



Record of an alleged extinct rodent: molecular analyses of the endemic *Octodon pacificus* from Chile

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Octodon (Octodontidae) is an endemic genus of rodents that is typical of southwestern South America and represented by 4 species. Octodon pacificus, commonly referred to as the Mocha Island degu, was initially described from specimens collected in 1959 at Mocha Island, a small coastal island located along the central coast of Chile. Fifty-seven years after its original collection, we report the discovery of a female O. pacificus carcass, identified by its morphological characteristics and its specific locality. In addition, based on the cytochrome b (Cytb) gene of the mitochondrial DNA obtained from O. pacificus and other congeneric species, we assessed phylogenetic relationships within the Octodontidae. Bayesian phylogenetic reconstruction indicated that O. degus represented the basal Octodon sp., followed by O. lunatus; O. bridgesii and O. pacificus were identified as sister taxa. Remarkably, the genetic divergence between O. bridgesii and O. pacificus is low, which suggests that 1 of 2 scenarios may be at play: the occurrence of a recent peripatric speciation process in O. pacificus, or the presence of O. bridgesii on Mocha Island. Documented collections of archeozoological material obtained from Mocha Island only include specimens of O. pacificus, a finding that supports our 1st proposed scenario. While the core of Mocha Island is a national reserve, strong anthropogenic landscape modifications have affected the coastal plains—the only known habitat of O. pacificus. Rodent control using killing traps and poison is a common practice on the island; therefore, population surveys and conservation initiatives are needed to conserve this endangered species.

El género *Octodon* (Octodontidae) se compone por cuatro especies de roedores endémicos del suroeste de América del Sur. *Ocotodon pacificus* fue descrito a partir de especímenes colectados en 1959 en Isla Mocha, una pequeña isla ubicada en la costa de Chile Central. Cincuenta y siete años después de su único registro, mediante un estudio morfológico, reportamos la identificación de una carcasa de una hembra de *O. pacificus* colectada en la localidad tipo para la especie. Adicionalmente, utilizando secuencias parciales del gen mitocondrial Cytb de esta y las otras tres especies del género, mediante un análisis Bayesiano se reconstruyeron las relaciones filogenéticas dentro de la familia Octodontidae. Con un elevado soporte de valores de probabilidad posterior, *Octodon degu* figura en un clado basal separado de un grupo hermano compuesto por *Octodon lunatus*, *Octodon bridgesii* y *O. pacificus*. La alta similitud genética observada entre *O. bridgesii* y *O. pacificus* es sugestivo de dos posibles escenarios: la ocurrencia de un evento de especiación peripátrica, o que *O. brigdesii* posee una población en la Isla Mocha. Análisis de osamentas de roedores en restos arqueológicos colectados en la isla, solo incluyen el diagnóstico de

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O. pacificus, lo que soporta nuestra primera hipótesis. Aun cuando el centro de Isla Mocha corresponde a una Reserva Nacional, la intensa actividad humana en las estrechas planicies costeras, ha modificado drásticamente el hábitat de *O. pacificus*. Los métodos comunes para el control de roedores, utilizando veneno y trampas son actividades comunes en la isla; por este motivo, se necesitan estudios poblacionales e iniciativas de conservación para proteger a esta especie amenazada.

Key words: Chile, endangered species, Octodon pacificus, Octodontidae, phylogeny, rodent

