Brain Volume of the Newly-Discovered Species *Rhynchocyon udzungwensis* (Mammalia: Afrotheria: Macroscelidea): Implications for Encephalization in Sengis

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Abstract

The Gray-faced Sengi (*Rhynchocyon udzungwensis*) is a newly-discovered species of sengi (elephant-shrew) and is the largest known extant representative of the order Macroscelidea. The discovery of *R. udzungwensis* provides an opportunity to investigate the scaling relationship between brain size and body size within Macroscelidea, and to compare this allometry among insectivorous species of Afrotheria and other eutherian insectivores. We performed a spin-echo magnetic resonance imaging (MRI) scan on a preserved adult specimen of *R. udzungwensis* using a 7-Tesla high-field MR imaging system. The brain was manually segmented and its volume was compiled into a dataset containing previously-published allometric data on 56 other species of insectivore-grade mammals including representatives of Afrotheria, Soricomorpha and Erinaceomorpha. Results of log-linear regression indicate that *R. udzungwensis* exhibits a brain size that is consistent with the allometric trend described by other members of its order. Inter-specific comparisons indicate that macroscelideans as a group have relatively large brains when compared with similarly-sized terrestrial mammals that also share a similar diet. This high degree of encephalization within sengis remains robust whether sengis are compared with closely-related insectivorous afrotheres, or with more-distantly-related insectivorous laurasiatheres.

Introduction

The Macroscelidea – or sengis – are small-bodied insectivorous mammals notable for their well-developed proboscis and robust hindlimb musculature. Their unique combination of physical, behavioral, and life history traits have been described as a `micro-cursorial adaptive syndrome’ [1] which includes small body size (<1 kg), a unique, highly cursorial locomotion, primarily myrmecophagous insectivory, relatively exposed sheltering habits, social monogamy, precocial litters, and female absentee neonatal care [2,3]. It has been proposed that this suite of traits enables sengis to occupy extremes of terrestrial habitats ranging from arid deserts to closed-canopy forests [1].

Morphological studies have traditionally included sengis in the polyphyletic group ‘Insectivora’ (with shrews, hedgehogs, moles, golden moles, tenrecs, and solenodons). Such morphological studies highlight the adaptive similarities among small-bodied insectivorous mammals irrespective of phylogeny. These similarities include small body size, shared features of the dentition, and relatively small brain size [4]. However, more recent studies [5,6] distinguished them from other insectivores, and recent molecular studies established the Macroscelidea as part of the supercohort Afrotheria, a monophyletic group with a very long evolutionary history [7], that contains five other orders: Proboscidea (elephants), Sirenia (manatees and dugongs), Hyracoidea (hyraxes), Tubulidentata (aardvarks), and Tenrecoidea (tenrecs and golden moles) [8-11]. Sengis are therefore relatively well-understood in terms of taxonomic position, behavioral ecology, and general morphology, but very little is known about their neuroanatomy.

