11 FOSSIL RODENTS FROM THE LATE MIOCENE URUMACO AND MIDDLE MIOCENE CUMACA FORMATIONS, VENEZUELA

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Rodents are one of the most diverse components of the current South American mammalian fauna, being known from more than 160 living and fossil genera. They made their first appearance in the fossil record of this subcontinent at least 31.5 Ma (earliest Oligocene; Wyss et al. 1993; Flynn et al. 2003; Hitz, Flynn, and Wyss 2006), according to dated strata from Chile. Putative older caviomorphs come from undated faunas of Santa Rosa, Peru (Frailey and Campbell 2004), but estimates of the age of the levels in which they occur are based on the stage of evolution of different mammal groups, and are therefore controversial. These Peruvian caviomorphs could be as young as Late Oligocene (Shockey, Hitz, and Bond 2004). This group of rodents that made an early appearance in South America is an endemic subgroup of hystricognath rodents and forms a clade called Caviomorpha (Wood and Patterson 1959; Adkins et al. 2001; Adkins, Walton, and Honeycutt 2003; Farwick et al. 2006; Huchon and Douzery 2001; Marivaux et al. 2002; Marivaux, Vianey-Liaud, and Jaeger 2004; Huchon et al. 2007; Veniaminova, Vassetzky, and Kramerov 2007; but see Bryant and McKenna 1995 and Candela 1999). It is a mystery how the earliest representatives of this group arrived in South America, since this subcontinent was isolated from other landmasses during most of the Tertiary. They most likely came from Africa by rafting, although some theories propose their entrance directly from Asia, where hystricognaths would have originated (Pook and Pook 1981; Marivaux et al. 2002).

The initial caviomorph diversification possibly occurred sometime during the Late Eocene, and a second important evolutionary radiation event occurred between the Middle and Late Miocene, with the appearance of forms that represent most living families (Vucetich, Verzi, and Hartenberger 1999). Living rodents include arboreal, cursorial, semiaquatic, gliding, and fossorial forms, with a body mass ranging between 7 and 90 kg, with the smaller end of the range represented by *Baiomys* species, the pygmy mice, and the larger end by *Hydrochoerus hydrochaeris*, the capybara. The fossil record of rodents shows that their diversity in body sizes and physical characteristics was even wider during the Tertiary, including one species that may have weighted around 1,000 kg at the end of the Pliocene/beginning of the Pleistocene of Uruguay, the dinomyid *Josephoartigasia monesi* (Rinderknecht and Blanco 2008; but also see Blanco 2008; Millien 2008). Some other examples of gigantism include forms from the Late Miocene from Urumaco, Venezuela, such as the neoepiblemid *Phoberomys pattersoni*.

Although the fossil record of South American mammals is rich, the record is strongly biased toward southern latitudes (Pascual, Ortiz Jaureguizar, and Prado 1996; Flynn and Wyss 1998), especially Patagonia and central Argentina. However, a few important deposits outside this region give some insight about the diversity in other areas, such as Salla-Luribay (Late Oligocene, Bolivia), Acre (Miocene, Brazil), and La Venta (Middle Miocene, Colombia). These intertropical faunas show that the faunas from northern South America displayed significant differences from coeval Patagonian ones, especially at specific and generic levels, from the Early Cenozoic. The fossil record from Venezuela is comparatively scarce and little known, but its mammals were diverse, and as explorations continue, new groups emerge. Although still poor, this Venezuelan record is important because it helps to improve knowledge of the Late Miocene South American mammals, so far well known only from Argentina and the Brazilian Acre.

The abbreviations used in the text are the following: AMU-CURS Alcaldía de Urumaco, Venezuela, Colección Urumaco Rodolfo Sánchez; CIAAP, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Coro, Venezuela; SA, Palaeontological collections of the Naturhistorisches Museum Basel, Switzerland; UNEFM, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela; UZH, Palaeontological Institut and Museum of the University of Zürich; P4 and p4, upper and lower fourth premolar respectively; M3 and m3, upper and lower third molar respectively; dp4, deciduous p4.

Neoepiblemidae

This family includes middle-sized to gigantic extinct rodents with bi- or multilaminar ever-growing cheek teeth (=euhypsodont), with a thick layer of interlaminar cement. Neoepiblemids have been recorded in Argentina, Venezuela, and Brazil in the Middle and Late Miocene and include *Phoberomys (=Dabbenea)*, *Neoepiblema (=Euphylus)*, and *Eusigmomys* (Bondesio, Pascual, and Vucetich 1975; Bondesio and Bocquentin-Villanueva 1988; Mones and Toledo 1989; Negri and Ferigolo 1999). Other genera are also sometimes included in this family, such as the lower and middle Miocene *Perimys* (Bondesio, Pascual, and Vucetich 1975; Vucetich 1994; Flynn et al. 2002; Kramarz 2002; Vucetich, Kramarz, and Candela 2010) and the Early Oligocene *Scotamys*, which was interpreted as allied to *Perimys*, and consequently also included within the Neoepiblemidae (Kramarz 2001).