Environmental changes in southern South America during the Miocene have shaped the evolutionary history of the Octodontidae, resulting in extinction of some species and adaptive changes in other species (Verzi et al. 2016). Therefore, a radiation process molded by an organism's adaptation to different habitats has led to the speciation of this group of rodents in western regions of southern South America (Muñoz-Pedreros 2000). Octodontid species diverged during the Miocene, about 9.0 million years ago (mya) (6.7-11.6 mya), with a 2nd burst occurring in the early Pliocene (Upham and Patterson 2012). Today, there are 14 extant species in the family Octodontidae: Aconaemys fuscus, A. porteri, A. sagei, Octodon degus, O. lunatus, O. bridgesii, O. pacificus, Octodontomys gliroides, Octomys mimax, Spalacopus cyanus, Tympanoctomys barrerae, T. kirchnerorum, T. aureus, and T. loschalchalerosorum (Patton et al. 2015). The genus Octodon is comprised of 4 species of aboveground generalists (Gallardo and Kirsch 2001), which are primarily distributed in Chile; their distribution extends to the Neuquén Province in Argentina (Patton et al. 2015). Octodon degus has the northernmost distribution in Chile, occupying the western slopes of the Andes between Vallenar and Curicó, up to a maximum of 1,200 m of elevation (-28.5666S, -70.7500W to -34.9833S, -71.2333W—Woods and Kilpatrick 2005); O. lunatus ranges from Limarí to Quilpué in central Chile (-30.6167S, -71.2667W to -32.7333S, -70.7W-Osgood 1943); O. bridgesii is distributed in Chile (-34.25S, -70.5667W to -38.5667S, -71.5667W) and Argentina (-40.1602S, -71.3575W-Redford and Eisenberg 1992; Patton et al. 2015); and O. pacificus occurs exclusively on Mocha Island (-38.3667S and -73.9333W), a small coastal island located off the coast of central Chile, within the Valdivian Rainforest region (Hutterer 1994). Currently, O. bridgesii is allopatrically distributed with respect to O. lunatus and O. degus, whereas in the past, these 3 species occurred in sympatry (Saavedra and Simonetti 2003). Human activities were responsible for the disappearance of O. bridgesii from the coastal and Andean regions of central Chile (Simonetti 1989; Saavedra and Simonetti 2003).

Octodon pacificus, commonly referred to as the Mocha Island degu, was described in 1994 from 3 females and 2 juvenile specimens collected in 1959 during a German zoological expedition to Mocha Island (Hutterer 1994). The species was identified as larger and heavier than the other Octodon spp., and it featured soft, long hair, which was brown and orange in color; the species also had a long tail, equaling 77% of its body and head length. Current information on these rodents has been restricted to the material collected in 1959, which has been maintained in the Alexander Koenig Research Museum in Bonn, Germany. While the finding of archeozoological material (bones and postcranial elements) on Mocha Island supports the long-term existence of *O. pacificus* (1,200–450 years ago [ya]—Saavedra et al. 2003), no living specimens have been observed or collected in the field since its original description in 1959.

The taxonomic relationship of *O. pacificus* is based entirely on morphology. Given the morphological characteristics of the species' skull and dentition, Hutterer (1994) grouped *O. pacificus* with *O. bridgesii* as its sister taxa, leaving *O. degus* and *O. lunatus* in a separate group. Subsequent molecular analyses of the genus *Octodon* revealed an alternate relationship, where *O. degu* was the basal species, and *O. bridgesii* and *O. lunatus* were sister taxa; the researchers did not include *O. pacificus* in this relationship (Gallardo and Kirsch 2001; Honeycutt et al. 2003; Upham and Patterson 2012). To clarify the evolutionary history of the genus *Octodon*, it is imperative that the genetic relationships among the 4 species are further assessed.

In this study, we report the rediscovery of the allegedly extinct *O. pacificus* at Mocha Island. Using partial mtDNA *Cytb* gene sequences, we reconstructed the phylogenetic relationships of the genus *Octodon*, and subsequently incorporated new data obtained from *O. pacificus*. We also discuss the conservation status and concerns associated with this rediscovered species.

MATERIALS AND METHODS

Study site and sample collection.—In December 2015, we conducted a small mammal survey at Mocha Island, a populated insular Chilean territory of about 48 km², located 34 km offshore from the Bío Bío region. Decades of anthropogenic landscape modifications led to the disappearance of the native Valdivian rainforest vegetation along the entire coast of the island. The native forest currently persists only within elevated areas of the central part of the island, which are now protected as a national reserve.

We spent a total of 800 traps nights in an area of approximately 3 ha during 3 field surveys in the southern part of Mocha Island (Fig. 1). On 29 December 2015, in the same area, a carcass of a female *Octodon* sp. was recovered from a lethal trap (-38.3955S, -73.9163W; 30 m above sea level) that was installed by local inhabitants to control the rodent population. Immediately after the carcass was discovered, a sample of muscle was obtained from the dead specimen and preserved in 95% ethanol. We also obtained tissues from other congeneric representatives: 10 muscle samples of *O. degus* from Bosque de Fray Jorge National Park (FJ, -30.6333S; -71.6666W), Las Chinchillas National Reserve (CHIN, -31.5005S; -71.1000W), Peñuelas National Reserve (PEN, -33.1666S; -71.4500W),

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Fig. 1.—Geographic distribution of *Octodon* species in Chile (based on Patton et al. 2015). White circles: collection sites of *O. degus* (this study), and white square: collection site of *O. lunatus* (this study).

and Til Til (TIL, -34.0666S; -70.95000W), and 2 muscle samples of *O. lunatus* from FJ (Fig. 1). The tissue collection of all 3 species was conducted under a Servicio Agricola Ganadero permit (number: 3348/2013), as well as with permission from the ethics committee of the Universidad de Concepción (18-2012; granted by Universidad de Concepción). The research on live animals followed the guidelines established by the American Society of Mammalogists (Sikes et al. 2011).

