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Variability and variation in *Dromiciops* Thomas, 1894 (Marsupialia, Microbiotheria, Microbiotheriidae)

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The genus *Dromiciops* Thomas is the only living representative of the order Microbiotheria. Throughout the history of the taxon, it was considered to comprise a continental and an insular form (*D. australis* and *D. gliroides*), a single species (*D. gliroides*), or, as recently described, 3 different species (*D. bozinovici*, *D. mondaca*, and *D. gliroides*). I analyzed the morphometric and morphologic variability (differences in morphological characters within a sample or species) and variation (differences in morphological characters among samples or species) in *Dromiciops.* Comparisons to test for secondary sexual dimorphism were made within and between continental and insular samples for localities with the largest samples available. Due to the lack of sexual dimorphism, males and females were analyzed together to test for: 1) differences between continental and insular samples; 2) differences between the arrangement of recently described species using a larger series of available specimens; and 3) clinal variation. Results support *Dromiciops* as composed of 1 valid species (*D. gliroides*), without clinal variation. Based on the samples I examined, several characters previously used as diagnostic for the 3 species previously recognized (e.g., incisive and palatal fenestrae, mandibular height) vary intraspecifically and are not valid as diagnostic.

El género *Dromiciops* Thomas es el único representante viviente del orden Microbiotheria. Durante su historia como entidad taxonómica, se consideró compuesto de una especie insular y otra continental (*D. gliroides* y *D. australis*, respectivamente), como una única especie (*D. gliroides*), o como se ha descrito recientemente, compuesta por tres especies diferentes (*D. bozinovici*, *D. mondaca* y *D. gliroides*). Los objetivos de este trabajo fueron analizar la variabilidad y variación morfométrica y morfológica en *Dromiciops.* Se realizaron comparaciones para probar la existencia o no de dimorfismo sexual en las muestras continentales e insulares y entre estas dos, usando las localidades con el mayor número de especímenes. Debido a la falta de dimorfismo sexual machos y hembras se analizaron juntos permitiendo testear la existencia de diferencias entre muestras continentales e insulares, analizar la propuesta reciente de separar *D. gliroides* en tres especies (dos de ellas nuevas) con una serie mayor de especímenes y testear la existencia de variación clinal. Basándome en los ejemplares examinados, muchos de los caracteres usados como diagnósticos para las tres especies recientemente reconocidas (e.g., fenestras incisivas y palatinas, alto mandibular), varían a nivel intraespecífico y no son válidos como diagnósticos.

Key words: marsupials, Monito del monte, morphology, species characteristics

The genus *Dromiciops* Thomas is the only living representative of the order Microbiotheria, a group of American marsupials more closely related to Australian marsupials than to any other American order (Szalay 1982a, 1994; but see Hershkovitz 1999). The history of this taxon as a separate entity from the other, most common American marsupials (Didelphimorphia) starts off with Reig (1955), who highlighted the differences of *Dromiciops* and included the species in a family that, until that moment, was only known from fossils (i.e., Microbiotheriidae—Reig 1955). Walter Segall's contributions on the anatomy of

the tympanic bullae in marsupials and insectivores added a unique character to this group: a completely closed bulla, which contained the tympanic ring (Segall 1969a, 1969b, 1970). Until 1982 and even later (see Reig et al. 1985, 1987; Hershkovitz 1992, 1999), microbiotheres were considered within Didelphidae (subfamily Microbiotheriinae—Simpson 1945; Ringuelet 1953; Ride 1964; Segall 1969a, 1969b, 1970); as a separate family within Didelphoidea (Kirsch 1977; Reig 1981; Marshall 1982); or basal to all other marsupials, living or extinct (Hershkovitz 1992, 1995, 1999).

Szalay (1982a, 1982b) separated the order Microbiotheria from Didelphimorphia in a comparative study of the tarsal anatomy of Old and New World marsupials, proposing the cohort Ameridelphia for all American marsupials, and Australidelphia for all the Australian forms plus *Dromiciops* and fossil microbiotheres (but see Hershkovitz 1992, 1995, 1999). Although all the information generated after 1990, mostly based on genetic and molecular studies, confirm the separation of *Dromiciops* from other American marsupials, its positioning within the Australian radiation has not reached a consensus (see Sharman 1982; Temple-Smith 1987; Kirsch et al. 1991, 1997; Westerman and Edwards 1991; Retief et al. 1995; Springer et al. 1998).