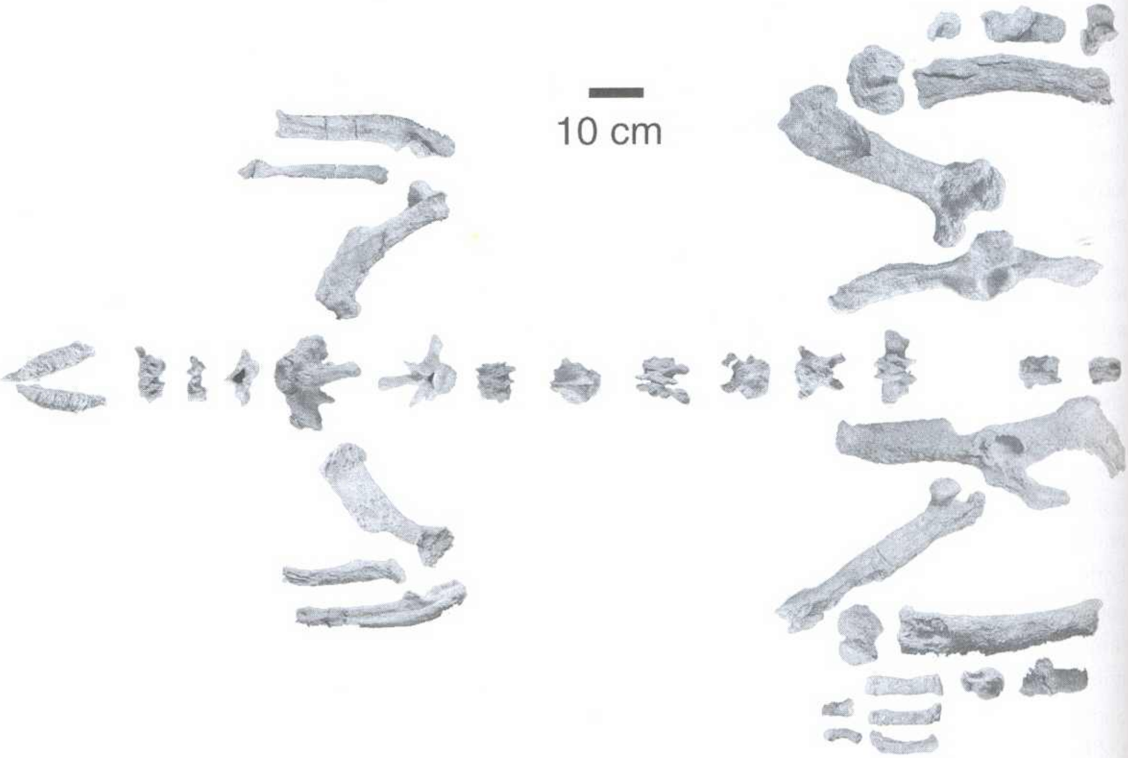

Fig. 11.1. Skeleton of the neoepiblemid *Phoberomys pattersoni* UNEFM-VF-020 (modified after Sánchez-Villagra, Aguilera, and Horovitz 2003) from the Urumaco Formation (Late Miocene, Venezuela).

Phoberomys

An almost complete skeleton of *Phoberomys pattersoni* Mones, 1980 (fig.11.1, and see fig. 11.2 for a life restoration) from the Urumaco Formation was found in 2000 by a team from the Universidad Francisco de Miranda led by O. Aguilera and reported by Sánchez-Villagra, Aguilera, and Horovitz (2003), in a study later expanded by Horovitz et al. (2006). *Phoberomys*, whose closest living relative is probably *Dinomys*, lived during the Late Miocene of Argentina, Brazil, and Venezuela. Sedimentary evidence indicates that *Phoberomys pattersoni* inhabited coastal wetlands consisting of lagoons of shallow waters separated from the coast by sandy barriers. The morphology of its teeth indicates that its diet was abrasive and probably included sea grasses. The locality in which the most complete specimen of *P. pattersoni* was found (Sánchez-Villagra, Aguilera, and Horovitz 2003) is Tío Gregorio (11° 14' 31" N, 70° 18' 40" W), with strata located at the top of the Urumaco sequence and stratigraphically close to the overlying Codore Formation.

With the discovery of the skeleton of *Phoberomys pattersoni* (UNEFM-VF-020), it was possible to estimate the body mass for this species in a more reliable way than had been possible before, since until then it was only known from isolated molars (Sánchez-Villagra, Aguilera, and Horovitz 2003). Based on the fusion of sutures in the skull and postcranium, we concluded that the skeleton belonged to an adult individual.

Fig. 11.2. Restoration of *Phoberomys pattersoni.* *Artwork by Jorge González.*

Analysis of humerus and femur shaft diameter (Biknevicius, McFarlane, and MacPhee 1993) yielded two different estimates for the body mass of *Phoberomys:* according to the humerus, its body mass was 436 kg, whereas according to the femur, 741 kg. The much greater robusticity of the femur than the humerus suggests that the hind limbs played a more important role in locomotion and weight support in this species, and therefore the latter was considered to yield an estimate closer to what its body mass must have been, about 700 kg. The forelimbs may have played a role in food manipulation as in living *Dinomys branickii.*

