Endocranial Volume and Optic Foramen Size in *Parapithecus grangeri*

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March 10, 2003

Contents

1   Introduction

The living anthropoids tend to have large brains, small olfactory bulbs and high acuity vision compared with other primates (Stephan et al., 1981; Baron et al., 1983). An interesting possibility is that an increasing emphasis on vision was in some way related to increases in brain size in the anthropoid lineage. It is certainly plausible that changes in sensory behavior would necessitate major changes in the brain. Comparative neuroanatomical data has suggested that brain size increases were related to growth in the parvocellular layers of the lateral geniculate nucleus, an early stage in the visual processing hierarchy (Barton, 1998).

It is therefore of particular interest to study brain size and the relative development of sensory structures in early anthropoid fossils. The discovery of a nearly complete skull (DPC 18651) of the species *Parapithecus grangeri* (see Simons this volume) affords us this opportunity. The Parapithecidae are widely regarded as a sister group to the living anthropoids (Kay and Fleagle, 1988; Ross et al., 1998; Simons, 2001). As such, they may retain primitive features which have been lost in the living anthropoids. DPC 18651 was embedded in a hard sandstone which preserved its shape. This sandstone fills the endocranial cavity, and the posterior part of the orbital cavity, obscuring the optic foramina. In order to examine these features, we performed an X-ray computed tomography (CT) scan of the fossil.

2   Methods

Imaging was performed at the high resolution CT facility at the University of Texas at Austin, using the ultra-high resolution subsystem with 1024 detectors. (Scanner built by Bio-Imaging Research, Inc., Lincolnshire, Illinois). Slices were acquired perpendicular to the Frankfort plane, in roughly coronal orientation. The following scanning parameters were used: 120 kV; .2mA; slice thickness 0.048 mm; field of view 45.5 mm. Images were reconstructed with a Laks convolution filter into 16 bit images, 1024x1024x1334 matrix, with voxel dimensions of .044 x .044 x .048 mm. These parameters give the ability to resolve objects on the order of .12 mm. Subsequent analysis was performed on a Linux workstation running Amira software (TGS, Inc. San Diego CA).

The position of interfaces between materials was calculated using the half maximum height (HMH) technique which sets the threshold halfway between the CT values on each side of an interface (Baxter and Sorenson, 1981; Spoor et al., 1993). Fig. 1 shows a coronal slice, and a plot of the CT values along a line passing through it. These values were used to determine the midpoint between the bone and matrix intensity levels. The threshold was then set at the midpoint, as shown in Fig. 1 C.

After determining HMH values, we used semi-manual image segmentation tools to segment out the endocranial cavity and the olfactory fossa. We determined the caudal end of the fossa based on the curvature of the surrounding

1

endocranial cavity and on the structure of more lateral parts of the fossa itself. We then calculated volumes for the brain and olfactory bulb from these segmentations.

Recently Kay and Kirk (2000) and Kirk and Kay (this volume) have detailed a method for studying visual acuity in fossil animals. One of the most important determining factors in visual acuity is the degree of summation of photoreceptors onto retinal ganglion cells. Kirk and Kay's optic foramen index (OFI), which is 100 times the ratio of optic foramen area to orbit area, correlates well with direct measures of summation.

Fig. 2 shows how we measured the cross section of the optic foramen in the CT data. We aimed to make our measurements comparable to the data for living animals collected by Kirk and Kay (this volume), who made measurements from the external (orbital) perspective. The plane of the optic foramen does not match the plane that the scans were taken in. We made our foramen measurements by resampling the data so that the plane of the foramen coincided with one of the orthogonal planes of the data set. We did this by first making a crude surface of the foramina. This was used to determine how much the data set should be rotated for the right and left foramina respectively. The resampling was then done using a lanczos filter. The surface area of each foramen was estimated from the resulting cross section, thresholded at the HMH level.

To compare statistically the olfactory bulb/brain relationship in *P. grangeri* with living groups of primates, we approximated the strepsirrhine and haplorhine distributions as bivariate normal, and constructed equal-frequency ellipses around them.

