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The Anatomy of the World's Largest Extinct Rodent
Marcelo R. Sánchez-Villagra, *et al.*
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Supporting Online Material

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Fig. S1

27 June 2003; accepted 13 August 2003

The Anatomy of the World's Largest Extinct Rodent

Marcelo R. Sánchez-Villagra,[1]* Orangel Aguilera,[2] Inés Horovitz[3]

Phoberomys **is reported to be the largest rodent that ever existed, although it has been known only from isolated teeth and fragmentary postcranial bones. An exceptionally complete skeleton of *Phoberomys pattersoni* was discovered in a rich locality of fossil vertebrates in the Upper Miocene of Venezuela. Reliable body mass estimates yield ~700 kilograms, more than 10 times the mass of the largest living rodent, the capybara. With *Phoberomys*, Rodentia becomes one of the mammalian orders with the largest size range, second only to diprotodontian marsupials. Several postcranial features support an evolutionary relationship of *Phoberomys* with pakaranas from the South American rodent radiation. The associated fossil fauna is diverse and suggests that *Phoberomys* lived in marginal lagoons and wetlands.**

Phoberomys belongs to the Caviomorpha, a diverse and endemic group of South American rodents that includes arboreal, cursorial, and fossorial forms and that ranges today in size between ~200 g and ~50 kg (*1*). The evolution of caviomorphs is recorded in a rich but geographically biased fossil record. The southern portion of South America contains most of the record (*2*); hence, discoveries in the northern tropics are of special significance. The Urumaco Formation in northwestern Venezuela contains one of the few examples of a diverse fauna of Upper Miocene vertebrates in the continent. Recent explorations resulted in the discovery of additional vertebrates in the upper and middle members of this formation, including the rodent reported here (table S1). Old and new discoveries make Urumaco one of the best-documented tropical Miocene fossil fauna of vertebrates in the world after La Venta in Colombia (*3*).

The Urumaco Formation is characterized by diverse faunal associations in continental (savannas), freshwater (swamps and rivers), estuarine (brackish), and marine (coastal lagoon, salt marsh, and sandy littoral) environments (table S1). Each assemblage can be correlated with a distinctive sedimentary environment. The following facies are apparent: shallow-water marine sediments rich in mollusks and fishes; brackish water rich in marine catfish; and swampy paleoenvironments rich in crocodilians and gavialids, in freshwater and marine turtles, and in freshwater catfish. These general sequences repeat several times in the outcrop (*4*). The skeleton reported here was found in brown shales interbedded with thin layers of coal.

Two specimens of *Phoberomys pattersoni* Mones 1980 (*5*) provide the basis for this report. One consists of an almost complete associated skeleton (Fig. 1A). The skull is poorly preserved and consists of a deformed palate with the upper molariform series and most of the dentaries, with molariform teeth and fragments of the incisors. An additional shattered partial skull, preserving most of the occipital and portions of the basicranial region, was also collected (Fig. 1B). Based on the degree of tooth wear and sutural fusion, we estimate that the specimens were adults at the time of death. The proximal epiphysis of the tibia and the distal epiphysis of the ulna are not fused to the diaphysis. However, it is possible that the animal was an adult, because no sutures can be recognized in the occipital region. In the pakarana *Dinomys*, probably the closest extant relative of *Phoberomys*, the epiphyses of long bones fuse late in ontogeny, some during adulthood (*6*). A description of the anatomy of the postcranial skeleton of *P. pattersoni* is presented in the supporting online material.

Allocation of the specimens to *P. pattersoni* is secured based on two diagnostic features of the last upper molar (*5*): the narrowing of the posteriormost portion at the level of the last three prisms, and the size (mesiodistal length: 41 mm; width: 20.7 mm) and relative proportions of this tooth. Based solely on tooth dimensions, *P. pattersoni* is slightly smaller than *P. insolita* and *P. lozanoi*, which have a M3 with a mesiodistal length of 47 and 48 mm, respectively. *Phoberomys*, together with the genera *Neoepiblema* and *Eusigmomys*, belongs to the fossil Family Neoepiblemidae, distributed in Argentina, Chile, Brazil, and Venezuela (*7*). Of all other species of Neoepiblemidae, cranial remains of only *Neoepiblema ambrosettianus* have been reported to date (*7*). This animal had a prominent sagittal crest, absent in *P. pattersoni*. Based on fragmentary dental remains, *Phoberomys* (and therefore the neoepiblemids) has been classified either with the chinchillas and viscachas (*8*), with the pakarana (*9*), or as the sister group to both (*10*). We plotted a set of 13 postcranial characters on a preexisting phylogenetic tree based on molecular data and found that several postcranial features support the association of *Phoberomys* with the pakarana (Fig. 2). This position for *Phoberomys* was the one that required the least number of steps.