Different equations for body mass estimation have been developed taking into account the dimensions of different elements of the skeleton, including the skull, the teeth, and limb bones. Similar estimates have been made based on teeth and limb bones for rodents of small and moderate size (up to 67 kg in the case of the fossil species *Castoroides leyseiorum,* after Hopkins 2008) but such is not the case for *Phoberomys pattersoni.* Estimates based on teeth yield a much smaller body size (234 kg) than those based on either humerus or femur (Hopkins 2008). Because of allometric growth, extrapolation of body mass estimations outside the observed range is potentially problematic in both cases (Biknevicius, McFarlane, and MacPhee 1993). Equations for body mass estimations are necessarily based on living species of caviomorphs (or on a taxonomically broader sample of rodents) that are much smaller than *Phoberomys.*

Allometry is potentially a problem because as the linear dimensions of an animal increase, so too do the area and volume, but they do so at different rates. Area increases as a function of the square of linear dimensions, and volume increases as a function of the cube of linear dimensions. For example, if an animal doubles its linear dimensions (length, breadth, and height), the area of its cross-section will be fourfold larger and its volume and body mass will be about eight times as large. The strength of any of its bones is a function of the area of the cross-section of the bone, so its structural supports will be four times stronger than in an animal half its linear size. The more two animals differ in size, the more they will differ in proportions. Dental dimensions are potentially even more problematic for body mass estimation than limb bone diameters because they are related to food consumption. Larger animals use proportionally less energy than smaller animals and therefore need to eat less in relation to their size. So teeth would not necessarily be expected to be proportional to body size when we compare animals of very different body sizes. Besides, the amount of food ingested and the surface area of teeth necessary to process it are expected to vary depending on diet and metabolic rate (cf. Vizcaíno, Bargo, and Cassini 2006). Therefore, the more closely the data used to estimate body mass are related to this variable, the better we can expect the body mass estimate to be. For this reason we consider information on thickness of limb bones (which necessarily evolved to the right size to support the corresponding body mass) to be more reliable than dental measurements in estimating body mass, even if one may be uncertain of the kind of locomotion the species may have displayed.

Phoberomys pattersoni was not alone in attaining an unusual body size in its family: all the species of the genus attained very large sizes. Remains of the various species of *Phoberomys* have been recovered in the Late Miocene of Argentina (*P. insolita*, *lozanoi*, *burmeisteri*, and *praecursor*), Brazil (*P. bordasi*), and Venezuela (*P. pattersoni*). The species *P. insolita*, *lozanoi*, *minima*, and *pattersoni*, were originally placed in the genus *Dabbenea* Kraglievich, 1926; however, Bondesio and Bocquentin Villanueva (1988) showed that *Dabbenea* was a synonym of *Phoberomys*. *P. pattersoni* is probably the second-largest species within its genus, after *P. insolita*: the length of the available M3 in *P. insolita* is 47 mm (Kraglievich 1940a), whereas that of *P. pattersoni* is approximately 41 mm. It is important to note, however, that in many species of mammals with euhypsodont (=ever-growing) teeth, crown size increases with age. Since the anatomy of most species of *Phoberomys* is poorly known and species diagnoses are based mostly on teeth, it is hard to assess whether differences in molar sizes are legitimate specific differences or just represent different ontogenetic stages of one another. The identification of the specimens from Urumaco as belonging to *Phoberomys pattersoni* is based on two diagnostic characters of M3 besides its size, namely the narrowing of the posteriormost portion at the level of the last three prisms and the relative proportions of this tooth (Sánchez-Villagra, Aguilera, and Horovitz 2003).

those reported by Mones (1980) in the original description of the species, however. Other rodent dental and postcranial remains have been recovered from the Urumaco sequence, most of which are smaller in size and different in morphology from those that have been identified as belonging to *Phoberomys pattersoni* (Horovitz et al. 2006).

Dinomyidae

Dinomyidae includes many species with multilaminar high-crowned cheek teeth, ranging from proto- to euhypsodont, the most recently described of which is the fossil *Josephoartigasia monesi* Rindernecht and Blanco, 2008 from Uruguay, the largest rodent species known, which may have weighed around 1000 kg. Uncontested reports of dinomyids start in the Middle Miocene (but see alternative below); the clade reached its highest diversity in the Late Miocene, and they are represented today by *Dinomys branickii*, the pacarana. *D. branickii* is about the size of a beaver and lives from Colombia and Venezuela to the north of Bolivia. Its typical habitat is low montane areas, and its diet consists of fruits, leaves, and tender shoots. Dinomyids were widely distributed in South America, but most of the fossil record is restricted to Argentina. The most recent systematic revision of the family was that by Mones (1981; see also Mones 1986). The only recent study of intraspecific or ontogenetic variation of representatives of this family is included in the revision of the genera *"Olenopsis"* and *Drytomomys* by Candela and Nasif (2006). The protohypsodont genus *Scleromys* (McKenna and Bell 1997, Kramarz 2006; Cerdeño and Vucetich 2007, and references cited therein) and the brachyodont *Branisamys* (Patterson and Wood 1982) have sometimes been included in Dinomyidae. If this latter affiliation is confirmed, the fossil record of Dinomyidae would extend back to the Late Oligocene. Three subfamilies are included in Dinomyidae: Dinomyinae, Eumegamyinae, and Potamarchinae. The former two consist of euhypsodont species and the last one of protohypsodont species. We follow Bondesio, Pascual, and Vucetich (1975) and Negri and Ferigolo (1999), who excluded *Phoberomys* and *Neoepiblema* from Dinomyidae and included them instead in Neoepiblemidae. Here we comment on previous discoveries of dinomyids and report new ones.