3   Results

The scans have good contrast between matrix and bone. In our 16 bit images, bone and matrix CT values typically differ by around 5000 CT units. This can be seen in the plot in Fig. 1 which represents the values through a region in the middle of the skull. It is also true in the areas around the optic foramen and olfactory bulb. Imaging artifacts are confined to a small amount of beam hardening around some of the thicker bones, too small to significantly effect our measurements.

The resolution of the scans is more than adequate to measure small structures such as the olfactory bulb and optic foramen. The optic foramen has linear dimensions an order of magnitude larger than the .12 mm resolution of these scans.

Fig. 1 A illustrates another feature of DPC 18651. In some regions the bones of the braincase have been worn away exposing the matrix of the endocranial cavity. However, based on the symmetry of the endocranial space in the images it is clear that very little endocranial matrix was lost, so this should not have a significant effect on measurements of endocranial volume.

2

3.1 Endocranial measurements

Fig 3 shows a computer generated surface of the skull of DPC 18651. In the bottom image the skull has been made transparent revealing the endocranial surface.

Our measurement of the brain volume of *P. grangeri* is 11,400 mm^3. In Fig. 4 we present a log brain size log body mass plot, which includes a number of living species. Various body mass estimates for *P. grangeri* from the literature are used (Kay and Simons, 1980; Gingerich et al., 1982; Conroy, 1987). Also included is a new estimate from Simons (this volume) based on post-cranial material. As the figure makes clear, *P. grangeri* had a small brain, even relative to the smallest estimate of body mass.

Our measure of *P. grangeri* olfactory bulb volume is 75.0 mm^3. Fig. 5 shows log olfactory bulb volume plotted against log brain volume for a number of living primates and *P. grangeri*. The value for *P. grangeri* lies near the bottom end of the strepsirrhine range. To assess this statistically, we also include the 95 % equal-frequency ellipses for anthropoids and strepsirrhines. The *P. grangeri* data point falls within both the strepsirrhine and anthropoid ellipses.

3.2 Estimation of degree of retinal summation

Table 1 gives our measurements for optic foramen area in *P. grangeri* along with two skull measures made directly on the fossil, and an OFI value calculated from all these. As can be seen from Fig. 6, the OFI of *P. grangeri* falls well within the range of living diurnal anthropoids.

4 Discussion

Our results show that, *P. grangeri* had a small brain for its body mass. In Fig. 4 we can see that even with the smallest available estimates of body mass, *P. grangeri* had a brain size more in line with the living strepsirrhines than the living anthropoids. This is consistent with results for *Aegyptopithecus zeuxis* in Simons (1993). It seems likely that the last common ancestor of *P. grangeri* and the living anthropoids retained the relatively small brain of its ancestors.

It is worth noting that body mass estimates for *P. grangeri* based on teeth and skull dimensions have probably been overestimates. Fig. 4 shows data for several large insectivores plotted alongside *P. grangeri* and the primates. If *P. grangeri* had a body mass around 3 kg, which is one value taken from the literature, then it had a brain relatively smaller than a number of living insectivores. Supporting the idea that previous estimates have been too high, Simons (this volume) provides body size estimates based on two tibiae and a humerus. All three are smaller than published values based on cranial measurements.

Fig. 6 shows that *P. grangeri* had an OFI well inside the range of living anthropoids. This suggests that it had low levels of summation in its retina, and relatively high acuity vision. The simplest scenario then is that the last

common ancestor of *P. grangeri* and the living anthropoids also had relatively high acuity.

Finally, Fig. 5 shows that the olfactory bulb of *P. grangeri* is similar in size to what one finds at the bottom end of the strepsirrhine range. It also falls above the value for any living anthropoid.

One possibility is that *P. grangeri* retains a relatively large olfactory bulb, which is the ancestral state. According to this possibility the line leading to living anthropoids would have undergone a reduction in olfactory bulb size after the divergence of the the Parapithecidae.