P. pattersoni is reported to have been the size of a rhinoceros (*1*, *11*, *12*). This rough estimate, based on isolated teeth, can be

[1]Universität Tübingen, Spezielle Zoologie, Auf der Morgenstelle 28, D-72076 Tübingen, Germany. [2]Universidad Nacional Experimental Francisco de Miranda, CICBA, Complejo Docente Los Perozos, Carretera Variante Sur, Coro, 4101, Estado Falcón, Venezuela. [3]Department of Organismic Biology, Ecology, and Evolution, 621 Young Drive South, University of California, Los Angeles, CA 90095–1606, USA.

*To whom correspondence should be addressed. E-mail: marcelo.sanchez@uni-tuebingen.de

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checked using the new postcranial material. Estimation of body mass in *Phoberomys* has two main limitations: We do not know what kind of locomotion the animal performed (*13*), and its body size was obviously an order of magnitude larger than that of the largest extant representatives of its group (*14*). Despite these caveats, having available both femora and humeri of the same specimen permits the calculation of a range of body mass. Femora and humeri provide the most reliable estimates because they do not share weight-bearing functions with other bones in their limb segments (*15*). The body mass is estimated using predictive equations based on anteroposterior diameters of humeral and femoral diaphyses. The equations are provided on the basis of data for 53 specimens representing 16 species of caviomorphs showing different locomotor habits (*15*). The anteroposterior diameter was measured at 35 and 65% from the distal end for the humeral and femoral shafts, respectively. The analysis yields body mass estimates of 436 kg using the humerus and of 741 kg using the femur (*16*).

Among caviomorphs and many other mammals, femoral sections tend to have greater anteroposterior diameters than do humeral sections of the same animal (*15*, *17*). *Phoberomys* had a gracile forelimb and a disproportionately robust hindlimb. Tibia and femur are particularly robust—much more so in *Phoberomys* in relation to the rest of the skeleton than is the case in most extant caviomorphs (*18*). It is likely that the hindlimbs of *Phoberomys* played a more impor-