Eumegamyinae

EUMEGAMYS

Kraglievich 1926 is a fossil genus previously known to occur only in Argentina from the Late Miocene until the Early Pliocene. Remains of an unidentified species of *Eumegamys* have been reported for Urumaco (Pascual and Díaz de Gamero 1969). The remains consist of two lower jaw fragments including several teeth. Some similarities have been noted between these remains and those of *E. paranaensis* from the Huayquerian

(Late Miocene) of Entre Ríos in northeastern Argentina (Pascual and Díaz de Gamero 1969). A partial lower incisor has been reported from Colonia, Uruguay (Calcaterra 1972), probably proceeding from Pliocene deposits, but the attribution to the genus is uncertain.

TETRASTYLUS

Ameghino 1886 occurred in Argentina in the Late Miocene. Paula Couto (1970) reported its survival until the Pleistocene in Lagoa Santa (Brazil). Linares (1990) reported the finding of remains of an undetermined species of this genus in Urumaco.

Potamarchinae, Cf. *Potamarchus*

Two upper right molars of medium size, one partial M3? (AMU-CURS-181; fig. 11.3; width, 6.65 mm) and an almost complete M3 (AMU-uncataloged; width, 6.35 mm; anteroposterior diameter, 7.2 mm; height 10.25 mm) were recently found in the lower member of the Urumaco Formation (coquina near town, coordinates: 11° 11' 380" N; 70° 15' 357" W). AMU-uncataloged has six laminae that become smaller posteriorly starting in the fourth lamina, whereas AMU-CURS-181 has only five preserved laminae. They have a thin interlaminar layer of cement; in each lamina the enamel layer of the posterior border is very crenulated and the labial border curves slightly posteriorly. Because of its small size, the crenulated layer of enamel, and being protohypsodont, these teeth resemble those of *Potamarchus* Burmeister, 1885. *Potamarchus* is an extinct genus known from Late Miocene deposits from Argentina. Linares (2004) mentioned

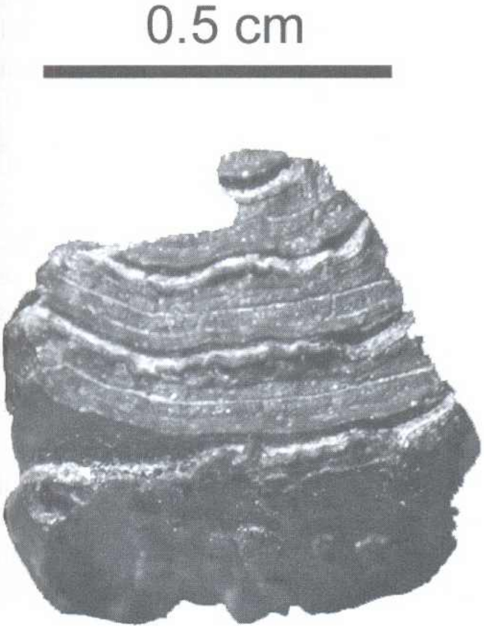

Fig. 11.3. *left* Upper right molar of dinomyid cf. *Potamarchus* AMU-CURS-181 (anterior to the bottom and labial to the left of image) from the Urumaco Formation (Late Miocene, Venezuela).

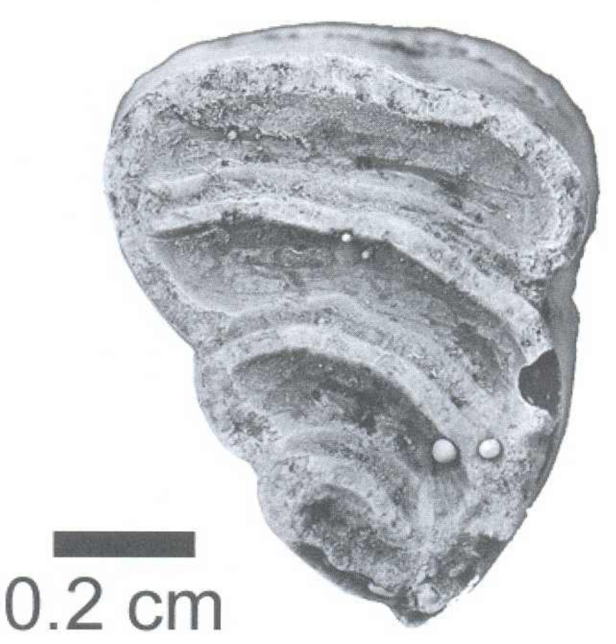

Fig. 11.4. *right* Cast of left lower p4 of an undetermined dinomyid genus and species UZH-Cast-A/V4660 (anterior to the bottom and labial to the left of image) from Cumaca Formation, Tuy Basin (Middle Miocene, Venezuela). The original specimen is deposited at the paleontological collections of the University of Montpellier.

the presence of *Potamarchus* for the middle portion of the Urumaco Formation, but the illustration of the specimen supporting this claim (Linares 2004, fig. 4D) is not clear or informative enough as to be able to verify this determination. Linares (2004) also listed *Olenopsis* as present in the lower member of the Urumaco Formation, a record requiring verification.

Dinomyidae Genus and species indet.