However, in Fig. 5 we have also plotted the 95 % equal-frequency ellipses for Anthropoids and Strepsirrhines. These show that statistically speaking, *P. grangeri* could fit with either group. One would not be surprised to see a modern strepsirrhine with an olfactory bulb of *P. grangeri's* size. But given the variation in our sample of modern anthropoids, it is also conceivable that a member of that group might have a similar brain-olfactory bulb relationship. A larger sample of modern species might allow us to exclude this.

These results suggest that high acuity preceded brain expansion in anthropoid evolution and that its development did not immediately result in brain expansion. However the development of high acuity would have opened up new possibilities favoring later brain expansion. Anthropoid primates show a number of behaviors which depend on acute vision. These include the detection of facial expression and individual identity, which led to an elaboration of the ventral processing stream of extrastriate visual cortex, and the visual guidance of precision manipulation, which led to similar elaboration of the dorsal stream. High acuity is a necessary but not sufficient neurobiological substrate for these behaviors. Perhaps high visual acuity initially evolved for foraging, and afterwards was co-opted for social behavior and precise object manipulation. The eyes of conspecifics are highly salient to anthropoid primates (Keating and Keating, 1982; Kyes and Candland, 1987; Parr et al., 2000). Direction of gaze and subtle movements of the eyelids and mimetic muscles surrounding the eyes and mouth provide vital information about the intentions of others. They do so on a much more rapid time scale than that afforded by olfactory cues. Making full use of this information required the elaboration of neural circuitry and expansion of the brain.

Our results also suggest that the last common ancestor of the Parapithecidae and the living anthropoids may have retained a large olfactory bulb. Since the total energy available to a mammal is governed by its body mass, and since brain structures are very expensive metabolically (Allman, 2000), it follows that when the neural substrate for a new behavioral adaptation evolves it must compete with pre-existing brain structures for limited energetic resources. We suggest that *P. grangeri* represents an early stage in anthropoid evolution before the olfactory system began to lose ground relative to higher order visual and executive cortical areas in this competition for energetic resources.

4

5   Conclusions

We find that *P. grangeri* had a small brain compared to living anthropoids. At the same time, the size of its optic foramen relative to its orbit suggests that it had low levels of summation and relatively high acuity vision, similar to living anthropoids. Thus, high acuity vision seems to have evolved prior to brain expansion in anthropoids. Olfactory bulb size in *P. grangeri* is typical of the bottom end of the range for living strepsirrhines. It is possible that *P. grangeri* has retained the ancestral condition in this respect, and that in the line leading to living anthropoids a reduction in olfactory bulb size post-dated the development of high acuity vision.

One hypothesis consistent with the above observations is that anthropoid visual acuity evolved originally for foraging. It was later co-opted for other tasks, such as social behavior and the precise manipulation of objects. The development of this second set of behaviors was associated with increases in brain size and reduction of the olfactory bulb.

6   Acknowledgments

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Endocranial Volume	11,400 mm^3
Olfactory Bulb Volume	75.0 mm^3
Optic Foramen Area	3.46 mm^2
Orbit Aperture	13.3 mm
Prosthion-Inion	65.8 mm
OFI	2.49

