High-Resolution Computed Tomography Study of the Cranium of a Fossil Anthropoid Primate, *Parapithecus grangeri*: New Insights Into the Evolutionary History of Primate Sensory Systems

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ABSTRACT

Extant anthropoids have large brains, small olfactory bulbs, and high-acuity vision compared with other primates. The relative timing of the evolution of these characteristics may have important implications for brain evolution. Here computed tomography is used to examine the cranium of a fossil anthropoid, *Parapithecus grangeri*. It is found that *P. grangeri* had a relatively small brain compared with living primates. In addition, it had an olfactory bulb in the middle of the range for living primates. Methods for relating optic foramen area and other cranial measurements to acuity are discussed. Multiple regression is used to estimate retinal ganglion cell number in *P. grangeri*. Given currently available comparative data, *P. grangeri* seems to have had retinal ganglion cell counts intermediate for living primates, overlapping with the upper end of the range for strepsirrhines and possibly with the lower end for anthropoids.

Key words: optic foramen; acuity; olfactory bulbs; endocranial volume

A bivariate plot of brain volume versus body mass for the living primates (Fig. 1B) shows that anthropoid primates have much larger brains than strepsirrhines. Excepting the human outlier, the anthropoid-strepsirrhine difference is the most striking feature on the plot. There are also important differences in sensory structures between the two groups. Living anthropoids tend to have higher-acuity vision and reduced olfactory bulbs relative to strepsirrhines (Baron et al., 1983; Ross, 2000). When in the evolutionary development of anthropoids did these characteristics evolve?

We recently used X-ray computed tomography (CT) to examine several features of the cranium of an early anthropoid from the Fayum of Egypt, *Parapithecus grangeri* (Bush et al., 2004). *P. grangeri* is considered to belong to the sister group of the living anthropoids (Kay and Fleagle, 1988; Ross et al., 1998; Simons, 2001). It therefore offers information on anthropoid ancestors before the divergence of platyrrhines and catarrhines. The nearly complete specimen (DPC 18651) was embedded in a hard

Grant sponsor: the National Institutes of Health; Grant number: EY11759; Grant sponsor: W.M. Keck Foundation for Discovery in Basic Medical Research at the California Institute of Technology; Grant sponsor: Frank V. Hixon Fund.

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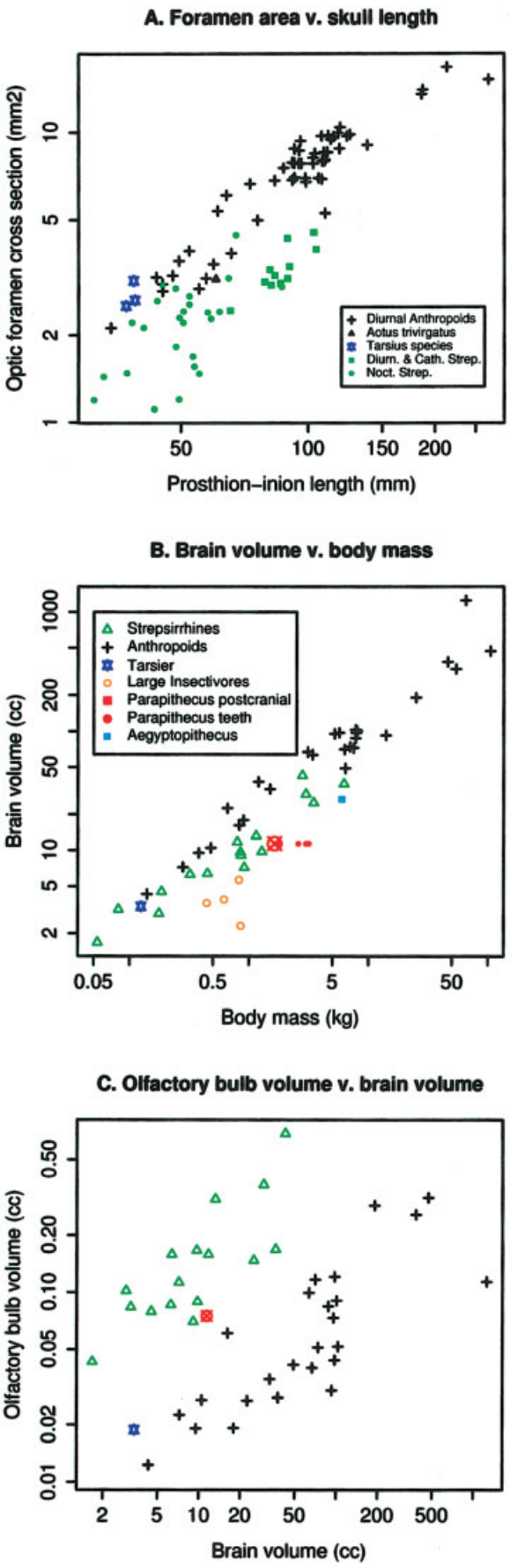
Received 20 May 2004; Accepted 1 July 2004
DOI 10.1002/ar.a.20113
Published online 6 October 2004 in Wiley InterScience (www.interscience.wiley.com).