In the taxonomic history of the genus, *Dromiciops* was separated into an insular form (*D. gliroides*) restricted to Chiloé Island (Chile), and a continental form (*D. australis*), with occurrence records for Argentina and Chile (Philippi 1893, 1894; Thomas 1894; Thomas 1919; Osgood 1943; Greer 1965). This taxonomic arrangement did not reach a consensus and was little used subsequently (see Martin 2008). Recently, Himes et al. (2008) recognized the existence of certain genetic structure within populations of *Dromiciops*, differences that were analyzed by D'Elía et al. (2016) who described 2 new species for the genus (but see Valladares-Gómez et al. 2017).

This study focuses on what has been described as intraspecific variability and variation following Yablokov (1974), including some aspects discussed by Bateson (1939), Simpson (1948), and Simpson et al. (2003). Variability, as used by these authors, is understood as "the presence of differences among individuals within a breeding population" (Simpson 1948), the magnitude of differences within a specific characteristic or trait, or changes associated with the transition from one characteristic to another. The measurement of intraspecific variability gives an idea of how a character or trait might differ within a population, providing insights into the evolution of a taxon, and describing "the potential or the propensity to vary" (Wagner and Altenberg 1996). The concept of variation as used here implies a different characteristic or state of a certain character (i.e., polymorphic) between individuals in a population, a sample, or species in a clade (Wagner and Altenberg 1996; Wagner et al. 1997). Therefore, to establish interspecific variation between characters, one must understand their intraspecific or intrapopulation variability.

Due to the taxonomic singularity of *Dromiciops*, this work has the following goals: 1) to characterize the genus morphologically and morphometrically; 2) to analyze the intraspecific variability for external and craniodental traits; 3) to test the distinction of insular and continental forms, as well as the groups recovered or described by Himes et al. (2008) and D'Elía et al. (2016); and 4) to test the existence of latitudinal (clinal) variability.

Materials and Methods

Variability and variation of cranial, mandibular, and dental characters are described for *Dromiciops* through the study of the holotype and specimens from several collections (Appendix I). Collections examined and their acronyms are as follows: AMNH, American Museum of Natural History, New York; BMNH, British Museum of Natural History, London; CML, Colección Miguel Lillo, Tucumán; CRUB-M, Centro Regional Universitario Bariloche, San Carlos de Bariloche; FMNH, Field Museum of Natural History, Chicago; LIEB-M, Laboratorio de Investigaciones en Evolución y Biodiversidad, Esquel; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires; MLP, Museo de La Plata, La Plata; UACH, Universidad Austral de Chile, Valdivia; and USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Skull measurements were integrated with external measurements, which were taken from skin labels or field catalogs, and include total length (TTL), head and body length (HBL), tail length (TL), hind-foot length (F), ear length (E), and weight (W). When HBL was not provided, it was calculated by subtracting TL from TTL. When TTL was not provided, it was calculated by the sum of HBL and TL.

Skull anatomy and description follows Wible (2003), with the exception of the palate for which Voss and Jansa (2003) were followed. Dental nomenclature follows Goin (2003). Upper and lower dentition are designated by uppercase and lowercase letters, respectively. Dental homologies follow Luckett (1993), in which the first 2 upper and lower premolars are considered unreplaced deciduous teeth. Therefore, teeth found in adult dentition of *Dromiciops* are designated as follows (from anterior to posterior): upper and lower incisors, I1–5 and i1–4; canines, C1 and c1; premolars, dP1–2 and dp1–2, and P3 and p3; and molars, M1–4 and m1–4. The single functional deciduous tooth in each jaw quadrant, when referenced, is designated dP3 or dp3. The presence of diastemas, which are represented by the symbol *D* (following Martin 2008), is described between canines and the 1st premolars, between premolars, and between the last premolar and the 1st molar.

