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Reconstructing the molecular phylogeny of giant sengis (Macroscelidea; Macroscelididae; *Rhynchocyon*)

Elizabeth J. Carlen [a,b,1], Galen B. Rathbun [a], Link E. Olson [c], Christopher A. Sabuni [d], William T. Stanley [e], John P. Dumbacher [a,b,*]

[a] Institute for Biodiversity Science and Sustainability, California Academy of Sciences, San Francisco, CA 94118, United States
[b] Department of Biology, San Francisco State University, San Francisco, CA 94132, United States
[c] University of Alaska Museum, Fairbanks, AK 99775, United States
[d] Pest Management Centre, African Centre of Excellence, Sokoine University of Agriculture, Morogoro, Tanzania
[e] Science & Education, Field Museum of Natural History, Chicago, IL 60605, United States

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ABSTRACT

Giant sengis (Macroscelidea; Macroscelididae; *Rhynchocyon*), also known as giant elephant-shrews, are small-bodied mammals that range from central through eastern Africa. Previous research on giant sengi systematics has relied primarily on pelage color and geographic distribution. Because some species have complex phenotypic variation and large geographic ranges, we used molecular markers to evaluate the phylogeny and taxonomy of the genus, which currently includes four species: *R. chrysopygus*, *R. cirnei* (six subspecies), *R. petersi* (two subspecies), and *R. udzungwensis*. We extracted DNA from fresh and historical museum samples from all taxa except one *R. cirnei* subspecies, and we generated and analyzed approximately 4700 aligned nucleotides (2685 bases of mitochondrial DNA and 2019 bases of nuclear DNA) to reconstruct a molecular phylogeny. We genetically evaluate *Rhynchocyon* spp. sequences previously published on GenBank, propose that the captive *R. petersi* population in North American zoos is likely *R. p. adersi*, and suggest that hybridization among taxa is not widespread in *Rhynchocyon*. The DNA sample we have from the distinctive but undescribed giant sengi from the Boni forest of northern coastal Kenya is unexpectedly nearly identical to *R. chrysopygus*, which will require further study. Our analyses support the current morphology-based taxonomy, with each recognized species forming a monophyletic clade, but we propose elevating *R. c. stuhlmanni* to a full species.

1. Introduction

The 19 extant species of sengis (elephant-shrews; Rathbun and Kingdon, 2006) in the mammalian Order Macroscelidea are restricted to the African continent and form two well-defined subfamilies, the soft-furred sengis (Macroscelidinae), with 15 extant species in four genera (*Elephantulus*, *Macroscelides*, *Petrodromus,* and *Petrosaltator*), and the giant sengis (Rhynchocyoninae), with four extant species in one genus (*Rhynchocyon*).

Despite their long evolutionary history (Novacek, 1984) and broad African distribution (Corbet and Hanks, 1968) in highly diverse habitats across much of Africa (Rathbun, 2009), sengis have proven to be taxonomically challenging, having relatively few discretely varying morphological traits with which to resolve their phylogeny and taxonomy (Corbet and Hanks, 1968). With the application of molecular genetics in the last several decades, some insights into extant sengi phylogeny and taxonomy have been gained. This work has shown that Macroscelididae are morphologically specialized, yet across a diversity of habitats, they maintain a stable life history and morphology that has masked some of their evolutionary and ecological diversity (Rathbun, 2009).

Abbreviations: 12s16s, 12S rRNA, valine tRNA, and 16S rRNA; AMNH, American Museum of Natural History; BLAST, basic local alignment search tool; BMNH, Natural History Museum, London; Bpp, Bayesian posterior probability; CAS, California Academy of Sciences; CASMAM, California Academy of Sciences Mammalogy; D-loop, hypervariable 5′ end of the control region; ENAM, Enamelin; FMNH, Field Museum of Natural History; IRBP, inter-photoreceptor retinoid-binding protein; MCMC, Markov Chain Monte Carlo; MCZ, Museum of Comparative Zoology; mlb, maximum likelihood bootstrap; MTSN, Museo Tridentino di Scienze Naturali; NCBI, National Center for Biotechnology Information; ND2, NADH dehydrogenase 2; PCR, polymerase chain reaction; RAxML, Random Axelerated Maximum Likelihood; RMCA, Royal Museum of Central Africa; SNP, single nucleotide polymorphism; UAM, University of Alaska Museum; vWF, Von Willebrand factor.

* Corresponding author.
E-mail address: jdumbacher@calacademy.org (J.P. Dumbacher).
[1] Present address: Department of Biology, Fordham University, Bronx, NY 10458, United States.

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Giant sengis, as their name indicates, are the largest members of the order, with body masses ranging from 300 g to 700 g. They are diurnal, swift quadrupedal forest-floor dwellers with proportionally long legs, a long sparsely-haired tail, and a long snout that can twist and probe in leaf litter in search of invertebrate prey. The golden-rumped sengi (*R. chrysopygus*) is the only giant sengi whose behavioral ecology has been studied in sufficient detail to reveal that its life history is unusual for a small mammal (Rathbun, 2009). Individuals form monogamous pairs on territories, shelter singly in leaf nests on the forest floor, and produce one relatively precocial offspring at a time (FitzGibbon, 1997; Rathbun, 1979).

