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THE LAST MYSTERY OF THE LAST HOPE: ON THE SUPPOSED OCCURRENCE OF "*MEGAMYS*" (MAMMALIA: RODENTIA) IN CUEVA DEL MILODÓN

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DURING more than a century, a "large rodent" usually referred to as "*Megamys*" (the use of quotation marks is explained below) was mentioned as integrating the faunal assemblage unearthed from the worldwide famous Cueva del Milodón (**CM**, hereafter). Briefly, this cave (51.56° S; 72.61° W), located near Puerto Natales in the Last Hope Inlet, southern Chile, has been, since its discovery in 1895 (*cf*. Martinic, 2000, p. 103), the source of a long array of paleontological and archeological material. Most of this material came from Late Pleistocene levels and was exhumed throughout systematic and unsystematic excavations. Emblematic findings consist of the almost "fresh" fragments of *Mylodon* skin. A detailed work guiding the reader across the many contributions produced around CM is the recent dissertation of Martin (2013; and references cited therein).

Shortly after their discovery, Rodolfo Hauthal was commanded by Francisco P. Moreno to make collections in CM. Hauthal's findings and notes were published in a triserial paper composed of a contribution by Hauthal (1899) himself, a second one by Roth (1899) and a third one by Lehmann-Nitsche (1899). That of Roth (1899) was devoted to describing the faunal elements retrieved from CM and emphasized on *Mylodon* remains. However, in page 446 of Roth (1899) and among the materials referred to the order Rodentia, a proximal fragment of femur belonging to a "large rodent" indicating "*… un roedor mucho más grande que el carpincho (*Hydrochoerus capybara*), pero es algo más chico que el* Megamys patagonensis" -freely translated "a rodent much larger than the capybara… although a little smaller than the *Megamys patagonensis*"- was mentioned. The author also recorded a few selected measurements of this material and compared them with those of *Hydrochoerus* (Roth, 1899, p. 447). Lehmann-Nitsche (1899, p. 408) enlarged the morphological description of the preserved portion of this femur and attributed the introduction of this taxon into the cave assemblage to human action. Roth's mention of a "large rodent" for CM was translated and reproduced in the influential contribution of Smith Woodward (1900, p. 76) as follows: "Large Extinct Rodent. The proximal end of the femur of a large rodent (no. 52) has already been recognized by Roth, and compared with the extinct *Megamys*. It cannot be more exactly determined". Subsequent articles, including the seminal study of Emperaire and Laming (1954, p. 185) "*Hauthal, en outre, avait exhumé quelques vestiges… d'un grand rongeur et d'un petit rongeur…*" -freely translated "Hauthal had also discovered traces… of a large rodent and a small rodent…"- and several other specific contributions (*e.g.*, Borrero, 1994; Latorre, 1998), also uncritically cited this finding.

It is hard to believe that no single claim highlighted the apparent incongruence in having a "large extinct rodent" supposedly allied to "*Megamys*" in a Latest Pleistocene faunal assemblage in high latitudes. The undisputed persistence of "*Megamys*" in southernmost Chile during more than a century can be probably explained arguing that most researchers who explored these topics were not familiar with paleontology (*e.g.*, Latorre, 1998) or, alternatively, mainly focused on *Mylodon* and allied megamammals (*e.g.*, Borrero, 1994). However, "*Megamys*" was later reported from an additional site not far from CM, Cueva Lago Sofía 1

(Prieto, 1991, p. 86–87; see also Borrero, 1994, p. 192; Jackson and Prieto, 2005, p. 116).

"*Megamys*" was a name historically used by several authors when referring to large and gigantic extinct rodents (see Mones, 1981). Although the type species of the genus, *Megamys patagonensis*, a form described by Orbigny and Laurillard (in Orbigny, 1837: pl. 8; 1842, p. 110; see also Mones, 1987) and based on materials recovered by the former in northeastern Patagonia, is considered a litoptern (see Kraglievich, 1926), *Megamys* auct., non Orbigny and Laurillard, 1837 were linked to several Dinomyidae (*cf.* Mones, 1981). Very few dinomyids, most of which were apparently tropical or subtropical animals, survived beyond the Late Miocene–Pliocene (Vucetich *et al.*, 2015). *Megamys patagonensis* was considered a Patagonian "*Megamys*" for decades and it was probably due to such understanding that the connection between the material from CM and a large rodent made by Roth (1899) was favored. Up to date, there is no single record of confirmed dinomyids from Patagonia after the Middle Miocene (Rinderknecht and Blanco, 2015).