sandstone, which filled the endocranial cavity and the posterior part of the orbital cavity. CT was used to examine these features, making estimates of endocranial and olfactory bulb volume. To address the question of visual acuity in *P. grangeri*, the area of the optic foramen was measured. This is the aperture through which the optic nerve passes as it carries information from the retina to the brain. Prosthion-inion length and orbit area were also measured. Kirk and Kay (2004) have recently provided data on these three measures for a large number of living primates.

Methodologies of Estimating Visual Acuity

The present study uses different methods than Bush et al. (2004) for estimating acuity in fossil primates. The argument for the change is as follows. Visual acuity depends on how many units there are sampling a particular slice of visual space. In the primate eye, we can treat the retinal ganglion cell (RGC) as such a unit. The visual field that a primate eye samples is probably about the same regardless of species. Given this, average acuity will simply be a function of the number of RGCs.

Previously, Bush et al. (2004) used the method of Kirk and Kay (2004), which uses summation as a proxy for acuity. Summation is a measure of the convergence of photoreceptors on RGCs. Primates with high acuity tend to have low summation, that is, more RGCs for a given number of photoreceptors. In the method of Kirk and Kay (2004), optic foramen area is used as a proxy for the total number of RGCs, and orbit size as a proxy for the total number of photoreceptors. The ratio between them is used to approximate summation. This estimate of summation is then taken to give an indication of acuity (with low summation corresponding to high acuity).

The problem with this method is the final assumption. If RGCs are the fundamental sampling unit, summation only matters insofar as it affects the number of RGCs. This can be illustrated with an example in which two different primates have the same number of retinal ganglion cells. In this example, the eyes of the two primates sample the same amount of visual space, but one of them has lower summation. Given our assumption of equal RGC numbers, the primate with the lower summation must therefore have less photoreceptors. If summation is used as a proxy for acuity in this example, it is necessary to conclude that the primate with less photoreceptors has higher acuity. In fact, to the extent that the RGC is the fundamental sampling unit, only the number of RGCs matters.

Fig. 1. **A:** Plot of optic foramen cross-section vs. prosthion-inion length for a large number of living primates. Data come from Kirk and Kay (2004). **B:** Brain volume vs. body mass on logarithmic axes. In addition to data from living primates, which come from Stephan et al., (1981), the data points for *Aegyptopithecus* and *Parapithecus* are shown. For *Parapithecus*, a number of body size estimates from the literature are included (Kay and Simons, 1980; Gingerich et al., 1982; Conroy, 1987). Data points are also shown for several large insectivores (Stephan et al., 1991). **C:** Olfactory bulb volume vs. brain volume for living primates and *Parapithecus*. Note that the data for living species are based on histological measurements and do not include the olfactory ventricle. The *Parapithecus* estimate does include this and therefore will be something of an overestimate relative to the living species.