Table 1: Our measurements including endocranial volume, olfactory bulb volume, optic foramen area and OFI. Also included are measurements made directly on the fossil of orbit aperture and prosthion-inion length which were used to calculate the OFI and plot it in Fig. 6
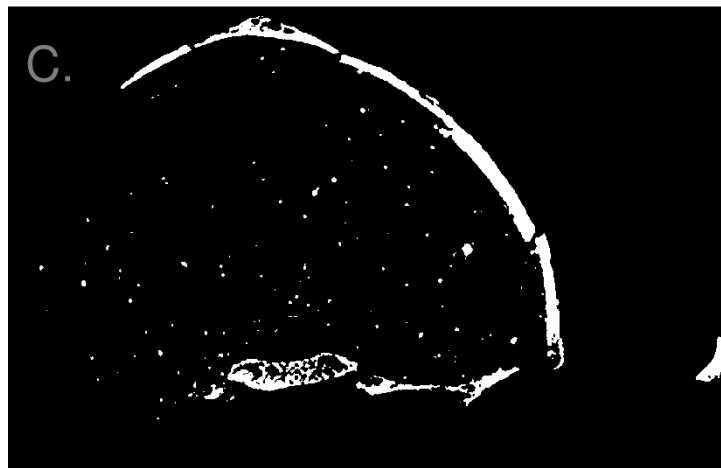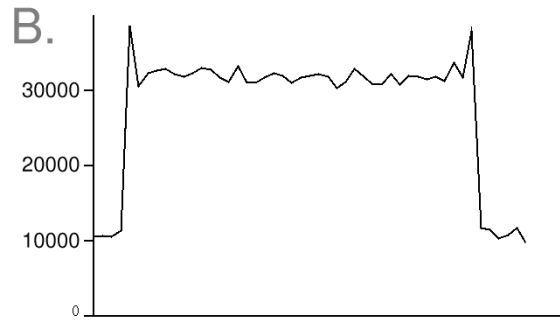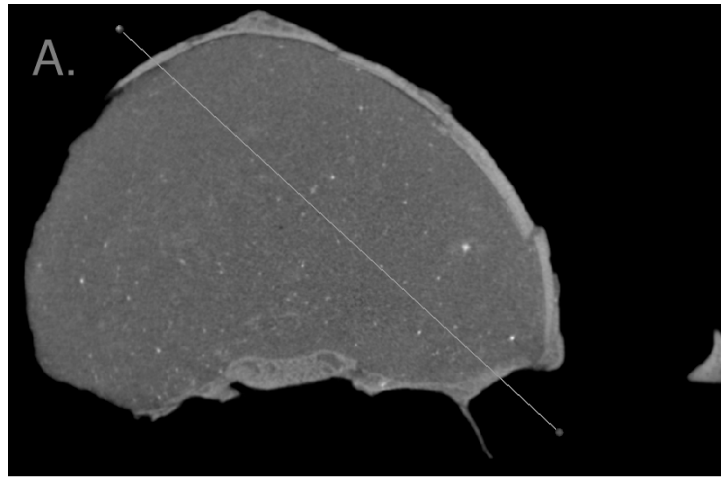
Figure 1: A. A coronal slice through the middle of the cranium. B. This graph represents the CT intensity values along the probe line which is visible in A. C. The slice from A. thresholded at the HMH value.
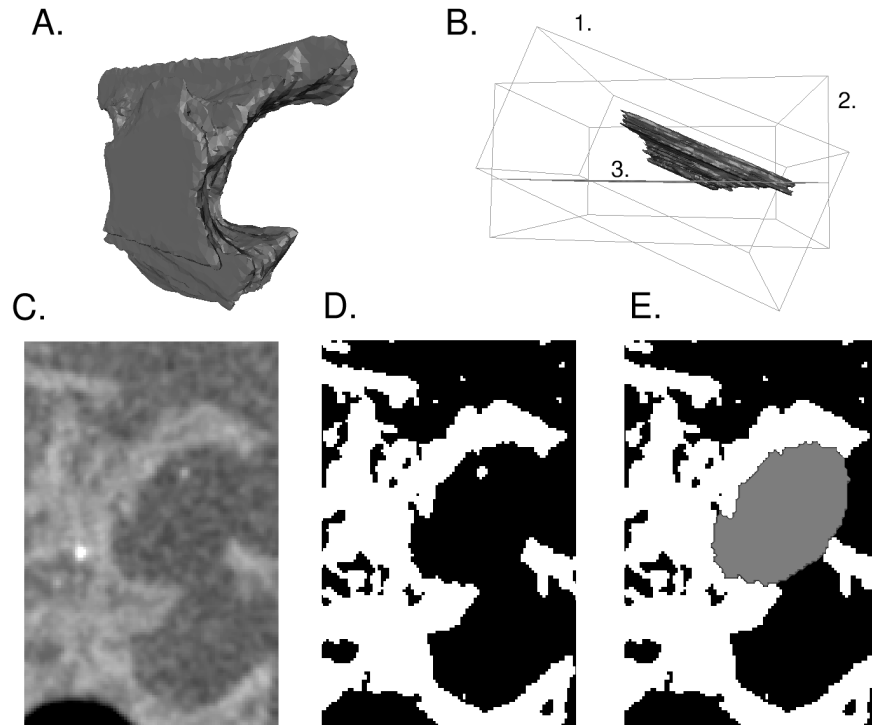
Figure 2: Illustration of measurement of left optic foramen. A. Crude surface of the bone around the optic foramen. B. Surface from a viewed from above. Bounding boxes show the rotated data set relative to the original data set. 1. Bounding box of original data set. 2. Bounding box of rotated data set. 3. Slice through the new data set which now lies in the plane of the foramen. C. View of the left optic foramen in new rotated data set. D. Left optic foramen thresholded at HMH level. E. Left optic foramen showing extent of surface area measure. The superior orbital fissure is visible below the optic foramen.
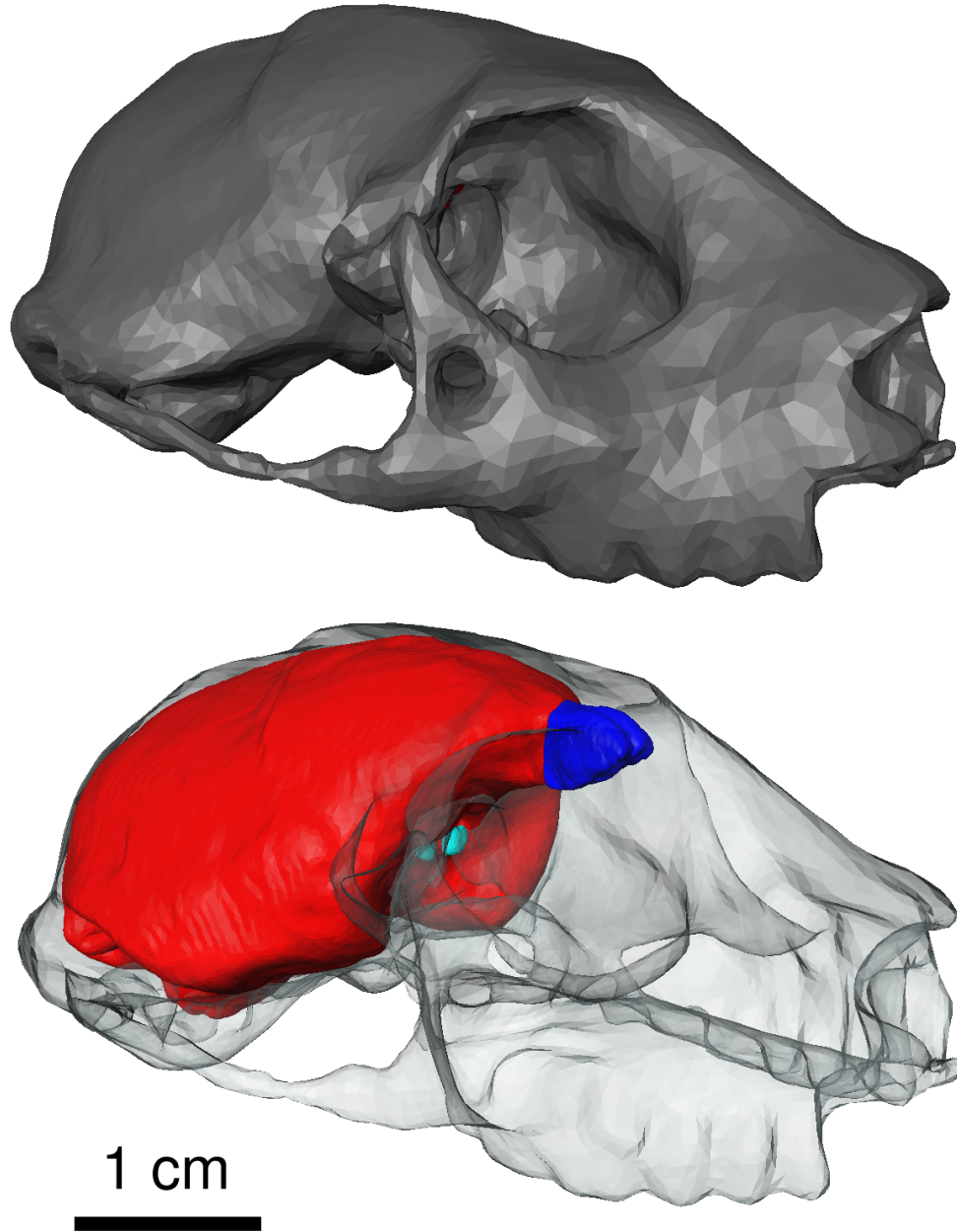
9

