase (Barton & Harvey 2000; Rilling & Insel 1998; Winter & Oxnard 2001; MacLeod, Chapter 7, this volume). It is also consistent with many analyses of human brain evolution that document morphological changes in relative lobe size and sulcal patterning in spite of little size difference compared with living great apes (Falk *et al.* 2000; Holloway 1974a, 1983a,b, 1984, 1995; Holloway & De la Coste-Lareymondie 1982; Tobias 1971a, 1983, 1991, 1995). Others have stressed the overall importance of brain size change in accounting for gross brain morphological evolution among hominids, so at least within this group the relative contributions of size and organization must be considered unresolved (Falk 1980a, 1987; Gibson *et al.* 2001; Preuss, Qi & Kaas 1999). Semendeferi and Damasio (2000) and Semendeferi *et al.* (1997) have shown that living

hominids including *Homo* differ little in the relative size of the frontal lobe, but that hylobatids have smaller frontal lobes, and gorillas may have unique cerebral proportions (see also MacLeod, Chapter 7, this volume). Visually, *Dryopithecus* appears to have comparatively small frontal lobes, but this is impossible to confirm without more complete material. If true, it would suggest independent expansion of this portion of the brain in living hominines and pongines.

CONCLUSIONS

A new cerebral size rubicon?

The idea of a critical brain mass defining a certain adaptive grade was common in interpreting the evidence of brain evolution in *Homo* (Falk 1980a, 1987; Holloway 1995; Jerison 1973; Tobias 1971a, 1995). Nonhominid catarrhine brain size evolution is labile, and in this way it is similar to the evolution of other biological attributes and their anatomical correlates (body mass, positional behavior, diet, etc.). Excluding *Homo*, brain size has been surprisingly stable in hominid evolution, despite

dramatic changes and diversity in body mass, diet, and positional behavior. It may be that the typical nonhuman hominid level of encephalization (a brain of at least 270g) represents a rubicon that allows for the production of great-ape-like levels of behavioral complexity. This is very close to the limits proposed by Jerison (1973) (Figure 14.3).

Which came first?

Brain size is correlated to many other biological variables (life history, ecological and social pressures) and it is likely that significant changes in brain size cannot occur without affecting other biologically critical variables (Aiello & Dunbar 1993; Aiello & Wheeler 1995; Clutton-Brock & Harvey 1980; Dunbar 1992; Falk 1987, 1990; Gibson *et al.* 2001; Holloway 1995; Kelley 1997; Martin 1983, 1990, 1996; Parker 1996; Parker & Gibson 1979; Smith 1991). The converse is probably also true, i.e., significant changes, particularly in life history variables, may very strongly affect brain mass evolution. Many other authors stress one or a few variables (diet, foraging, social relations, group size, body size, positional behavior, etc.) as critical to the evolution of higher levels of intelligence in hominids, but this intelligence is made possible by the presence of a large brain, whether brain mass is the direct result of selection or not.

The earliest, albeit suggestive, evidence of hominoid-like brain mass is in *Proconsul*, which also appears to exhibit a hominoid-like life history (Kelley 1997; Chapter 15, this volume). Selection may have operated on one or more life history variables (rate of maturation, length of infancy, number of offspring, age of first birth, etc.) or on brain mass directly. The *Proconsul* individual on which our brain and body mass calculations were based was the size of a large monkey, most of which have smaller brains. This suggests that body mass selection was not the prime mover for brain mass increase, at least in *Proconsul*. The ecology and diet of *Proconsul* were not remarkable, as far as we can tell (Andrews, Begun & Zylstra 1997; Kay & Ungar 1997; Teaford & Walker 1984; Ungar & Kay 1995; Walker 1997; Walker & Teaford 1989; Singleton, Chapter 16, this volume). One unusual aspect of *Proconsul* is the combination of incipiently hominoid-like capabilities in the hip joint, wrist joints, and phalanges along with the absence of an external tail (Beard *et al.* 1993; Begun *et al.* 1994; Kelley 1997; Ward 1993, 1997a; Ward, Walker & Teaford 1991; Ward *et al.* 1993). It is possible that

Proconsul, which is for the most part larger than hylobatids, responded to the challenges of negotiating an arboreal setting with incipiently hominoid-like encephalization and postcranial anatomy. However, *Proconsul* was clearly not a suspensory hominoid, so that arboreal challenges, while reminiscent of those on which Povinelli & Cant (1995; see Gebo, Chapter 17, Hunt, Chapter 10, this volume) focus, would have been qualitatively different. At any rate, the initial phase of hominoid brain evolution is represented by the evidence of *Proconsul*.

Dryopithecus was a suspensory great ape and had a large brain but *Oreopithecus*, which was at least as suspensory but somewhat smaller in size, did not. The positional behavior of *Sivapithecus* is not completely clear, though most indications point to some degree of arboreality with suspensory postures in most species (Rose 1983, 1984, 1986, 1989, 1997; Spoor, Sondaar & Hussain 1991). *Lufengpithecus* postcrania are very poorly known and almost undescribed, but indications are that it was as suspensory as *Dryopithecus* and *Oreopithecus* (Begun pers. obs.). Both Asian fossil great apes were large and both probably had large brains. All four fossil great apes have distinctive dental and gnathic morphologies indicative of diverse dietary preferences (Singleton, Chapter 16, this volume). However, while *Oreopithecus* was a specialized folivore the other three taxa were all frugivores of one sort or another.