Morphological data.—To perform a morphological analysis, we used the terminology of Wood and Wilson (1936) and Woods and Howland (1979), including the following corporal dimensions: 1) body: total, tail, hindfoot and ear lengths; and 2) skull: greatest length, zygomatic width, interorbital width, nasalia length, nasalia width, diastema length, upper toothrow crown lengths, P4–P4 width, and widths of both upper I1. All measurements were obtained using a Mitutoyo caliper (0.01 mm; Mitutoyo Corporation, Japan) and are given in millimeters. These measurements were compared to the dimensions of the paratype and holotype of *O. pacificus*, as well as with those of the *O. bridgesii* and *O. lunatus* specimens. Necropsy

was performed and full-body radiography was analyzed with the aim of determining whether fetuses were present. The skull and body were placed in ethanol and deposited in the zoological collection of the Universidad de Concepción under accession number MZUC-UCCC: 44277 (skull), 44278 (body), and 44279-44281 (3 young).

Molecular methods.-DNA was extracted using a simple salt method described in Aljanabi and Martínez (1997). The mtDNA Cytb gene was selected for genetic analyses due to the availability of Cytb sequences in GenBank for several octodontine rodents. An approximately 1,000-base pair (bp) fragment of the Cytb gene was amplified using the primers MVZ05, MVZ16, MVZ108, and MVZ127 (Leite and Patton 2002). Specifically, the reactions contained 1 µl of DNA at 20 ng/µl, 1× reaction buffer, 1.5 mM of MgCl₂, 200 µM of each dNTP, 0.4 µM of each primer, and 0.8 units of Taq DNA polymerase Platinum (Invitrogen, Thermo Fisher Scientific, Waltham, Massachusetts), with a final reaction volume of 40 µl. The polymerase chain reaction (PCR) protocol has 2 phases as described by Korbie and Mattick (2008): 1) 10 min at 95°C, and 11 cycles of 95°C for 15 s; a touchdown of annealing temperature at 60°C-50°C for 30 s, with 1 cycle at each annealing temperature of 1°C interval, and 72°C for 45 s; 2) 35 amplification cycles at 95°C for 15 s, 50°C for 30 s, and 72°C for 45 s; and a final extension period of 30 min at 72°C. PCR products were visualized on 1% agarose gel with sodium borate (SB) buffer and RedGel; they were run for 20 min at 200 V, and amplicons of expected size were purified and sequenced bi-directionally at Macrogen, Inc. (Seoul, South Korea). The sequences were assembled and the polymorphic sites were confirmed by eye from the chromatograms using Sequencher v. 5.1 (Gene Codes, Ann Arbor, Michigan). Sequences were deposited in GenBank under the accession numbers KX298475-KX298482 (Supplementary Data SD1).

Phylogenetic reconstruction.—Sequences of all Octodon spp., including O. bridgesii (n = 1) obtained from GenBank (KJ742651), as well as Ctenomys (Ctenomyidae) and Trichomys (Echimyidae; Supplementary Data SD1), were

19.5

5.9

10.7

10.6

11.2

8.2

4.3

19.6

5.9

10.8

10.3

11.1

7.8

4

Nasalia length

Nasalia width

Width P4-P4

Diastma length

Upper toothrow, crowns

Upper toothrow, alv.

Width of both upper I1

aligned using the Clustal X software (Thompson et al. 1997). The sequence of Thrichomys laurentius (Echimyidae, Thomas 1904) was used as the outgroup. A Bayesian-inferred phylogenetic tree was constructed using MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). The evolutionary model was selected using jModelTest 0.1.1 (Guindon and Gascuel 2003; Posada 2008) and the Akaike Information Criterion (AIC). The best-fit model of nucleotide substitution was GTR+I+G. Two Bayesian analyses were run for 2,000,000 generations, with sampling performed every 1,000 generations. The SD of split frequencies was < 0.01, indicating that both runs had converged. Additionally, the potential scale reduction factor (PSRF-Gelman and Rubin 1992) was very close to 1 for all parameters, indicating that we had adequately sampled their posterior distributions. A consensus tree was visualized in FigTree 1.2.2 (Rambaut 2009). Genetic distances at intra- and interspecific levels for Octodontinae and *Ctenomys* spp. were calculated with MEGA 6 (Tamura et al. 2013).