A left lower p4 (original specimen housed in the paleontological collections of the University of Montpellier; cast UZH-Cast-A/V4660; fig. 11.4) was found in Cumaca Formation, Tuy Basin, Middle Miocene (Macsotay, Peraza, and Wehrmann 1995). Bermúdez (1966) reported fish scales and teeth from this formation, and in addition, Macsotay, Peraza, and Wehrmann (1995), Macsotay et al. (1998), and Wesselingh and Macsotay (2006) reported the presence of coprolites, crocodile teeth, turtle carapace fragments, and freshwater gastropods. The molluscan *Tryonia* from this formation has interesting biogeographic implications: it suggests a close biogeographic affinity between northern Venezuelan and western Amazonian faunas during the Middle Miocene (Wesselingh and Macsotay 2006, p. 65).

Macsotay, Peraza, and Wehrmann (1995) assigned the left lower p4 (UZH-Cast-A/V4660) to *Prolagostomus* sp. (Chinchillidae). It is a small (anterior width, 4.1 mm; posterior width, 7.02 mm; anteroposterior diameter 8.51mm), high-crowned tooth, probably euhypsodont. The latter cannot be established with certainty because the base of the tooth is missing, but the tooth is much higher than in any potamarchine genus. It is long and pointed anteriorly, and its structure is simple, with four laminae and three flexids. The hypoflexid is very long and reaches almost the lingual wall. The other two flexids, which are anterior to the hypoflexid, open over the lingual wall. The anteriormost flexid is the shortest of the three. The enamel is thick and continuous around the entire tooth, becoming thinner in the anterior side of each lamina. The morphology of UZH-Cast-A/V4660 is similar to that of the p4 of all *Tetrastylus* species, but the laminae are somewhat broader and the tooth is more pointed anteriorly. It differs from the p4 of *Drytomomys*, another small dinomyid, because UZH-Cast-A/V4660 has only four laminae (as in *Scleromys*), whereas *Drytomomys* has five. The anterior end of UZH-Cast-A/V4660 differs from that of dp4 in known dinomyid taxa in its pointed shape.

Hydrochoeridae

This group of caviomorphs, the capybaras, which includes the largest living rodents, has a fossil record that extends back to the Late Miocene of South America, and the group migrated more recently to North America and the West Indies. Capybaras are today represented by one or two species (*Hydrochoerus hydrochaeris* and *H. isthmius*). They were thought to be highly diversified during the Late Miocene (Mones 1991, and literature cited therein), but Vucetich et al. (2005a) and Vucetich and Deschamps (in press) questioned their suprageneric systematics, drastically reducing their diversity, and proposed a different scheme of evolution for this family. These authors accepted only one genus for the Late Miocene, *Cardiatherium* Ameghino 1883, with several species.

Some specimens pertaining to hydrochoerids have been reported for Urumaco and referred to cf. *Cardiatherium* and *Kiyutherium* (Linares 1990; Mones 1991, and literature cited therein). Following Vucetich et al. (2005a), Deschamps et al. (2007), and Vucetich and Deschamps (in press), we tentatively consider all this material as *Cardiatherium* sp.

Other Rodent Postcranial Remains of Uncertain Familial Affinities from the Urumaco Formation

Horovitz et al. (2006) reported several additional specimens of rodents of uncertain affinities of large size (including the possibility of their being *Phoberomys*) from the Urumaco Formation. One of the specimens, CIAAP-1438, consists of two fragments of the skull and the right jaw, left humerus, both femora, proximal right ulna, proximal radius, left astragalus, and two vertebrae (see humerus and femur in fig. 11.5). Humerus and femur are more gracile than in *P. pattersoni* UNEFM-VP-020.