Taken as a whole, large body mass, suspensory positional behavior, and brain size in fossil great apes do not offer unambiguous support for a clambering hypothesis of the evolution of a distinctive great ape intelligence (Povinelli & Cant 1995). *Proconsul* was relatively large for an arboreal primate but non-suspensory with a small brain compared with hominids. *Dryopithecus* and probably *Lufengpithecus* and *Sivapithecus* overlap with *Proconsul* in body mass but are more suspensory and larger brained. *Oreopithecus* is in the same size range and is highly suspensory but had an even smaller brain than *Proconsul*. This is not to say that the Povinelli and Cant hypothesis is falsified by the paleontological evidence, since we do not know whether or not any fossil great ape clambered in the manner they propose. It could be that most fossil great apes broadly fit the predictions of the Povinelli and Cant hypothesis, but *Oreopithecus*, the fossil great ape they proposed as a good fit, does not. Why?

Oreopithecus has a highly specialized dentition and postcranial morphology suggestive of uniquely specialized folivory and exclusive, highly suspensory arboreality (Harrison & Rook 1997; Kay & Ungar 1997).

Some have suggested that *Oreopithecus* was bipedal and terrestrial, but this is based on a questionable reconstruction of the foot, and a very poorly preserved innominate and set of vertebrae (Köhler & Moyà-Solà 1997; Moyà-Solà, Kohler & Rook 1999; Rook *et al.* 1999). In contrast, there are many clear-cut suspensory arboreal characters of the *Oreopithecus* postcranium (Harrison & Rook 1997; Jungers 1987; E. E. Sarmiento & Marcus 2000; S. Sarmiento 1987; Straus 1963; Szalay & Langdon 1986). Whatever the positional behavior of *Oreopithecus*, the diversity of opinions probably reflects its lack of close modern analogues. It is possible that *Oreopithecus*, while suspensory, was unlike any living hominoid in the details of its positional behavior. It has been likened by some to sloths (Wunderlich, Walker & Jungers 1999), and may have been not a clamberer but a slowly (?stereotypically) moving suspensory quadruped, which may explain its departure from the prediction of Povinelli and Cant (see Hunt, Chapter 10, Gebo, Chapter 17, this volume).

The pattern of brain size diversity in fossil great apes more closely matches broad patterns of diet. Hominid-like craniodental characters of *Dryopithecus*, *Sivapithecus*, and *Lufengpithecus* are associated with specialized hominid-like frugivory (large incisors, robust, elongated anterior palates, large postcanine dentitions, large brains), all absent from the highly folivorous *Oreopithecus* (Singleton, Chapter 16, this volume). A dietary shift may instead be associated with brain size increase in early great apes. Or, it may be that all of these factors (life history, diet, and positional behavior) are necessary to account for the evolution of the early hominid brain.

Fossil great apes tell us much about the timing of the origin of hominoid and hominid-like characters of the brain, and set some broad parameters for understanding the causes of these changes and their relationship to the evolution of intelligence. The biggest difficulty in interpreting this evidence is the bias intrinsic in the fossil record that turns the attention of researchers to behavior very closely related to or constrained by morphology. The fossil evidence of great apes is not suitable for testing hypotheses of social cognition, communication, group size, technical abilities, or foraging strategies. They do tell us, however, that many of the anatomical correlates of large brain mass (and by extension, intelligence) in living hominids, whether they are prime movers in great ape intelligence evolution or not, were already present in the fossil great apes of the late Miocene.

ENDNOTE

1 Stem catarrhine, or stem hominoid, etc., refers to a taxon that cannot be attributed to any living taxon but that is essentially more closely related to the taxon to which it is a stem than to anything else. A stem catarrhine is more closely related to Old World monkeys and apes than to other primates, but is not more closely related to either Old World monkeys or apes. A stem hominoid is a hominoid but is no more closely related to hylobatids than to hominids. On a related nomenclatural issue, there is some debate on the species designation of the specimen of *Proconsul* that provides evidence of the brain (KNM RU-7290). In my view it is a female *Proconsul nyanzae*, while Walker *et al.* (1993) regard it as *Proconsul heseloni*. Radinsky (1974) analyzed this same specimen when it was known as *Dryopithecus* (*Proconsul*) *africanus*, following Simons and Pilbeam (1965). It was at that time accessioned in the collections of the British Museum, with the catalogue number BMNH 32363. Falk (1983a) uses the old catalogue number but assigns the specimen to *Proconsul africanus*, following Le Gros Clark and Leakey (1951). The specimen was returned to Kenya and given the new catalogue number used here. The genus *Proconsul* is probably in need of revision, which accounts for the differences of opinion between Walker *et al.* and myself. For the purposes of this chapter it does not matter, because the body and brain mass estimates used to assess relative brain size come from the same specimen.

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