How can RGC number be estimated from osteological measurements? Kirk and Kay (2004) measured optic foramen area, prosthion-inion length, and orbit area in a large sample of living primates. Their argument was that optic foramen area is related to RGC number. We agree, but there is also considerable variation in optic foramen area that is not related to RGC number. As Figure 1A shows, larger diurnal anthropoids tend to have a larger optic foramen. This is true despite the fact that those diurnal anthropoids that have been examined have roughly the same number of RGCs (Tetreault et al., 2004). Optic foramen cross-section increases with body size, but RGC number seems not to. This scaling of optic foramen diameter may reflect systematic variation in axon diameter or the size of the opthalmic artery. Figure 1A also reveals a grade difference between anthropoids and strepsirrhines. Anthropoids have a larger foramen area at a given skull size. It is quite likely that this difference corresponds to the large difference in RGC number between the two groups.

The RGC number in fossils might be addressed using bivariate plots like that in Figure 1A. But this method depends on the supposition that the grade difference mentioned above really does correspond to an RGC number difference. It would be better to use osteological measures and RGC counts from living species to develop regression equations for predicting RGC number. The ideal approach is to use multiple regression with RGC count as the dependent variable and several osteological measures as predictor variables. This will isolate the portion of variation in the predictors that is related to RGC count.

Kirk and Kay (2004) point out that increases in RGC number may be distributed unevenly between the fovea and periphery, so that increases in RGCs may not correspond to increases in maximum acuity. This is indeed a possible problem. However, in our opinion it is not one that can be addressed with currently available data. In principle, if one had estimates of the number of foveal RGCs in living primates, the multiple regression method could be used with foveal RGCs as the dependent variable.

MATERIALS AND METHODS

Imaging was performed at the high-resolution CT facility at the University of Texas at Austin using the ultra-high-resolution subsystem with 1,024 detectors (scanner built by Bio-Imaging Research, Lincolnshire, IL). Slices were acquired perpendicular to the Frankfort plane in roughly coronal orientation. The following scanning parameters were used: 120 kV; 0.2 mA; slice thickness 0.048 mm; field of view 45.5 mm. Images were reconstructed with a Laks convolution filter into 16 bit images, 1,024 $\times$ 1,024 $\times$ 1,334 matrix, with voxel dimensions of 0.044 $\times$ 0.044 $\times$ 0.048 mm. These parameters gave an effective resolution of about 0.12 mm, which is more than adequate for examining structures such as the optic foramina and the olfactory bulbs. Subsequent analysis was performed on a Linux workstation running Amira software (TGS, San Diego, CA). The half-maximum-height technique was used to determine the position of interfaces between materials (Baxter and Sorenson, 1981; Spoor et al., 1993).

To address acuity in *P. grangeri*, osteological measurements were used to predict total RGC count. Equations were developed using living species. The values for *P. grangeri* were then plugged into these. The osteological measurements of Kirk and Kay (2004) were combined with RGC measurements (see Table 3 of Bush and Allman, 2004 in this issue). There are 11 species for which both types of measurement are available. The data set from Kirk and Kay (2004) includes three osteological measurements: optic foramen area, prosthion-inion length, and orbit area. Ideally, one would use all three of these as predictors for RGC count (or at least try it with all three, potentially eliminating one if it did not add enough predictive power). However, there are too few data points to use three predictors. Instead, two combinations of two predictors are used: foramen area and orbit area on the one hand, and foramen area and prosthion-inion length on the other. Since foramen area is more closely related to RGC count than the other two ($R^2 = 0.80$ vs. 0.52 and 0.55 for orbit and prosthion-inion), it makes sense to include it in both regressions. Using foramen area and skull length to predict RGC count, $R^2 = 0.89$ ($P = 0.0002$) is obtained. Using foramen area and orbit area, $R^2 = 0.85$ ($P = 0.0005$) is obtained.

Our measurement of the olfactory fossa in *P. grangeri* is compared with measurements in living species by Baron et al. (1983). It is important to note that the measurements of Baron et al. (1983) do not include the olfactory ventricle. Our estimate based on the volume of the olfactory fossa does include the ventricle and is therefore likely to be something of an overestimate relative to the data of Baron et al. (1983). All statistical analysis was done using the R package (Ihaka and Gentleman, 1996).