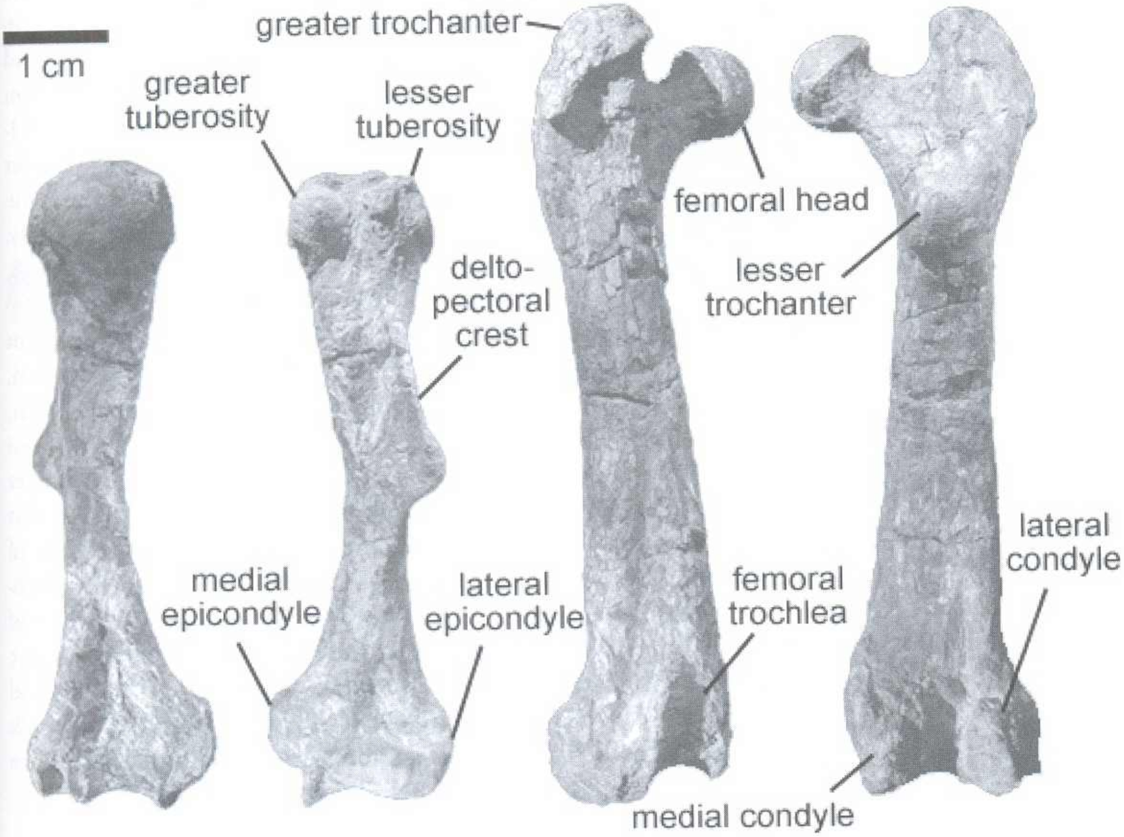

Fig. 11.5. Left humerus and right femur of an undetermined rodent CIAAP-1438 in posterior and anterior views, from the Urumaco Formation (Late Miocene, Venezuela).

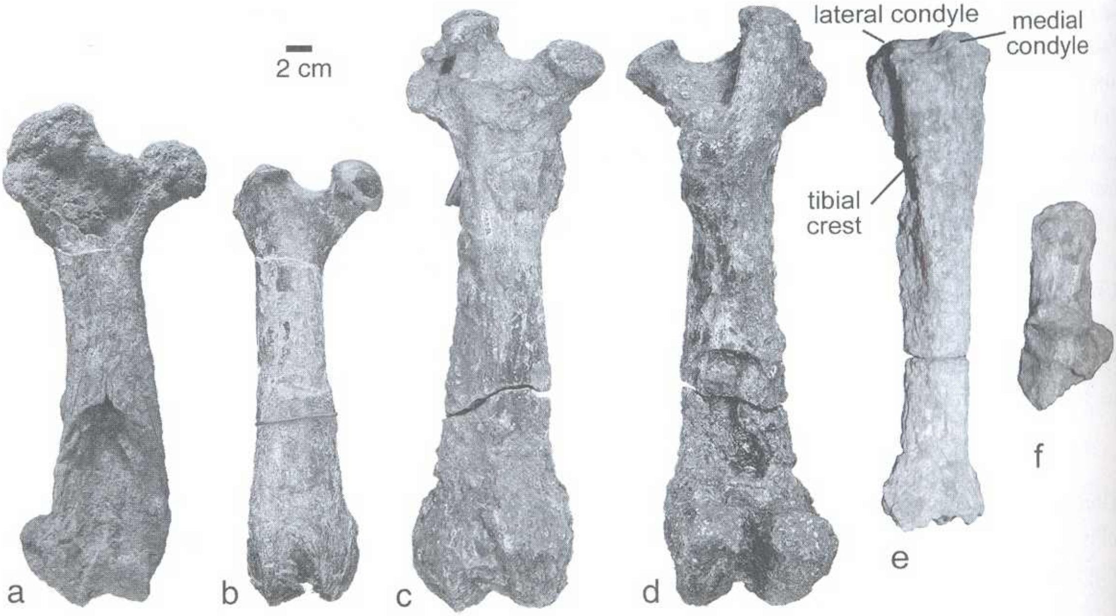

Fig. 11.6. A: Right femur of *Phoberomys pattersoni* UNEFM-VF-020. Errata note: Scale bars for pelvis, femur, and lateral view of tibia of *Phoberomys pattersoni* UNEFM-VF-020 in Horovitz et al. 2006 (figs. 7, 8, and 10) should have been labeled "3 cm" instead of "2 cm." B: Mirror image of right femur of undetermined rodent SA-259 from Savonetta River, Trinidad, reportedly of Late Miocene age (Schaub 1935). Right femur in anterior (C) and posterior (D) views, and tibia (E) and calcaneum (F) in anterior view, AMU-CURS-56, 55 and 54, respectively, of an undetermined rodent from the Urumaco Formation (Late Miocene, Venezuela).

That report also included a left humerus and right femur, catalogued as CIAAP-441 and 442 respectively, which were found a few meters apart, although it is not clear if they belonged to the same individual. The proportions of the two bones are different from those of *Phoberomys pattersoni* UNEFM-VF-020, but the humeral deltoid crest is very long and extends to the proximal portion of the bone, similar to that in *P. pattersoni* UNEFM-VP-020 (Horovitz et al. 2006). An isolated humerus, UNEFM-VF-010, from the Urumaco Formation (Horovitz et al. 2006), smaller than that of *Phoberomys pattersoni* UNEFM-VF-020, also differs from the latter in that its deltoid crest is not continuous with its greater tuberosity.