RESULTS

We captured 281 rodents (a success rate of 31.6%) using Sherman traps; the rodent species were Abrothrix longipilis (n = 221), A. olivaceus (n = 32), and Rattus rattus (n = 18). No Octodon was captured with the Sherman traps.

Morphological characteristics.-The fur color of the collected specimen matched the pattern found for O. pacificus, as described by Hutterer (1994). The color of the pelage of O. pacificus is brown-orange, with brighter orange tips observed on the hairs of the underside. Octodon degus have agouti-colored fur, a lighter venter, and white ear tufts. Octodon lunatus have an agouti color that is very similar to that of O. degus, but with softer and longer pelage. The color of the pelage of O. bridgessi is a mixture of brown and yellow, not orange (Hutterer, 1994). Likewise, the morphological measurements of the skull and body of the specimen were concordant with the dimensions of O. pacificus, as detailed in the original description. The total length and tail length are generally longer in O. pacificus when

18.0

5.8

8.7

9.3

10.7

8.6

4.2

15.6

5.3

8.8

9.5

10.1

6.2

3.6

5	· í			Ĩ			
	This study	O. pacificus		O. bridgesii	O. lunatus	O. degus	
		Holotype	Paratype				
Total length	375	380	390	323 (250-370)	360 (328-382)	266.5 (200-307)	
Tail length	180	170	165	138.3 (102-167)	157 (152-161)	111.4 (81–138)	
Hindfoot	38	40	42	38.5 (34-40)	40.7 (40-42)	35.5 (31-40)	
Ear	18.7	20	20	22 (20-23)	28	24.7 (19-31)	
Greatest length	48.5	46.3		41.8-44.8	46.5	43.3	
Zygomatic width	25.2	25.9	25.3	23.7-23.9	23.8	23.9	
Interorbital width	9.1	10	86	8 1-9 0	9.1	10.3	

19.5

5.6

10.6

10.9

11.3

8.2

4.2

17.6

5.1-5.8

8.1-9.9

9.5-10.0

9.6-10.6

6.5-7.7

3.1-3.7

Table 1.—External and cranial measurements of Octodon pacificus from this study compared to the holotype and paratype measurements described by Hutterer (1994). Measurements (averages and ranges) of other Octodon species were obtained from Redford and Eisenberg (1992).

compared to the measurements of *O. bridgesii*; likewise, the ear is smaller in *O. pacificus* than in the other *Octodon* spp. (Table 1). Pictures of the analyzed skull are presented in Fig. 2. The necropsy procedure and radiographic study of the adult female identified at least 6 unborn pups (Fig. 3).

Phylogenetic analysis.—We analyzed a 1,093-bp fragment of the *Cytb* gene for all 4 *Octodon* spp. We identified 1 haplotype from *O. lunatus* (n = 2) and 6 haplotypes for *O. degus* (n = 10). The Bayesian phylogenetic reconstruction illustrates the genus *Octodon* as a monophyletic clade within the Octodontidae family, exhibiting a high posterior support value (0.99–1; Fig. 4). *Octodon degus* is basal to the remaining *Octodon* with a polytomy of *O. degus* haplotypes from FJ and CHIN, and another clade with haplotypes from PEN and TIL. *Octodon lunatus* branches off second, while *O. bridgesii* and *O. pacificus* represent sister taxa. The genetic distance between *O. bridgesii* and *O. pacificus* is very low (0.3%). This value is similar to the variation at the intraspecific level observed within *O. degus* (0.2–0.9%; Table 2), and it is lower than the genetic distance between several *Ctenomys* spp. (0.5–0.8%; Supplementary Data SD2). Only 4 polymorphic sites were identified between *O. bridgesii* and *O. pacificus*, whereas 57 polymorphic sites were found between *O. lunatus*, *O. bridgesii*, and *O. pacificus* (there were 139 polymorphic sites for the entire *Octodon* data set).