Figure 3: Surfaces of *P. grangeri* skull and braincase. The lower image shows the skull rendered transparent revealing the endocranial cavity. Dark blue represents the olfactory bulbs and light blue represents the optic nerves.
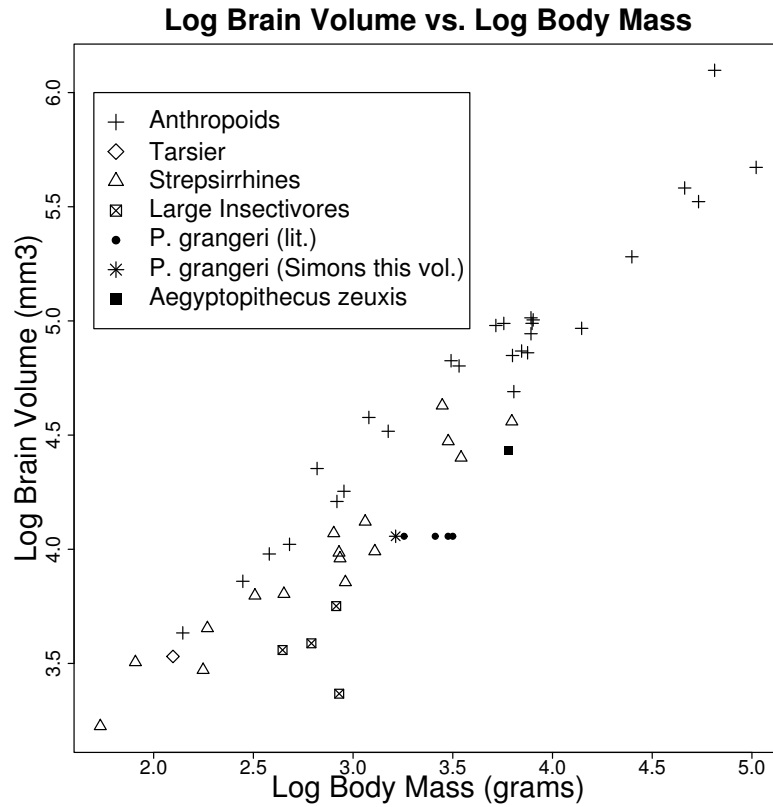
Log Brain Volume vs. Log Body Mass