A total of 22 measurements were taken from crania, mandibles, and teeth of adults (as indicated by completed tooth eruption) as follows: greatest cranial length (GCL); zygomatic breadth (ZB); palatine length (PL); palate width at canines (CW); palate width at M3 (PWM3); interorbital constriction (LINOR); nasal length (NSL); braincase width (BW); condylobasal length (CBL); distance between bullae (BB); maximum length and width of the bulla (LB and WB, respectively); mandibular width (MW); mandibular height at m3 (MHm3); length from the anteriormost point of the 1st upper premolar to the

posteriormost point of the last upper molar (dP1–M4); length from the anteriormost point of the 1st upper molar to the posteriormost point of the last upper molar (M1–M4); length from the anteriormost point of the 1st lower premolar to the posteriormost point of the last lower molar (dP1–m4); length from the anteriormost point of the 1st lower molar to the posteriormost point of the last lower molar (m1–m4); length and width of the 3rd upper and lower molar (LM3, WM3, Lm3, and Wm3, respectively; Fig. 1).

Measurements of adults were used to assess intraspecific variability, including possible sexual dimorphism. Mosimann's variables were calculated for each linear measurement by dividing specimen measurements by the geometric mean of the measurements of all the specimens (Mosimann 1970). In this way, shape variables (independent of size) were calculated and used in the sexual dimorphism and principal component analyses (PCAs; see below). This methodology was previously used in Meachen-Samuels and Van Valkenburgh (2009), Morales and Giannini (2010), and Schiaffini et al. (2017). As proposed by Rice (1989), a standard Bonferroni ($P = \alpha/n$) correction was used on P-values for the analyzed variables, with $P = 0.008$ and 0.002 for external measurements with α-values of 0.05 and 0.01; and $P = 0.0023$ and 0.00045 for craniodental variables with α-values of 0.05 and 0.01, respectively.

A non-parametric Kruskal–Wallis analysis of variance (ANOVA) was performed to test for sexual dimorphism, using 3 localities with specimen numbers > 10 (i.e., La Picada, $n = 45$; Valdivia, $n = 18$; Fundo San Martín, $n = 13$). To test for morphometric differences between insular and continental forms (i.e., the "traditional" distinction between *D. gliroides* and *D. australis*), sexual dimorphism was analyzed independently for all insular and continental specimens through a non-parametric Kruskal–Wallis ANOVA. This was followed by the same type of ANOVA to test for differences between continental and insular samples. To test for morphometric differences between the species recently recognized by D'Elía et al. (2016), 4 PCAs on the covariance matrix (based on Mosimann's variables as discussed above) were preformed: 1) including all external and craniodental measurements; 2) only using external measurements, excluding weight; 3) only with craniomandibular and dental measurements; and 4) only with dental measurements. These PCAs were performed with standardized measurements to test for intraspecific dispersion, and to include specimens from localities scattered throughout the species range, which could not be analyzed using the above ANOVAs. The number of principal components (PCs) used was selected following Cattell (1966). A multivariate analysis of variance (MANOVA) was performed between the different PCs to test for significant differences between each of them, and the groups recognized by D'Elia et al. (2016), and separating Chiloé Island. The existence of clinal variability was tested by regressing latitude with the first 2 axes from each PCA (Martin 2013). All statistical analyses were performed using InfoStat (Di Rienzo et al. 2010).