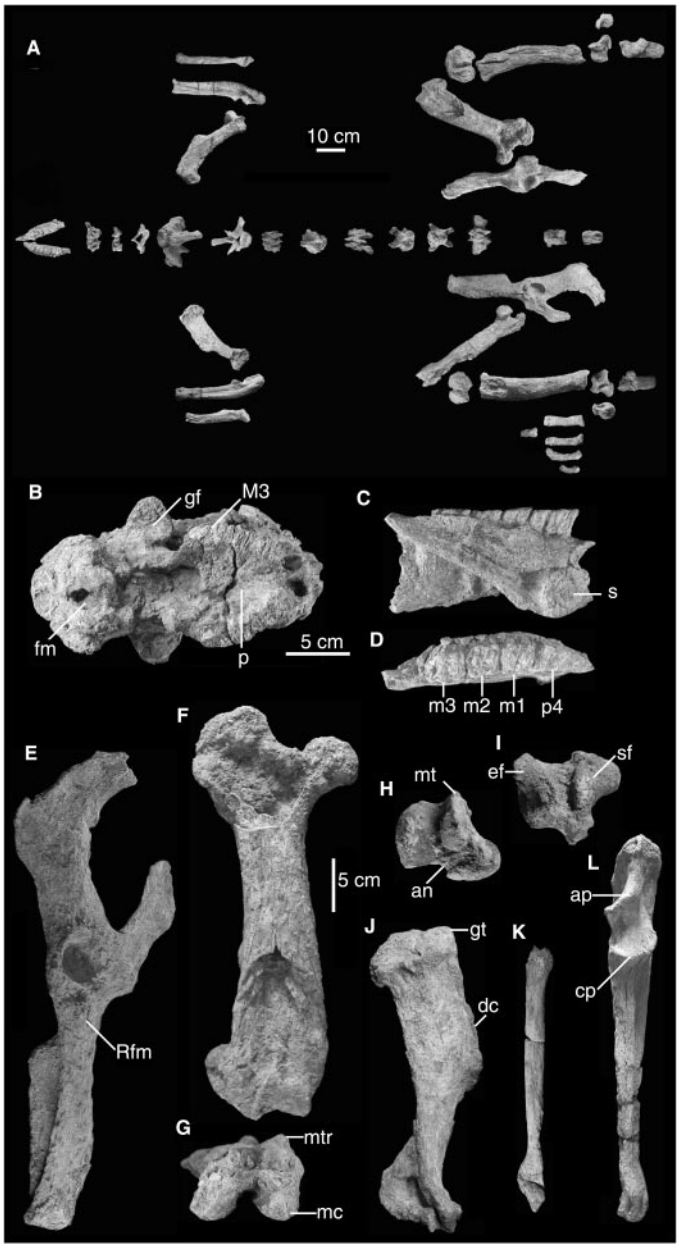


Fig. 1. *Phoberomys pattersoni*. (**A**) Entire array of elements of skeleton (Universidad Nacional Experimental Francisco de Miranda, UNEFM-VF-020) in different views, collected at Tío Gregorio (11° 14′52″N, 70°18′18″W), in the northern part of the town of Urumaco. Most of the skeleton is preserved with the exception of several bones from the hands and feet, the scapulae, and the ribs. Thirteen vertebrae are preserved, including the atlas. (**B**) Additional shattered partial skull in ventral view (UNEFM-VF-021), preserving most of the occipital and portions of the basicranial region. Collected in El Hatillo, sector Taparito (11°14′31″N/70°14′44″W). (**C**) Lingual and (**D**) occlusal view of the left dentary of UNEFM-VF-020. (**E** to **L**) Miscellaneous bones of UNEFM-VF-020. (E) Left innominate, lateral view; (F) right femur, anterior view; (G) right femur, distal view; (H) astragalus, dorsal view; (I) astragalus, ventral view; (J) humerus, flexor aspect; (K) radius; (L) right ulna, anterior view. Abbreviations: an, astragalar neck; ap, anconeal process; cp, coronoid process; dc, deltoid crest; ef, ectal facet; fm, foramen magnum; gf, glenoid fossa; gt, greater tubercle; mc, medial condyle; mt, medial trochlea; mtr, medial trochlear ridge; p, palate; Rfm, Rectus femoris muscle attachment; s, mandibular symphysis; sf, sustentacular facet. Bars: (A), 10 cm; (B) to (D), 5 cm; (E) to (L), 5 cm.

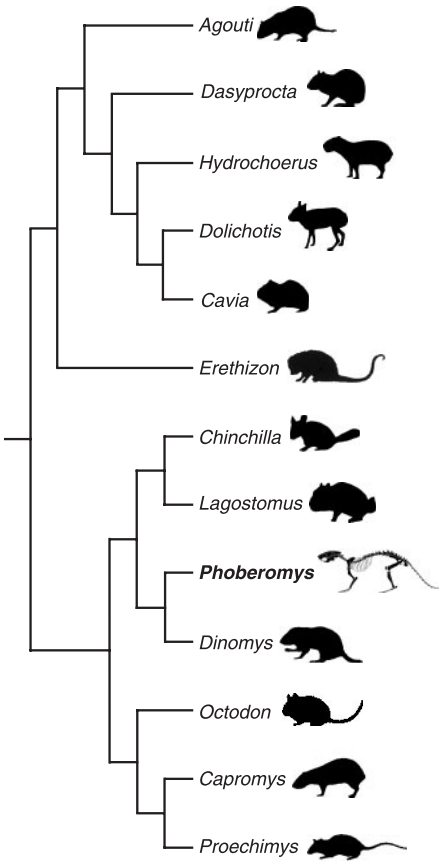


Fig. 2. Phylogenetic position of *Phoberomys* superimposed on a phylogeny of caviomorph rodents (*23*) compared in this study. Thirteen characters and 29 character states were examined in 13 caviomorphs. Relationships among taxa were based on a parsimony analysis of molecular data (*23*, *24*), and *Phoberomys* was added to that tree in several alternative positions, using the scaffold approach (*25*). The morphological characters were optimized in these different topologies. The most parsimonious placement for *Phoberomys* was as sister group of *Dinomys* (47 steps), three steps shorter than the hypothesis of sister group relationship with chinchillas and viscachas and indeed at least three steps shorter than any other hypothesis. Based only on dental traits, *Phoberomys* has been classified together with the chinchillas and viscachas, with the pakaranas (*Dinomys*), or as sister group to both. Several postcranial traits support the pakarana hypothesis, represented in this tree: Rectus femoris muscle attachment in pelvis forms an elongated crest; medial and lateral ridges of femoral trochlea convergent proximally; medial condyle wider than lateral condyle in posterior view of femur; medial ridge of astragalar trochlea protrudes posteriorly further than lateral one; anconeal process of ulna extends further cranially than coronoid process. Some of these shared-derived character states of *Dinomys* and *Phoberomys* evolved convergently in other caviomorphs. See supplementary information for a complete list of characters, the character matrix, and a list of specimens examined.