Recently, a new species of giant sengi (*Rhynchocyon udzungwensis*) was discovered in Tanzania [12]. Prior to dissection of one of the specimens, we were able to perform magnetic resonance imaging (MRI) scans in order to measure the brain volume of the new species. In light of the taxonomic repositioning of sengis and the limited number of published data on sengi brain size, the discovery of *Rhynchocyon udzungwensis* provides an opportunity to re-analyze the relationship between brain size and body size in sengis. Thus, the goal of this study is to analyze brain/body allometry within sengis and compare this pattern of brain scaling to that of similarly-sized insectivore-grade terrestrial mammals. Here we compare sengis with closely-related afrotherian insectivorous tenrecs (Tenrecidae) and golden moles (Chrysochloridae), as well as more-distantly related laurasiatherian insectivores including Solenodontidae, Talpidae, Erinaceidae, and Soricidae. We are interested in determining 1) whether *R. udzungwensis* is similar to
Figure 1. Phylogeny of genera included in the present analysis. A dendrogram illustrating the phylogenetic relationships among the genera investigated in the present study [11,13-18].
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| Family          | Genus          | Species       | Body mass (g) | Brain mass (mg) | Source |
|-----------------|----------------|---------------|---------------|-----------------|--------|
| Solenodontidae  | Solodon        | paradoxus     | 672           | 4723            | [21]   |
| Tenrecidae      | Tenrec         | ecaudatus     | 852           | 2588            | [21]   |
| Tenrecidae      | Setifer        | setosus       | 237           | 1516            | [21]   |
| Tenrecidae      | Hemicentetes   | semispin      | 116           | 839             | [21]   |
| Tenrecidae      | Echinops       | telfairi      | 87.5          | 623             | [21]   |
| Tenrecidae      | Oryzorictes    | talpoides     | 44.2          | 580             | [21]   |
| Tenrecidae      | Microgale      | cowani        | 15.2          | 420             | [22]   |
| Tenrecidae      | Limnogale      | mergulus      | 92            | 1150            | [21]   |
| Tenrecidae      | Microgale      | dolsoni       | 31.9          | 557             | [21]   |
| Tenrecidae      | Microgale      | talazaci      | 48.2          | 766             | [21]   |
| Tenrecidae      | Micropotamog   | lamottei      | 64.2          | 800             | [21]   |
| Tenrecidae      | Micropotamog   | ruwenzorii    | 96.8          | 1134            | [21]   |
| Tenrecidae      | Potamogale     | velox         | 618           | 4152            | [21]   |
| Chrysochloridae | Chlorotalpa    | stuhlmanni    | 40.2          | 736             | [21]   |
| Chrysochloridae | Chrysochlori   | asiatica      | 49            | 700             | [21]   |
| Erinaceida      | Atelerix       | algirus       | 736           | 3264            | [21]   |
| Erinaceida      | Erinaceus      | europaeus     | 849           | 3367            | [21]   |
| Erinaceida      | Hemiechinus    | auritus       | 235           | 1880            | [21]   |
| Erinaceida      | Echinosorex    | gymnurus      | 823           | 6084            | [21]   |
| Soricidae       | Sorex          | alpinus       | 11            | 262             | [21]   |
| Soricidae       | Sorex          | cinereus      | 5.2           | 168             | [21]   |
| Soricidae       | Sorex          | fumeus        | 8.4           | 241             | [21]   |
| Soricidae       | Sorex          | minutus       | 4.4           | 115             | [21]   |
| Soricidae       | Sorex          | araneus       | 10.2          | 216             | [21]   |
| Soricidae       | Microsorex     | hoyi          | 2.6           | 96              | [21]   |
| Soricidae       | Neomys         | anomalus      | 11.6          | 282             | [21]   |
| Soricidae       | Neomys         | fodiens       | 15.3          | 328             | [21]   |
| Soricidae       | Blarina        | brevicauda    | 19.7          | 393             | [21]   |
| Soricidae       | Cryptotis      | parva         | 9.9           | 245             | [21]   |
| Soricidae       | Anourosorex    | squamipes     | 20.1          | 389             | [21]   |
| Soricidae       | Crocidura      | attenuata     | 9.3           | 209             | [21]   |
| Soricidae       | Crocidura      | flavescens    | 29.3          | 414             | [21]   |
| Soricidae       | Crocidura      | giffardi      | 82            | 545             | [21]   |
| Soricidae       | Crocidura      | hildegardaeae | 10.2          | 213             | [21]   |
| Soricidae       | Crocidura      | occidentalis  | 28            | 440             | [22]   |
| Soricidae       | Crocidura      | russels       | 11.1          | 197             | [21]   |
| Soricidae       | Crocidura      | suaveolens    | 10.3          | 190             | [21]   |
| Soricidae       | Crocidura      | jacksoni      | 12.7          | 250             | [21]   |
| Soricidae       | Crocidura      | leucodon      | 13.5          | 190             | [21]   |
| Soricidae       | Suncus         | etrescus      | 1.9           | 62              | [21]   |
| Soricidae       | Suncus         | murinus       | 33.8          | 383             | [21]   |
| Soricidae       | Scutisorex     | somereni      | 63.4          | 640             | [21]   |
| Soricidae       | Sylvisorex     | granti        | 3.9           | 165             | [21]   |
| Soricidae       | Sylvisorex     | megalura      | 5.5           | 188             | [21]   |
| Soricidae       | Ruwenzorisor   | suncoides     | 18.2          | 370             | [21]   |
| Soricidae       | Myosorex       | babaulti      | 17            | 360             | [21]   |
| Talpidae        | Talpa          | europaea      | 82.1          | 1024            | [21]   |
| Talpidae        | Talpa          | micrura       | 41.4          | 816             | [21]   |
| Talpidae        | Parascalops    | breweri       | 53.8          | 880             | [21]   |
other sengis in its relative brain size, and 2) whether the relative brain sizes of sengis overlap that of other insectivore-grade terrestrial mammals. Figure 1 illustrates the phylogenetic relationships of the taxa used in this study [11,13-18].

Materials and Methods

Brain mass was measured from a preserved adult specimen (MTSN 8069) of R. udzungwensis described by Rovero et al. [12] as a partially-eaten carcass abandoned by a raptor. The carcass was collected under permit from the Tanzania Commission for Science and Technology [12]. Although parts of the pelvis and hindlimb had been consumed, the head was intact and well-preserved. To estimate brain volume we performed high-resolution 3D spin echo scans (TR = 81.6 ms, TE = 21.7 ms, Matrix = 512 x 512 x 256, Voxel size = 270 μm x 270 μm x 390 μm) using a 7-Tesla high-field MR imaging system (Bruker Biosystems).