Figure 4: Brain volume plotted against body mass on logarithmic axes for *P. grangeri* and a collection of primate species. We use a number of published estimates of *P. grangeri*'s body mass: Kay and Simons (1980); Gingerich et al. (1982); Conroy (1987), as well as an average of three post-cranial estimates from Simons (this volume). Also plotted is data for *Aegyptopithecus zeuxis* from Simons (1993), and four large insectivores from Stephan et al. (1981, 1991).
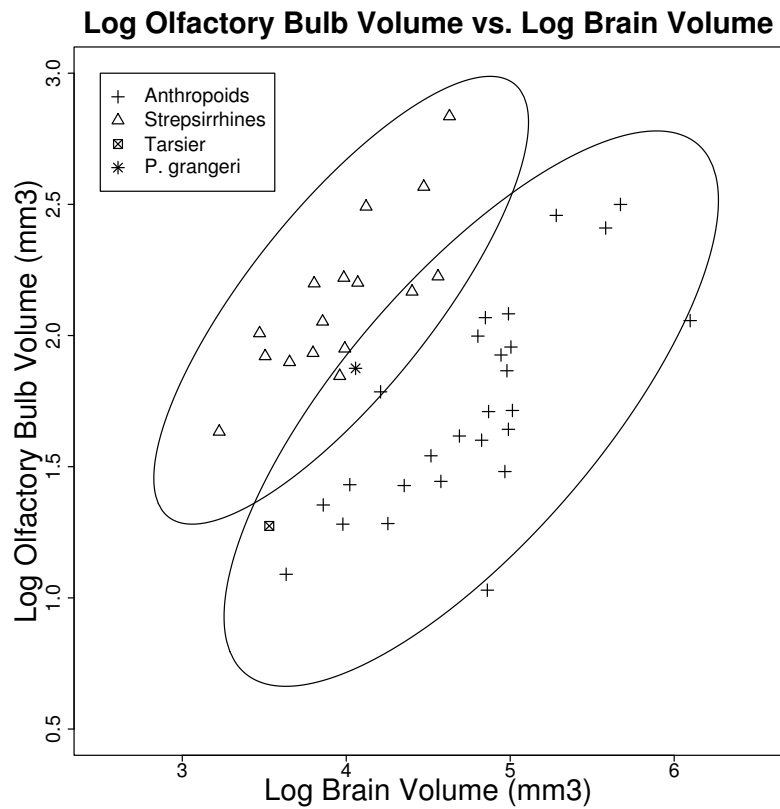
Figure 5: Olfactory bulb volume plotted against brain volume on logarithmic axes for a number of living species and *P. grangeri*. Included are the 95 % equal-frequency ellipses for each group. Data from living species are from Baron et al. (1983).