RESULTS

Figure 2 illustrates a number of surfaces made from the data and includes slices through the olfactory bulbs and the optic foramen. The endocranial volume for *P. grangeri* was measured at 11.4 cm^3. Figure 1B shows that this is small relative to *P. grangeri*'s body size. Included are data points corresponding to several different estimates of body size. Even with the smallest estimates of body size, *P. grangeri* falls well below the range of living anthropoids, more in the range of the living strepsirrhines.

The olfactory fossa of *P. grangeri* had a volume of 75 mm^3. A plot of olfactory bulb size vs. brain size is given in Figure 1C, where *P. grangeri* is plotted against data from a number of living species (Baron et al., 1983).

The estimated foramen area for *P. grangeri* was 3.46 mm^2. Combining this with measures of prosthion-inion length and orbit area (65.8 mm and 13.3 mm^2, respectively), multiple regression equations were used to estimate retinal ganglion cell number. Using foramen area and prosthion-inion length as predictors, the number of RGCs was estimated at 670,000. Using foramen area and orbit area, the number of RGCs was estimated at 967,000.

DISCUSSION

The results of the present study reinforce the point that brain expansion happened independently in a number of primate groups. The small size of our endocranial measurement in *P. grangeri* is consistent with a previous measurement on *Aegyptopithecus zeuxis*, which is also plotted in Figure 1B (Simons, 1993). The Fayum anthropoids did not have large brains. The larger implication of this is that brain expansion must have happened independently in several primate groups. Both *Parapithecus* and *Aegyptopithecus* have small brains even compared with strepsirrhines. Given the small brain size of ancestral primates (Radinsky, 1970;

