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ARTICLE

DIVERSITY AND BODY SIZE IN GIANT CAVIOMORPHS (RODENTIA) FROM THE NORTHERN NEOTROPICS—A STUDY OF FEMORAL VARIATION

M. GEIGER,[1] L. A. B. WILSON,[2] L. COSTEUR,[3] R. SÁNCHEZ,[4] and M. R. SÁNCHEZ-VILLAGRA[*,5]
[1]Paläontologisches Institut und Museum, Universität Zürich, 8006 Zürich, Switzerland, madeleine.geiger@pim.uzh.ch;
[2]School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington NSW 2052, Australia, laura.wilson@unsw.edu.au;
[3]Naturhistorisches Museum Basel, Augustinergasse 2, CH-4001 Basel, Switzerland, loic.costeur@bs.ch;
[4]Smithsonian Tropical Research Institute, Box 0843- 03092, Balboa, Ancon, República de Panamá, rodolfosanchez128@hotmail.com;
[5]Paläontologisches Institut und Museum, Karl-Schmid-Strasse 4, CH-8006 Zürich, Switzerland, m.sanchez@pim.uzh.ch

ABSTRACT—New discoveries of numerous fossil femora from giant caviomorph rodents from the Miocene of Venezuela and a specimen of a Miocene giant rodent from Trinidad in the collections of the Naturhistorisches Museum in Basel made possible the first examination of taxonomic, ontogenetic, and functional variation in these animals. We provide comparisons of femoral shape, metrics, and growth (epiphyseal closure), finding that four morphotypes are distinguishable based largely on degrees of robustness or gracility. This indicates that the diversity of giant caviomorphs was larger than previously known; *Phoberomys pattersoni* was not the only giant caviomorph that inhabited the Miocene of the northern Neotropics. The study of cortical cross-sectional area of fossils serves to estimate the body mass for two giant caviomorphs at 420–580 kg. The first description of patterns of bone microstructure in three fossil giant caviomorph femora reveals similarities to extant rodents: absence of Haversian tissue and presence of layers of lamellar followed by reticular-like bone.

INTRODUCTION

The ecomorphological diversity of caviomorph rodents (Hystricognathi) includes semiaquatic, terrestrial, arboreal, scansorial, and fossorial forms, all part of a Neotropical radiation with the oldest record in the middle Eocene (Antoine et al., 2011). The body size range of the clade is expanded by an order of magnitude when considering fossil forms (Rinderknecht and Blanco, 2008), for which a large diversity is recorded in the Cenozoic (Vucetich et al., 1999). Some of the largest caviomorphs belong to the Neoepiblemidae, and *Phoberomys* Kraglievich, 1926, is the largest among these. Most findings of this genus are based on isolated teeth, thus the report of a partial skeleton of *P. pattersoni* Mones, 1981, from the Urumaco Formation (late Miocene) in the northwest of Falcón State, Venezuela, was significant (Sánchez-Villagra et al., 2003). A phylogenetic analysis suggested a sister-group relationship of *Phoberomys* with *Dinomys*, the pacarana (Horovitz et al., 2006). Moreover, the study of morphological peculiarities of the skeleton and teeth indicated that these animals might have used the forelimbs for food manipulation and that their diet was abrasive, most probably including sea grasses (Horovitz et al., 2006, 2010). In the last 10 years, numerous expeditions by the last author, Orangel Aguilera (Aguilera, 2004), and colleagues have resulted in the discovery of several remains of giant rodents from Urumaco, some of which were illustrated or treated briefly by Horovitz et al. (2006, 2010). Most of these remnants are femora, perhaps because of their great robustness compared with other bones of the postcranium.

Of significance in this context is a large rodent femur reported by Schaub (1935) from the Springvale Beds, Caroni County, Trinidad. This formation is also Late Miocene in age (Kugler, 2001; Horovitz et al., 2010) and related to the Codore Formation in the Urumaco Sequence (Kugler, 2001), which forms the upper contact with the Urumaco Formation.

Here, we include the currently known fossil giant caviomorph femora from Urumaco and the Springvale Beds in one study that integrates three different approaches, in order to gain insights into the paleobiology of these animals. First, we provide comparisons of femoral peculiarities through morphology-based (descriptions and measurements) and ontogeny-based (epiphyseal closure) investigations. Second, we complement body mass estimates for *P. pattersoni* with calculations based on two giant caviomorph specimens. Third, we provide the first description of patterns of bone microstructure in three fossil giant caviomorph femora.

Institutional Abbreviations—**AMU-CURS**, Alcaldía de Urumaco, Colección Urumaco Rodolfo Sánchez, Urumaco, Venezuela; **CIAAP**, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Coro, Venezuela; **NMB**, Naturhistorisches Museum Basel, Basel, Switzerland; **UNEFM**, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela, **ZMUZH**, Zoologisches Museum der Universität Zürich, Zurich, Switzerland.

MATERIALS AND METHODS

Measurements

We took five measurements from seven fossil femora with calipers to the nearest 0.01 cm. Measurements were chosen to reflect the morphological peculiarities of the specimens, in addition to being easy to reproduce and measureable on as many of the fossils as possible. The measurements were modified from Knussmann (1980), Herrmann et al. (1990), and Buikstra and Ubelaker (1994) and are defined as follows (Fig. 1):

[*]Corresponding author.