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tant role in locomotor propulsion than the forelimbs, which were probably important in food manipulation. Because of this, the body mass estimation based on the femur is more reliable: *P. pattersoni* probably weighed ~700 kg. With *Phoberomys*, the size range of the order is increased and Rodentia becomes one of the mammalian orders with the widest size variation, second only to the Diprotodontia (kangaroos, koalas, wombats, and possums) (fig. S1).

The fossil record of Caviomorpha is extensive, with 140 fossil genera recognized in a recent review (*8*), but no form competes with *Phoberomys* in terms of size. *Artigasia magna* from the upper Pliocene of Uruguay is reported to be gigantic, but its lower teeth are only ~60% the size of those of *P. pattersoni* (*19*). *Artigasia*, like most fossil rodents, is known based only on dental and mandibular parts.

The paleoenvironment in which *P. pattersoni* was found and the associated fauna indicate that this rodent was either semiaquatic or foraged in or near water, as capybaras do. *P. pattersoni* had a deep and massive horizontal ramus of the mandible, correlated with a high degree of hypsodonty. *Phoberomys* clearly had an abrasive diet, perhaps consisting of seagrasses. Potential predators could have been the many crocodiles reported from Urumaco, including some of the largest forms that ever existed, such as *Purussaurus* spp. Contemporaries included *Stupendemys geographicus*, the world's largest turtle (*20*).

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Amazonia 1492: Pristine Forest or Cultural Parkland?

Michael J. Heckenberger,[1]* Afukaka Kuikuro,[4] Urissapá Tabata Kuikuro,[4] J. Christian Russell,[2] Morgan Schmidt,[3] Carlos Fausto,[5] Bruna Franchetto[5]

Archaeology and indigenous history of Native Amazonian peoples in the Upper Xingu region of Brazil reveal unexpectedly complex regional settlement patterns and large-scale transformations of local landscapes over the past millennium. Mapping and excavation of archaeological structures document pronounced human-induced alteration of the forest cover, particularly in relation to large, dense late-prehistoric settlements (circa 1200 to 1600 A.D.). The findings contribute to debates on human carrying capacity, population size and settlement patterns, anthropogenic impacts on the environment, and the importance of indigenous knowledge, as well as contributing to the pride of place of the native peoples in this part of the Amazon.

Was the Amazon a natural forest in 1492, sparsely populated and essentially pristine, as has been traditionally thought? Or, instead, were parts of it densely settled and better viewed as cultural forests, including large agricultural areas, open parklands, and working forests associated with large, regional polities (*1*–*3*). Despite growing popularity for the latter view (*4*–*6*), entrenched debates regarding pre-Columbian cultural and ecological variation in the region remain unresolved due to a lack of well-documented case studies (*7*, *8*). Here, we present clear evidence of large, regional social formations [circa (c.) 1250 to 1600 A.D.] and their substantial influence on the landscape, where they have altered much of the local forest cover. Specifically, archaeological research in the Upper Xingu (Mato Grosso, Brazil), including detailed mapping and excavations of extensive earthen features (such as moats, roads, and bridges) in and around ancient settlements, reveals unexpectedly complex regional settlement patterns that created areas of acute forest alteration.

The Upper Xingu is unique in the southern peripheries of the Amazon as the largest contiguous tract of tropical forest still

[1]Department of Anthropology, [2]Land-Use and Environmental Change Institute, [3]Department of Geography, University of Florida, Gainesville, FL 32611, USA. [4]Associação Indígena Kuikuro do Alto Xingu, Parque Indígena do Xingu, Mato Grosso, Brazil. [5]Department of Anthropology, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, Rio de Janeiro 20940–040, Brazil.

*To whom correspondence should be addressed. E-mail: mheckenb@anthro.ufl.edu

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