Fortunately, in order to address the "*Megamys*" occurrence in CM, the material studied by Roth (1899) is housed in the Museo de La Plata (**MLP,** División Paleontología Vertebrados, Museo de La Plata, La Plata, Argentina) under the number MLP 94-VIII-10-67. A first question is, due to it was never figured, if this bone corresponds to that originally described by Roth (1899, p. 446–447). The material is marked with a "52" written in pencil in accordance with the number reported by Roth (1899, p. 446). A second number also marked in pencil on the bone surface reads "49" and was stricken-through apparently with the same pencil employed to mark "52". According to the list provided by Roth (1899), "49" corresponds to a canid tibia. Beyond numbers, the material at hand is a fragment of a proximal right femur limited to the femoral head (*capitis*), the neck and the lesser trochanter. The preserved fragment proves consistent with Roth' description and the additional notes provided by Lehmann-Nitsche (1899). Finally, the measurements provided by this author (Roth, 1899, p. 447; therein alluded to under the number "54", a confident *lapsus calami*) are almost the same as ours (Tab. S1 - Supplementary Information) and we can therefore reach the conclusion that both Roth and the present authors are dealing with the same piece.

Clearly, the material is a small fragment of femur and its identification is clouded by the fact that the bone surface is poorly preserved. Almost the entire femoral head is meteorized and only a small fragment of compact tissue indicating the original surface survived. As for the *fovea capitis*, a well-defined structure in a regularly preserved femoral head, is almost undistinguishable, thus suggesting that bone removal was deep. Even though there is no indication of a marked suture of the head epiphysis suggesting that the femur belongs to an adult individual, the bone erosion also conceals the border between head and neck. The material is broken to the external portion of the femoral head and nothing can be appreciated of the greater trochanter and the trochanteric fossa.

In spite of all the aforementioned limitations, MLP 94-VIII-10-67 contains enough anatomical information to allow a taxonomical identification (Fig. 1; Tab. S1 - Supplementary Information). The similarities detected with respect to the same element in camelids, particularly *Lama guanicoe*, are many and include general aspects of the morphology and size of the femoral head and the neck as well as the morphology, the magnitude and the relative medial location of the lesser trochanter, the development of the crest for insertion of iliopsoas muscle, and the expression of the preserved portion of the intertrochanteric crest (which is poorly developed at the proximal end of the lesser trochanter). Minor differences between the studied fossil and *L. guanicoe*, including a somewhat longer neck and a head more proximally directed, can be partially attributed to size-age variation. However, fine morphological details, particularly those with respect to the head, are hard to address in MLP 94-VIII-10-67 due to poor bone preservation.

In order to verify Roth's original hypothesis (1899), MLP 94-VIII-10-67 was compared with several living and extinct caviomorph rodents, and particularly with the large living caviomorph *Hydrochoerus*, the single extant dinomyid (*Dinomys*) and several giant extinct eumegamyids and neoepiblemids (Kraglievich, 1932: fig. 9; Biknevicius *et al.*, 1993: fig. 3; Mones, 1997: fig. 9A–B; Horovitz *et al.*, 2006: fig. 8A–B; Geiger *et al.*, 2013). The differences observed between caviomorph femora and camelids (Fig. 1) are more than trenchant as the former are characterized by greatly distinguishable rounded heads more medially oriented with respect to the proximal-distal axis of the bone, especially

longer necks, and lesser trochanters not medially located. Also, in the caviomorphs herein examined, the trochanteric fossa is extended more distally (at about the level of the base of neck) than in camelids. In MLP 94-VIII-10-67, there is no evidence of the trochanteric fossa in the comparable preserved region of the femur and its proximal position, a feature consistent with camelids –in which the fossa trochanteric is essentially restricted at the level of the greater trochanter–, is therefore indicated. Additionally, the distinctive crest (for the attachment of iliopsoas muscle) extended distally from the lesser trochanter in MLP 94-VIII-10-67 and *Lama guanicoe* is poorly developed or absent in large caviomorphs while the intertrochanteric crest is more conspicuous in the latter. To our best understanding, the femur fragment collected from CM by Hauthal and referred to a "large rodent" by Roth (1899), who then considered it