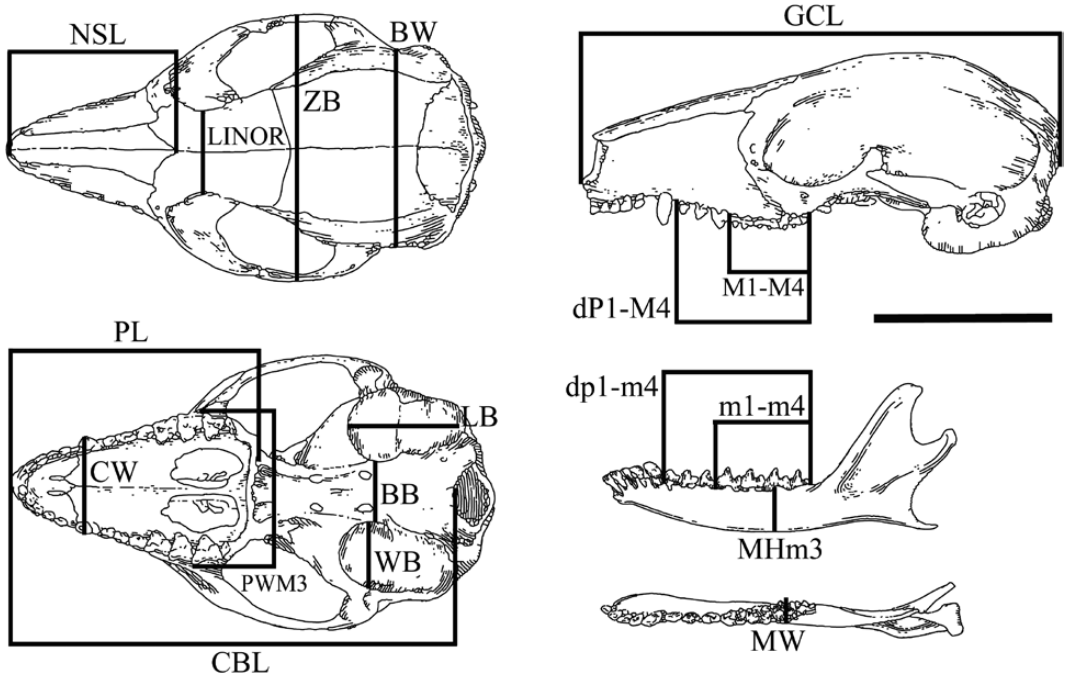

Fig. 1.—Diagrammatic views of skull and mandible of *Dromiciops* illustrating measurements taken: greatest cranial length (GCL); zygomatic breadth (ZB); palatine length (PL); palate width at canines (CW); palate width at M3 (PWM3); interorbital constriction (LINOR); nasal length (NSL); braincase width (BW); condylobasal length (CBL); distance between bullae (BB); maximum length and width of the bulla (LB and WB, respectively); mandibular width (MW); mandibular height at m3 (MHm3); length from the anteriormost point of the 1st upper premolar to the posteriormost point of the last upper molar (dP1–M4); length from the anteriormost point of the 1st upper molar to the posteriormost point of the last upper molar (M1–M4); length from the anteriormost point of the 1st lower premolar to the posteriormost point of the last lower molar (dP1–m4); length from the anteriormost point of the 1st lower molar to the posteriormost point of the last lower molar (m1–m4).

Due to the large number of specimens analyzed, a morphological description following Martin (2008) is done to characterize the cranium, mandibles, and teeth of *Dromiciops*, providing an opportunity to discuss some of the characters used as diagnostic for the species recognized by D'Elía et al. (2016), and the previous separation between insular and continental forms.

Results

A total of 141 adults of *Dromiciops* was studied, coming from ca. 30 localities spread throughout the species known distribution (Appendix I). Of these, 106 (~82%) come from 17 localities in Chile, with a latitudinal range from −37.4333°S to −43.1096°S; 25 specimens (~18%) come from 9 localities in Argentina, with a latitudinal range from −40.19417°S to −42.549°S. Three localities in Chile produced ca. 56% of the studied specimens (La Picada, n = 45; Valdivia, n = 21; Fundo San Martín, n = 16), while the majority of other localities have less than 6 specimens available (Appendix I). These localities have been recently attributed to *D. gliroides* (i.e., La Picada) and *D. mondaca* (i.e., Valdivia and Fundo San Martín) by D'Elía et al. (2016).

Intraspecific morphometric variability.—No significant differences were found between the sexes in any of the external, craniomandibular, and dental measurements analyzed for the 3 localities with the largest numbers of specimens (Table 1). Similarly, no differences were found between continental males and females, or those from Chiloé Island (Table 2). Finally, an ANOVA between all males and females pooled together was performed, and no differences were found between the sexes (Table 3). Also, no qualitative differences were found in any studied characters between males and females of *Dromiciops*, within the 3 localities with the most specimens, continental and island samples, and all samples pooled together (see below).