Here we report a new femur, tibia, and calcaneum (AMU-CURS-56, 55 and 54 respectively, fig. 11.6C–F) reportedly found in association (Rodolfo Sánchez, pers. comm. 2008), and an isolated right calcaneum AMU-CURS-uncatalogued (fig. 11.7) from the Urumaco Formation. The femur AMU-CURS-56 is cracked and not in very good condition, but it is evident that it is substantially larger than that of *P. pattersoni* UNEFM-VF-020 but relatively more gracile, with a greater trochanter that is massive but not quite as much as in *P. pattersoni*. The head is slightly incomplete, but the greater trochanter was probably the taller of the two. The neck is directed slightly more proximally than in *Phoberomys pattersoni*, where it is more medially oriented. The total length of this femur (measured from the greater trochanter to the distal end) is 445 mm; the length of the femur from (the slightly incomplete) femoral head to the distal end is 420 mm. The shaft of the femur is not well enough preserved to report reliable diameter measurements. The associated tibia and calcaneum (AMU-CURS-55 and 54) are still undescribed.

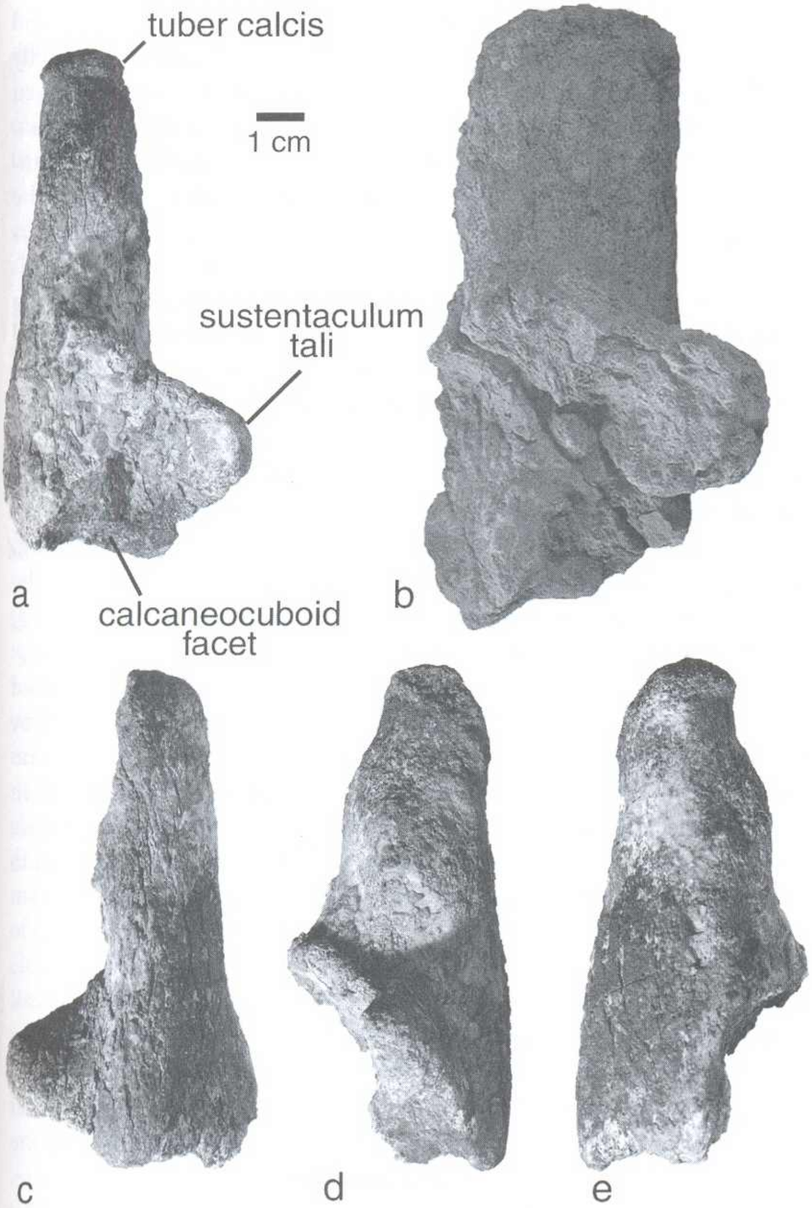

Fig. 11.7. Left calcaneum of undetermined rodent AMU-CURS-uncatalogued from the Urumaco Formation (Late Miocene, Venezuela) (A and C–D) and mirror image of right calcaneum of *Phoberomys pattersoni* UNEFM-VF-020 to facilitate comparisons (B).

The isolated right calcaneum, AMU-CURS-uncatalogued (fig. 11.7), is different from that of *P. pattersoni* in that the tuber calcis is deeper dorsoventrally than wider (for example as in *Hydrochoerus*, *Erethizon*, and *Proechimys*, among living caviomorphs). The tuber calcis also differs from that of *Phoberomys* in that it becomes thinner (both dorsoventrally and mediolaterally) toward the posterior end, and it displays a constriction dorsally, medially, and partially laterally, just anterior to the tip. In the anterior area of the calcaneum, the ectal, sustentacular, and calcaneucuboid facets are partially preserved, although not much is left of the ectal facet.