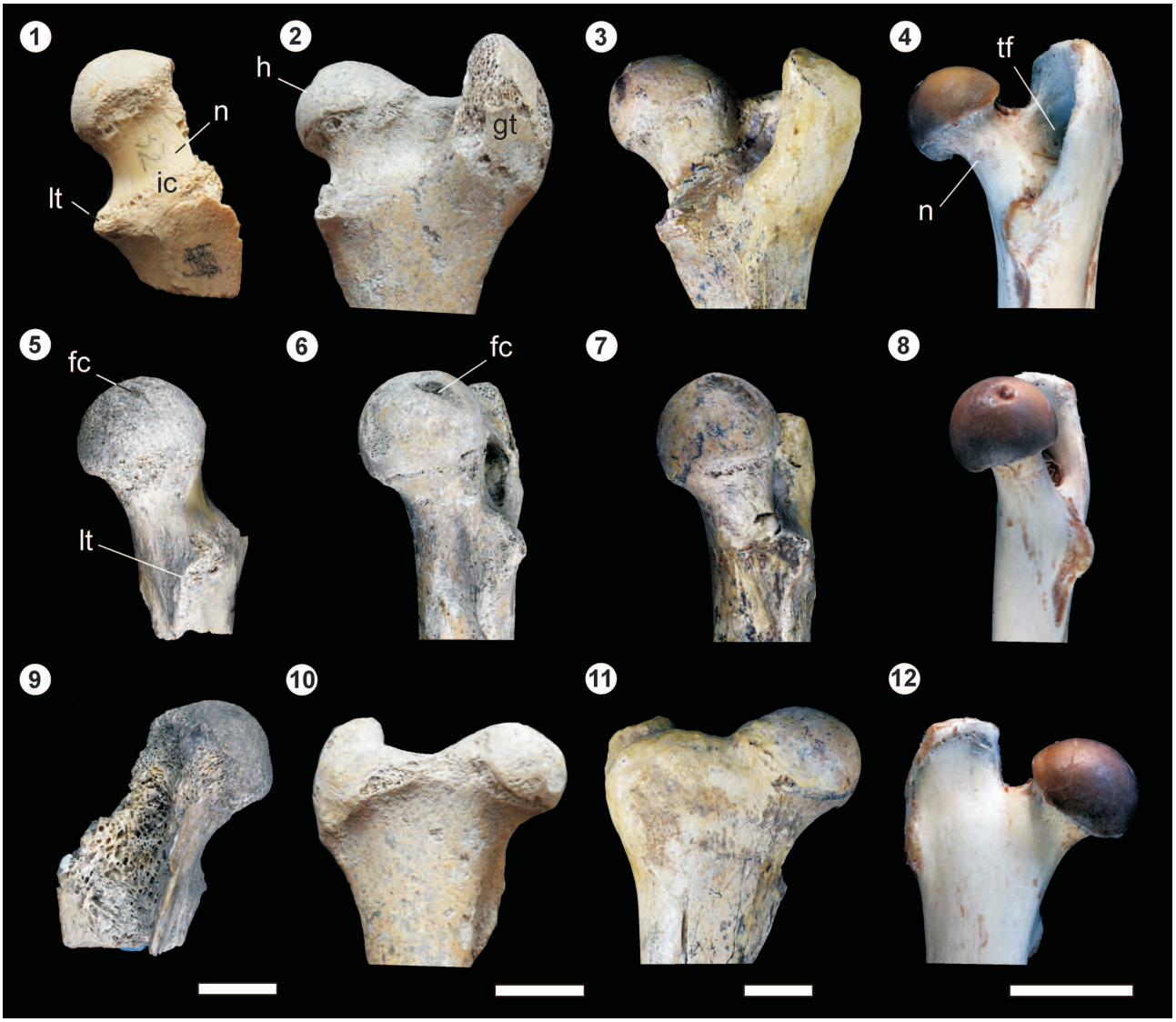

Figure 1. 1, 5, 9, Proximal femora comparisons among "*Megamys*" from Cueva del Milodón (**MLP** 94-VIII-10-67); **2, 6, 10,** the living camelid *Lama guanicoe* (**MLP** 86-III-25-22); **3, 7, 11,** the extinct camelid *Hemiauchenia* sp. (**MLP** 62-VII-27-161); **4, 8, 12,** the largest living caviomorph rodent *Hydrochoerus hydrochaeris* (**MLP** without number). From upper to bottom rows; posterior (caudal), medial and anterior (craneal) views, respectively. Abbreviations: **fc,** *fovea capitis*; **gt,** greater trochanter; **h,** head; **ic,** intertrochanteric crest; **lt,** lesser trochanter; **n,** neck; **tf,** trochanteric fossa. Scale bars= 30 mm.

"*Megamys*", belongs to a member of the family Camelidae and probably to a morphotype similar to that of *L. guanicoe*. Independently, Martin (2013, p. 257) reached the same conclusion herein presented by briefly mentioning that, in her inventory of the materials collected by Hauthal and housed in MLP, "*El número 52 pertenece a un gran roedor. Sin embargo, actualmente bajo este número hay un fémur de camélido*" (freely translated "Number 52 belongs to a large rodent. However, there is a femur of camelid currently under this number"). Camelids prove widespread in southern South American Quaternary localities (*e.g.*, Martin, 2013 and the references cited therein) and many remains of this taxon were unearthed from CM (Roth, 1899).

Roth (1899) probably misinterpreted MLP 94-VIII-10-67 due the particular morphology that meteorization produced on the *capitis*, mostly erasing the *fovea* and giving a bell-shape to the bone. In fact, a general resemblance is observed with respect to the femora of the largest known rodents (*cf.* Geiger *et al.*, 2013). Regarding the additional record of "*Megamys*" for Cueva Lago Sofía 1 (Prieto, 1991), the material actually belongs to a camelid. Apparently, the excavators of this site misinterpreted an isolated incisor as a rodent one and associated this finding with the record of "*Megamys*" of CM. Although not explicitly connected, this "*Megamys*'s incisor" is the same that was later referred to the camelid *Vicugna* (Prieto and Canto, 1997; F. Martin, comm. pers.).