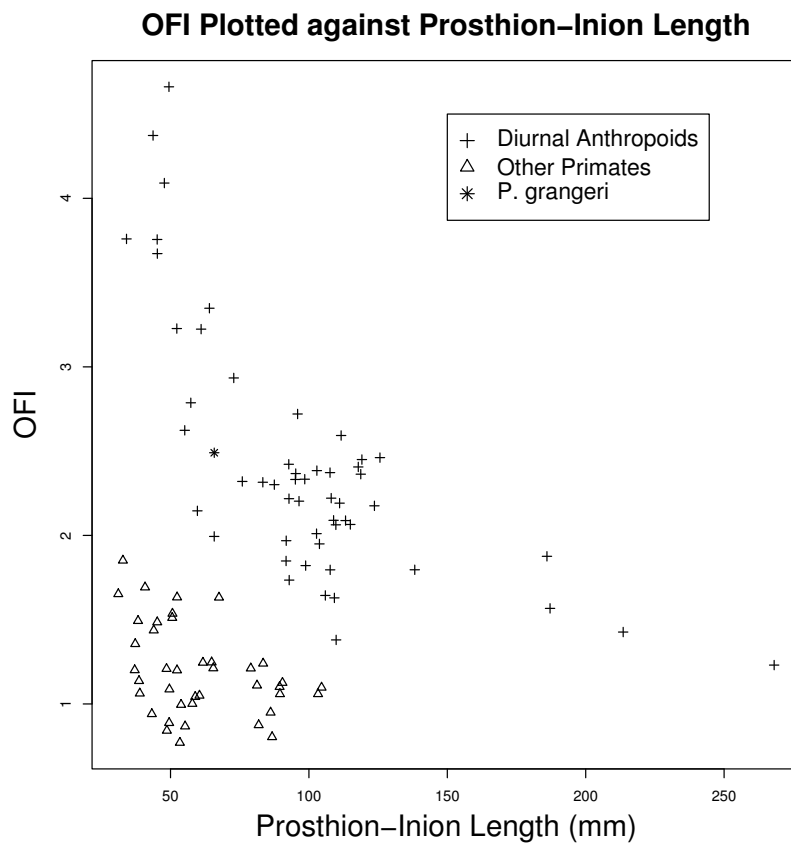**OFI Plotted against Prosthion–Inion Length**

Figure 6: OFI for *P. grangeri* plotted with data from living primates. Living primate data is from Kirk and Kay, this volume.