In the 65 years between 1847 and 1912, ten species and four subspecies of *Rhynchocyon* were described. Corbet and Hanks (1968), using mostly distinctive pelage color patterns (Fig. 1) and allopatric distributions (Fig. 2), conducted a thorough taxonomic revision of the order, resulting in only three recognized giant sengi species. The golden-rumped sengi (*R. chrysopygus*) is monotypic and occurs in coastal Kenya. The black-and-rufous sengi (*R. petersi),* has two subspecies: *R. p. adersi* from islands off Tanzania and *R. p. petersi* from mainland Tanzania and Kenya (Fig. 2). The checkered sengi (*R. cirnei*) has six subspecies: *R. c. cirnei* from Mozambique and southern Malawi, *R. c. shirensis* from the Shire Valley of southern Malawi, *R. c. reichardi* from Tanzania, Malawi, and Zambia highlands, *R. c. hendersoni* from highlands of northern Malawi, *R. c. macrurus* from southeastern Tanzania lowlands, and *R. c. stuhlmanni* from the Congo Basin and western Uganda (Fig. 2). *Rhynchocyon c. shirensis* was a new taxon (Corbet and Hanks, 1968), whereas the other subspecies had previously been described as full species. Corbet and Hanks (1968) also noted that *R. c. stuhlmanni*

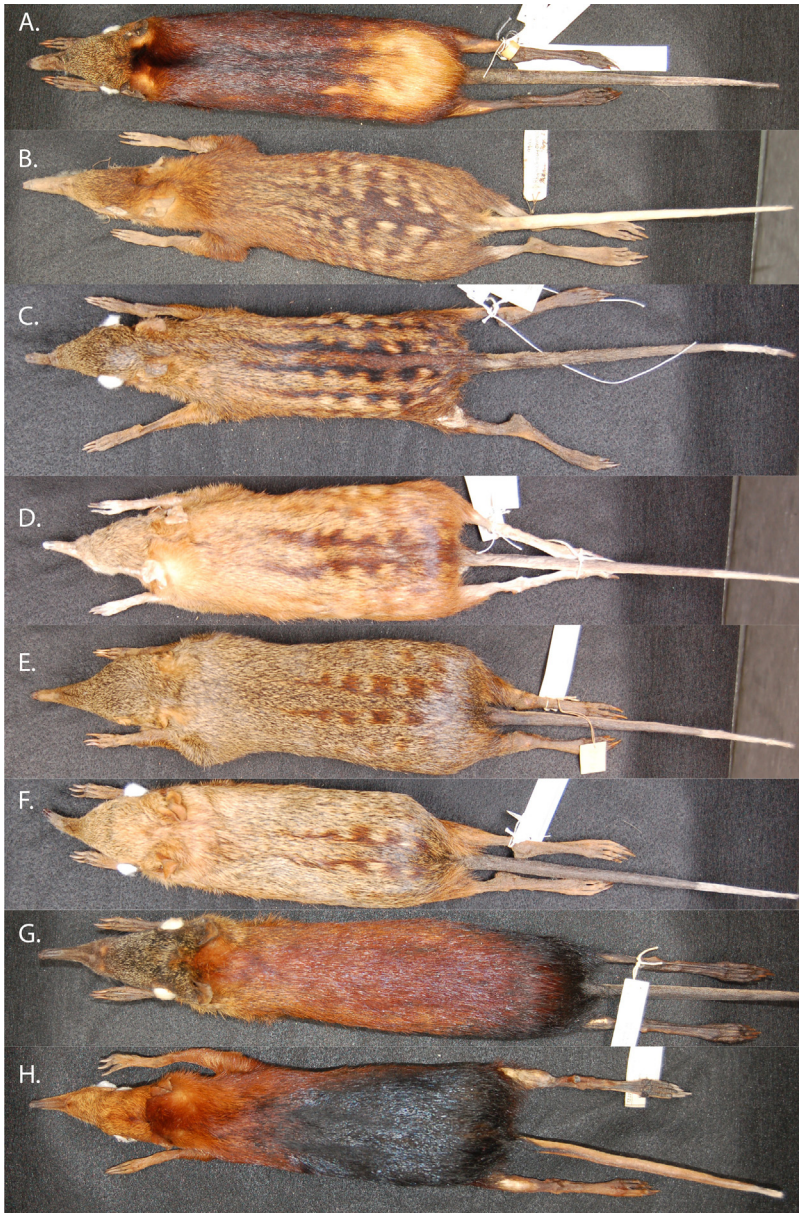

Fig. 1. Study skins showing the color patterns of *Rhynchocyon* taxa (see text for museum abbreviations associated with following catalog numbers). From top to bottom: (A) *R. chrysopygus* CAS MAM 24526; (B) *R. cirnei stuhlmanni* AMNH 49462 (light form of cline), (C) *R. cirnei reichardi* CAS MAM 28535; (D) *R. cirnei macrurus* AMNH 179301 (light form of cline), (E) *R. cirnei shirensis* AMNH 161777; (F) *R. cirnei cirnei* CAS MAM 29358; (G) *R. udzungwensis* CAS MAM 28043; (H) *R. petersi petersi* CAS MAM 30667. The Boni *Rhynchocyon* is not represented, but is superficially similar to *R. udzungwensis*, as are the clinal dark forms of *R. c. macrurus* from southeastern coastal Tanzania and *R. cirnei stuhlmanni* from western Uganda (see Corbet and Hanks, 1968).