In order to control for statistical non-independence due to phylogeny, we performed additional tests using a phylogenetic generalized least squares (PGLS) regression model with Pagel’s lambda [24,25]. PGLS analyses were conducted with the caper software package [26] in the R computing environment [27] using branch lengths from Bininda-Emonds et al. [28].

Results

Segmentation of the R. udzungwensis MRI (Figure 2) yielded a brain volume of 6.883 cc. When multiplied by the specific gravity of brain tissue, the brain mass is calculated to be 7.131 g. This represents the largest brain in the present dataset, followed by the brains of Echinosorex and two other Rhynchocyon species. With a body mass of 710 g, R. udzungwensis is surpassed in body size by several other species of Erinaceidae and Tenrecidae. When the brain size of R. udzungwensis is compared with the four other species of Macroscelidea in the dataset, the R. udzungwensis datapoint falls on the allometric trend line defined by the two smaller-bodied Elephantoidea species and the two larger-bodied Rhynchocyon species (Figure 3). Although the sample size is small, this indicates that the brain mass of R. udzungwensis is consistent with what would be expected in a sengi of its body mass.

RMA regression of body mass on brain mass for all species yields a best-fit line with a slope of 0.71 (n = 57, R² = 0.94, p<0.001; 95% CI: 0.67–0.76). For inter-specific tests, we compare on residual scores (to detect differences in line elevation/intercept) and fitted scores (to detect shifts along a common slope) [23].

Table 1. Cont.

| Family       | Genus    | Species    | Body mass (g) | Brain mass (mg) | Source |
|--------------|----------|------------|---------------|-----------------|--------|
| Talpidae     | Scalopus | aquaticus  | 115            | 1310            | [21]   |
| Talpidae     | Desmana  | moschata   | 443            | 4000            | [21]   |
| Talpidae     | Galemys  | pyrenaicus | 59.7           | 1329            | [21]   |
| Macroscelidida | Elephantulus | fuscipes | 57             | 1330            | [22]   |
| Macroscelidida | Elephantulus | myurus    | 45.1           | 1270            | [19]   |
| Macroscelidida | Rhynchocyon | stuhlmanni | 490           | 6100            | [22]   |
| Macroscelidida | Rhynchocyon | peteri    | 471            | 5400            | [20]   |
| Macroscelidida | Rhynchocyon | udzugwensis | 710          | 7131            | Present Study |

Dataset of body size and brain size for insectivorous mammals used in the present analysis. doi:10.1371/journal.pone.0058667.t001

Figure 2. Maximum intensity projections of the R. udzungwensis MRI. Two views of the R. udzungwensis MRI visualized as maximum intensity projections with the brain highlighted in white. A) Antero-lateral oblique view. B) Superior view, scale bar = 5 cm. doi:10.1371/journal.pone.0058667.g002
brain allometry in: 1) sengis versus all other insectivores, 2) sengis versus other afrotherian insectivores only, 3) sengis versus laurasiatherian insectivores, and 4) afrotherian insectivores (including sengis) versus laurasiatherian insectivores. The results of each of these comparisons are summarized in Table 2.

When the sample is grouped according to Macroscelidea (n = 5) versus all other insectivores (n = 52), the test for heterogeneity of slopes indicates that the slopes of the two lines are statistically indistinguishable (common slope = 0.66; 95% CI: 0.63–0.70). Residual axis scores indicate that the best-fit line describing Macroscelidea has a significantly larger y-intercept than the line describing other insectivores ($X^2 = 142.36, p<0.001$).

We repeated this comparison using the PGLS model to control for phylogeny. Pagel’s lambda was 0.880, indicating a strong
Table 2. Summary of results.

| Comparison                      | Test for heterogeneity of slopes | Common slope (95% CI) | WALD test for difference in elevation/intercept | WALD test for shift along common slope |
|---------------------------------|----------------------------------|-----------------------|-----------------------------------------------|----------------------------------------|
| sengis vs. other insectivores   | \( p = 0.336 \)                  | 0.66 (0.63–0.70)      | \( X^2 = 142.36, p < 0.001 \)                 | \( X^2 = 9.847, p = 0.002 \)            |
| sengis vs. other afrotherian    | \( p = 0.163 \)                  | 0.65 (0.55–0.70)      | \( X^2 = 76.94, p < 0.001 \)                 | \( X^2 = 3.632, p = 0.057 \)            |
| insectivores only               |                                  |                       |                                               |                                        |
| sengis vs. laurasiatherian      | \( p = 0.229 \)                  | 0.67 (0.64–0.72)      | \( X^2 = 110.471, p < 0.001 \)              | \( X^2 = 11.846, p = 0.001 \)           |
| insectivores only               |                                  |                       |                                               |                                        |
| afrotherian insectivores vs.    | \( p = 0.626 \)                  | 0.70 (0.65–0.74)      | \( X^2 = 0.864, p = 0.353 \)                | \( X^2 = 13.829, p < 0.001 \)          |
| laurasiatherian insectivores    |                                  |                       |                                               |                                        |

Statistical comparisons of brain/body allometry among the insectivores in the present sample. Results indicate that sengis have relatively larger brains for a given body size compared with other insectivore-grade mammals.