DISCUSSION

We report a new record of an insular endemic species that was alleged to be extinct. No further reports of this species were documented after its original description from the material collected in 1959 (Hutterer 1994), with the exception of a few archaeozoological skeletal remains (1,200–450 ya—Saavedra et al. 2003). Our morphological analyses revealed that the body, skull, and dentition morphometry were concordant with the dimensions of the type specimens



Fig. 2.—Lateral (a) and ventral (b) view of the skull, and the occlusal view of upper molars (c) of the collected Octodon pacificus.



Fig. 3.—Full-body radiograph of the studied specimen of Octodon pacificus with osteological evidence of 6 fetuses observed.



Fig. 4.—Bayesian phylogenetic reconstruction among the *Octodon* species, with several other members of the family Octodontidae included. Posterior support values are indicated on each node.

(holotype and paratype) of O. pacificus, which strongly suggest that the collected specimen indeed corresponds to the endangered species. However, our genetic analysis of Cytb sequences revealed a low genetic distance (0.3%) between this species and its sister, O. bridgesii, suggesting that the taxonomic status of O. pacificus should be carefully assessed. While the genetic divergence within O. bridgesii has yet to be evaluated, the low genetic divergence observed for the Cytb gene between these 2 Octodon spp. could be interpreted as intraspecific genetic variation, which would challenge the status of O. pacificus as a full species. One might argue that the discovered specimen is of O. bridgesii and not O. pacificus. However, O. bridgesii has not been reported on Mocha Island, and the closest mainland distribution to the island is Nahuelbuta (-33.6166S; -79.0333W). On the other hand, the minor genetic divergence of O. pacificus could be the result of a recent peripatric speciation process, implying that an original founder effect occurred on the island. The larger body size of O. pacificus with respect to O. brigdesii and the other continental Octodon spp. could be the result of insular evolution (Lomolino 2005; Lomolino et al. 2012). Further molecular assessments including nuclear markers are needed to ascertain the evolutionary history of *O. pacificus*.

Biodiversity conservation on islands is a major global concern due to the high endemism and extinction rates of insular biota (Alcover et al. 1998). Octodon pacificus from Mocha Island is not an exception. Since its original description in 1959, no live specimens have been reported, rendering the status of this rodent as a critically endangered species (IUCN 2015). While the central region of Mocha Island has been declared a national reserve (Verdugo 1989), human settlements and agricultural activities along the shoreline have degraded most of the potential habitat of O. pacificus. In addition, the local people often use lethal traps to control rodent populations. These factors likely serve as primary threats to the remaining O. pacificus populations. We were unable to capture O. pacificus, and this species was not caught during previous small mammal surveys. The Sherman traps that were used in our survey are generally capable of capturing semifossorial and social rodents, such as Octodon. However, Tomahawk traps were shown to be most effective in capturing O. degus (Burger et al. 2009). This highlights the importance of trap type in specimen capture,

Table 2.—Pairwise genetic distances between species of *Octodon* (different populations of *Octodon degus* are treated separately). In bold is the genetic distance between the studied *O. pacificus* and *O. bridgesii*.

	O. degus (FJ1)	O. degus (CHIN1)	O. degus (PEN1)	O. degus (PEN2)	O. degus (TIL1)	O. degus (TIL2)	O. lunatus	O. bridgesii
O. degus (FJ1)								
O. degus (CHIN1)	0.005							
O. degus (PEN1)	0.009	0.009						
O. degus (PEN2)	0.009	0.009	0.002					
O. degus (TIL1)	0.007	0.007	0.002	0.002				
O. degus (TIL2)	0.009	0.006	0.003	0.003	0.002			
O. lunatus	0.099	0.099	0.101	0.103	0.101	0.101		
O. bridgesii	0.099	0.098	0.099	0.101	0.099	0.097	0.051	
O. pacificus	0.099	0.098	0.099	0.101	0.099	0.097	0.049	0.003

and future surveys should consider using Tomahawk-style traps to increase the trapping success rate. It is critical to note that the female analyzed in this report was pregnant with at least 6 young, indicating that the population of this threatened species is still reproductively active. More individuals of *O. pacificus* from Mocha Island and a larger sample of *O. bridgesii* are required to better understand the evolutionary history of *O. pacificus*.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Table of all *Octodon* sequences and representatives of the Octodontinae subfamily obtained from GenBank with respective accession numbers and references.

Supplementary Data SD2.—Table of genetic distances between species of *Ctenomys*. In bold the lowest genetic distance calculated between several pairwise *Ctenomys* species.

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