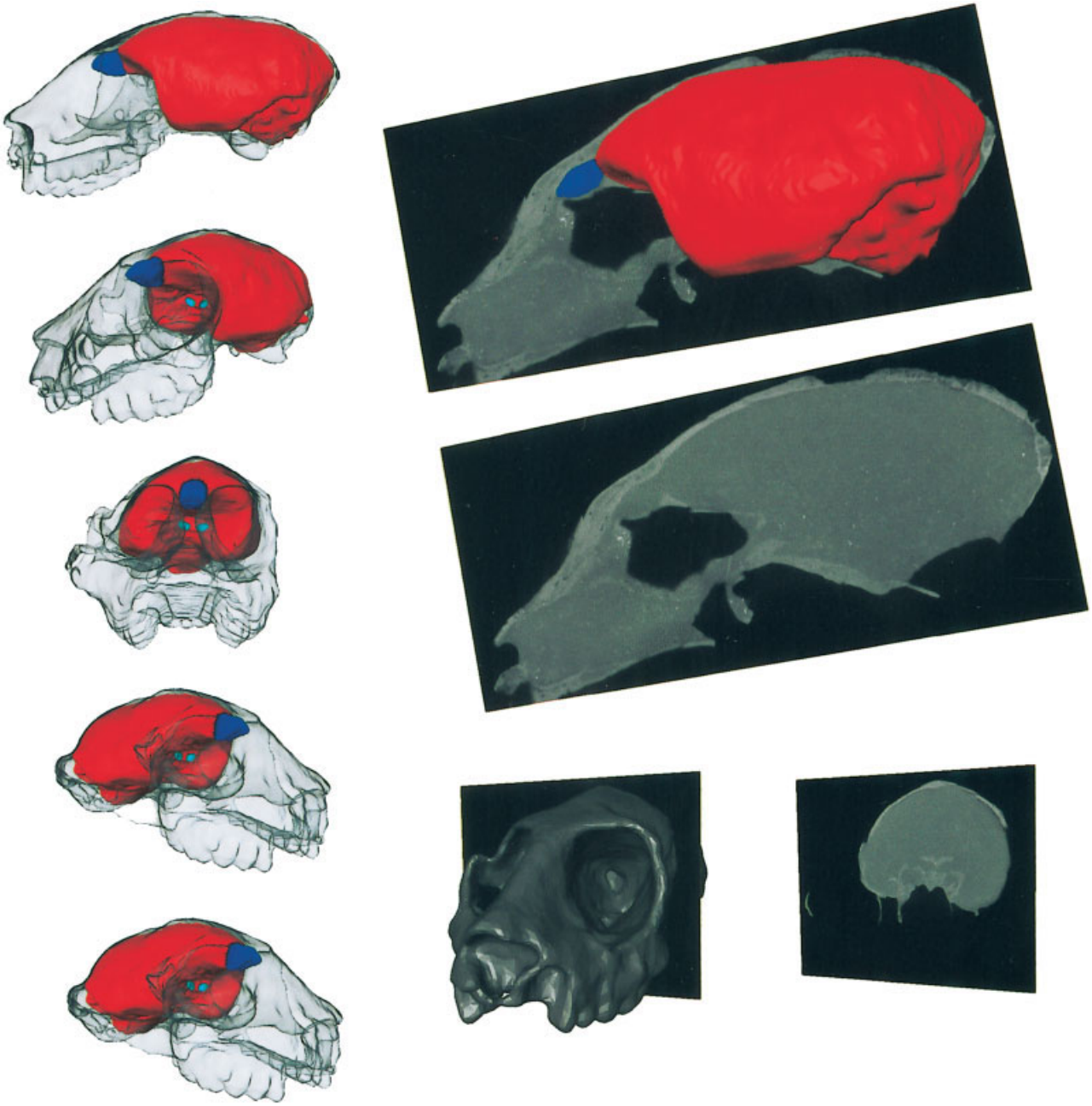


Fig. 2. The column at the left is surfaces made from our CT data set. They show the endocranial cavity (red) along with the olfactory bulbs (dark blue) and the optic foramina (light blue). The surface of the skull is rendered transparent. At right, a sagittal slice through the data set reveals the olfactory bulbs, and a coronal slice through the optic foramina is also shown.

Jerison, 1973), this suggests that the last common ancestor of strepsirrhines and anthropoids had a brain smaller than most living strepsirrhines. So independent brain expansion has happened in one or more strepsirrhine groups. In addition, the claim that *Aegyptopithecus* had a small brain for its body size is bolstered by our *Parapithecus* result. Because *Aegyptopithecus* is thought to be a catarrhine, its small brain size suggests an independent brain expansion in platyrrhines and catarrhines.

It has been argued that *P. grangeri* was more folivorous than other Fayum anthropoids (Kay and Simons, 1980). We note that its brain is small even relative to living folivores. Our brain size measurement also suggests that body mass estimates made for *P. grangeri* based on teeth and skull dimensions have probably been overestimates. Several of these would put *P. grangeri* at a brain size grade equivalent to living insectivores, which we regard as unlikely.

In Figure 1B, the olfactory bulb volume of *P. grangeri* appears to fall around the bottom end of the range for strepsirrhines. However, as was mentioned above, the data points for living species do not include the olfactory ventricle. Our measurement of the olfactory fossa in *P. grangeri* does include this and is therefore likely to be something of an overestimate relative to the living species in Figure 1B. Because the size of olfactory ventricle varies greatly between taxa, the magnitude of this overestimate is not possible to estimate accurately (Smith and Bhatnagar, 2004). What can be said is that even considering the potential error, *P. grangeri*'s olfactory bulb volume fell in the middle of the range for living primates, quite possibility intermediate between that of living anthropoids and strepsirrhines.

Our two estimates of RGC number for *P. grangeri* define a range that extends from well within the strepsirrhine range up to the bottom end of the anthropoid range (for comparison with living species, see Table 3 of Bush and Allman, 2004, this issue). The low end of the human intraspecies range falls around this level (Jonas et al., 1992). Thus, it is not possible to reach strong conclusions about visual acuity in *P. grangeri*. The weaker conclusions of the present study more accurately reflect the current state of knowledge.

Counting retinal ganglion cells in living primates is straightforward, and many such measurements have been made in recent years (Tetreault et al., 2004). As more measurements are made, and as more well-preserved early anthropoid fossils are recovered, it will be possible to reach conclusions about acuity in these animals with reasonable confidence.

ACKNOWLEDGMENTS

The authors thank Matthew Colbert for assistance with scanning, as well as Chris Kirk, Richard Kay, and Tim Smith for suggestions regarding the analysis. This is Duke Primate Center publication number 787.

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