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Discussion

The recent discovery of new extant species of sengi has increased the number of known species of Macroscelidea and more may yet be described [29–31]. Dumbacher and colleagues [31] recently elevated the two subspecies of *Macroscelides* to species level using a combination of genetic and morphological markers. In 2008, Smit et al. discovered *Elephantulus plicatus* during an investigation of genetic biogeography in South African sengis [30]. Also in 2008, Rovero et al. reported the discovery of *Rhinchoycon udzungwensis* from isolated high-elevation forests of Tanzania [12]. *R. udzungwensis* has the largest body mass of any extant sengi yet discovered. There is a paucity of data on brain size in macroscelidians, but in the present study we are able to compare the brain size of the newly-discovered *Rhinchoycon* specimen with data from four other species of Macroscelidea. Our analyses indicate that *R. udzungwensis* exhibits a brain mass that is within the confidence intervals of the regression line described by the small-bodied *Elephantulus* and the large-bodied *Rhinchoycon*. These results suggest a consistent pattern of brain allometry within Macroscelidea, although additional data collection on other sengis will be necessary in order to quantify this relationship more precisely.

Very little is known about brain allometry in Macroscelidea compared with other insectivores, especially following the taxonomic repositioning of sengis from ‘Insectivora’ into Afrotheria. Stephan et al. [21,22] provide the most comprehensive dataset of brain- and body-size among insectivores (including size of individual brain structures). They report brain-size values for three species of Macroscelidea (incorporated here), but the authors recognized that Macroscelidea had likely been incorrectly placed within ‘Insectivora’ and therefore excluded the sengis from their analyses.

Our inter-specific comparisons using the new phylogenetic rubber indicate that macroscelidians have relatively large brains when compared with similarly-sized terrestrial mammals that also share a similar diet. This high degree of encephalization within sengis appears to hold whether sengis are compared with closely-related insectivorous afrotheres, or with more-distantly-related insectivorous laurasiathères. In fact, the brain-body allometry of Macroscelidea may be more similar to larger-brained non-insectivorous groups such as Rodentia or Lagomorpha, rather than smaller-brained insectivores.

An alternative interpretation that sengis have relatively smaller bodies must also be considered. The earliest sengis are primarily known from dental specimens, Grossman and Holroyd [32] use published equations [33,34] for reconstructing small mammal body mass from dental dimensions to reconstruct the body mass of early sengis. These reconstructions indicate that the earliest Macroscelidians such as *Chambus* [35,36] and *Nemenchatherium* [37] were similar in body size to modern macroscelidene sengis such as *Elephantulus* or *Petrodromus*. Early members of the modern sengi subfamilies *Rhinchoyconinae* (*Myothyranthocyon* [38,39]) and *Macroscelidinae* (*Msweng* [40]) are similar in size to their living relatives. Thus, there is little evidence to suggest that sengis underwent body size reduction during their evolution.

The functional significance of sengi encephalization remains unclear. But there are some suggestions from the literature that merit further study. Using electrophysiology, Dengler-Crish et al. [41] found a large somatosensory representation of the proboscis, vibrissae, and tongue in the cortex of the South African sengi *Elephantulus edwardsi*. And using immunohistochemistry, Pieters et al. found cholinergic neurons present in the cochlear nucleus and both colliculi of the Eastern Rock sengi *Elephantulus myurus* that are not present in hyraxes, rodents, and primates, possibly suggesting an auditory adaptation for predator avoidance [19]. Additionally, Sherwood et al. found that the giant elephant shrew *Rhinchoycon petersi* exhibits a high density of
calcoxin interneurons, a trait which they find to be derived from the stem mammal condition [20].

In relation to our analysis, sengis differ radically from other insectivores in their locomotor behavior, especially as it pertains to predator avoidance mechanisms. Modern sengis move very quickly and with notable agility, most likely by a uniaxial, cursorial/saltatorial mode of locomotion [2,42] using their relatively longer hindlimbs to generate a bounding motion. By contrast, most other insectivore-grade mammals move comparatively slowly. Furthermore, sengis create and maintain a complex trail system that they use for escaping predators [43-45]. Perhaps in the future, the underlying neuronal mechanisms for these behaviors, and many others, will help to explain the pattern of sengi brain allometry observed here.

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