The sustentaculum is shorter anteroposteriorly than in *Phoberomys*, and its morphology is unusual because this process extends anteriorly slightly beyond the anterior edge of the sustentacular facet. The facet is raised relative to the more anterior, nonarticular portion of the sustentaculum. Although its preservation is poor at its anterior end, it seems that the sustentaculum converged with the body of the calcaneum anteriorly at the level of the calcaneocuboid facet, that is, at the anterior tip of the calcaneum. The calcaneocuboid facet is elongated, and its major dimension is oriented in the direction laterodorsal to medioventral. It may be missing its dorsolateral end or else the calcaneum displays a flat dorsolaterally directed triangular facet on its anterolateral area. The ventralmost point of the calcaneocuboid facet protrudes anteriorly slightly beyond the rest of the facet. This facet is concave both dorsoventrally and slightly mediolaterally and is directed mostly distally and slightly mediodorsally in its distal end. There is an anteroposteriorly elongated depression on the dorsal surface of the body of the calcaneum lateral to the sustentaculum. The length of the calcaneum is 111.52 mm (although it may possibly be missing a very small anterior portion), the tuber calcis is 65.17 mm long, and the maximum width of the calcaneum is 55.65 mm.

The right femur of a large rodent, SA-259 (fig. 11.6B), was recovered from reportedly Late Miocene rocks in Savonetta River, Trinidad, by Schaub (1935). It is shorter than that of *P. pattersoni* UNEFM-VF-020 and it is similar to AMU-CURS-56 in general proportions. It differs from both in that the greater trochanter is relatively smaller in girth and height, being about as high as the head. The orientation of the neck is similar to that of AMU-CURS-56. The total length of SA-259 is 368 mm.

Discussion

The Late Miocene record of caviomorph rodents from Venezuela is still very scant and possibly biased, since only middle- and large-sized species have been found so far. Small species of caviomorphs (e.g., spiny rats) are abundant and diverse in Recent American intertropical faunas that are similar in some respects to the fauna that existed in Urumaco during the Late Miocene, but no such small species have been recovered there.

The Late Miocene represents the acme of gigantic caviomorphs. The most spectacular specimens in conservation and completeness have been recovered in Urumaco, but gigantic rodents were diverse all along the Neotropics from central Argentina to northern South America and the Antilles. Besides members of Neoepiblemidae, Dinomyidae, and Hydrochoeridae from South America, another example of gigantism is the well-known *Amblyrrhiza inundata*, which belonged to the Heptaxodontidae, a caviomorph family from the central and eastern Caribbean. *A. inundata* occurred in Anguilla and St. Martin during the Quaternary and may have coexisted with humans; according to some estimates, some individuals probably reached a body mass over 200 kg (Biknevicius, McFarlane, and MacPhee 1993), about the size of a black bear. Heptaxodontidae is most probably related to the Dinomyidae+Neoepiblemidae clade (Vucetich et al. 2005b).

Teeth are among the most common remains in the paleontological vertebrate record because of their enamel cover, the most resistant tissue of vertebrates. In most mammals, or for that matter vertebrates, teeth do not change in size or configuration once erupted, other than changes to some degree of the occlusal surface relief caused by wear. This means that tooth size and occlusal configuration can provide a reliable source of information for species definition for most mammals. However in some mammals, teeth continue growing once erupted, a phenomenon—hypsodonty—leading to high-crowned teeth. There are different criteria to classify hypsodont teeth. Mones (1982) considered protohypsodont those teeth that stop growing at some point during the life of an individual, and euhypsodont those that grow through life. In hypsodont teeth, change in size and occlusal morphology can be significant. For example, cheek teeth of capybaras (Hydrochoeridae) are highly variable in occlusal morphology, especially lower p4-m3 and upper M3 (Kraglievich and Parodi 1921; Kraglievich 1940b; Pascual and Bondesio 1968; Reig, Soriano, and Ojasti 1970; Mones 1975, 1991; Vucetich et al. 2005a). This diversity in tooth morphology represents both individual variability and ontogenetic change (Mones 1991, figs. 7–10). Vucetich et al. (2005a) have provided one of the most detailed studies on species demarcation in fossil capybaras. Capybaras are born with all cheek teeth already erupted, even with occlusal wear, and teeth keep growing in all dimensions as long as skull and mandible grow, as in other euhypsodont mammals (Francis 1960; Kramarz 2002). Differently from other groups of euhypsodont mammals, the occlusal morphology in capybaras keeps changing as the tooth grows, implying that the base of the tooth keeps folding allometrically through all or most of the animal's lifetime. The morphology of the occlusal surface becomes more complex with age. Accordingly, different morphologies were interpreted by Vucetich et al. (2005a) as members of an ontogenetic series, that is, as semaphoronts of one species (sensu Hennig 1966).

Several rodent species from Urumaco may represent examples of particular ways of growth in euhypsodont and multilaminated cheek teeth. They deserve to be studied bearing in mind ontogenetic trajectories in order to elucidate their actual diversity. Given the diversity in postcranial morphology described above, it seems likely that more than one species of large rodent coexisted in northern Venezuela and Trinidad. The scarcity of associated dental and postcranial remains and the uncertainties associated with taxonomy of multilaminated euhypsodont teeth do not allow a more precise assessment of taxonomic diversity of the region at this time.

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