With the discarding of "*Megamys*" from CM, only a single caviomorph rodent, *Ctenomys magellanicus*, integrates the Late Pleistocene faunal assemblage (Roth, 1899; Simonetti and Rau, 1989). Latorre (1998, p. 79) listed the rodent *Lagostomus maximus* for CM (see also Prieto, 1991, p. 86, there reported as *Lagostomys trichodactylus*) and, although we failed to detect any reference supporting the occurrence of such chinchillid, our survey of the paleontological collections of the Natural History Museum of London yielded materials from CM which belong to this family. Under number M 8787, a fragmentary lower jaw, a femur and a tibia lacking the proximal portion but preserving the articulate part of the feet with soft tissues are housed. Both morphology and measurements (not shown) indicate that these remains can be attributed to *Lagidium*, a widespread Andean chinchillid. There are populations of one species of this genus, *Lagidium wolffsohni*, in the Magallanes region, near CM (Texera, 1973). M 8787 probably pertains to the bunch of material recovered from the cave by Charles Milward and sold *ca.* 1898 to the Natural History Museum by Albert Konrad (*cf.* Martinic, 2000, p. 109–110).

In conclusion, the revision of a small fragment of femur from CM's Late Pleistocene assemblage and originally referred to a "large extinct rodent" allowed us to resolve two questions. First, the potential survival in southernmost Chile of a gigantic rodent; the studied remain belongs to a camelid. Second, the necessity to explain how this taxon goes to the extinction; confidently "*Megamys*" can be extirpated from the assemblages recorded in paleontological and archaeological sites in the southern tip of South America. The "*Megamys* affair" and the ramifications of the matter along a century clearly demonstrate the value of accurate taxonomic primary identifications.

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