As for the arrangement proposed by D'Elía et al. (2016) into 3 species, and the separation between continental and insular forms (*D. australis* and *D. gliroides*, respectively), results of the PCA for all measurements (Supplementary Data SD1), external measurements only (Supplementary Data SD2), craniodental measurements (Supplementary Data SD3), and dental measurements (Supplementary Data SD4) revealed no significant morphometric differences (see also Fig. 2; Supplementary Data SD5–SD7). The first 2 PCs explained 68%, 88%, 62%, and 66% of the total variation, respectively. Results of the MANOVA performed between the different PCs and the classification criteria of D'Elía et al. (2016) and specimens from Chiloé Island as separate showed no significant differences between groups (Table 4; Supplementary Data SD8–SD10). Due to this lack of morphometric differentiation, average measurements for

Table 1.—Results of a non-parametric Kruskal–Wallis analysis of variance (ANOVA), calculated from Mosimann's variables, for differences between males and females of *Dromiciops*, for 3 localities with the largest number of specimens. Number of specimens per locality (n), and by sex are indicated for the 3 sites (La Picada, Valvidia, and Fundo San Martín, all in Chile). Asterisks mark significant differences (if existent) for Bonferroni-corrected values, following Rice (1989). See text for variable abbreviations.

Variables	La Picada (n = 45; 21 ♀, 24 ♂)		Valdivia (n = 21; 6 ♀, 15 ♂)		Fundo San Martín (n = 16; 6 ♀, 10 ♂)	
	H	P-value	H	P-value	H	P-value
TTL	0.03	0.8588	0.98	0.3208	1.68	0.2227
HBL	0.14	0.7042	0.03	0.8687	2.77	0.1045
TL	0.03	0.8680	0.62	0.4323	1.52	0.2448
F	0.81	0.3524	0.98	0.3155	0.21	0.6881
E	0.04	0.8449	0.01	0.9324	2.63	0.1245
W	0.09	0.7581	1.19	0.2738	0.11	0.7972
GCL	5.90E-04	0.9806	2.29	0.1636	1.09	0.3929
ZB	0.01	0.9226	0.46	0.5414	0.27	0.6786
PL	0.12	0.7332	2.34	0.1394	1.8	0.25
PWM3	0.06	0.806	0.02	0.9133	0.07	0.9048
LINOR	1.78	0.1752	0.15	0.7399	0.15	0.7619
CW	0.17	0.6776	0	> 0.9999	1.35	0.2857
BW	2.05	0.1513	0.05	0.8503	0.07	0.9405
NSL	0.76	0.3815	1.04	0.3354	0.82	0.4167
CBL	0.03	0.865	1.29	0.2909	1.42	0.2857
BB	0.01	0.9418	0.38	0.5748	1.35	0.2857
WB	0.14	0.7014	1.01	0.3497	4.27	0.0357
LB	3.94	0.0465	0.48	0.5301	0.6	0.5
MW	0.08	0.7433	0.02	> 0.9999	0.27	0.6667
MHm3	0.37	0.5397	0.72	0.4503	0.6	0.5119
m1–m4	0.21	0.6347	1.72	0.2168	0.6	0.6429
dp1–m4	0.01	0.9027	0.01	0.9664	0.82	0.4286
Lm3	0.64	0.4044	6.1	0.007	0.42	0.5952
Wm3	0.48	0.4571	0.86	0.4629	0.15	> 0.9999
dP1–M4	0.01	0.9028	0.02	0.8951	2.02	0.1786
M1–M4	0.05	0.8244	0.38	0.5748	2.82	0.119
LM3	2.41	0.1009	0.38	0.5385	1.35	0.4643
WM3	0.01	0.915	2.38	0.1678	0.82	0.6429

Table 2.—Results of a non-parametric Kruskal–Wallis analysis of variance (ANOVA), calculated from Mosimann's variables, for differences between males and females of *Dromiciops*, with specimens from all continental localities, and Chiloé Island. Number of specimens per locality (*n*), and by sex are indicated for each sample. Asterisks mark significant differences (if existent) for Bonferroni-corrected values, following Rice (1989). See text for variable abbreviations.

Variables	Continental (n = 119; 71 ♀, 48 ♂)		Chiloé Island (n = 8; 4 ♀, 4 ♂)	
	H	*P*-value	*H*	*P*-value
TTL	–0.42	> 0.9999	0.43	0.7
HBL	–0.51	> 0.9999	0.43	0.7
TL	–1.13	> 0.9999	0.05	> 0.9999
F	–2.04	> 0.9999	0.33	0.7
E	3.47	0.0561	0.05	> 0.9999
W	2.12	0.1449	0.43	0.7
GCL	–27.81	> 0.9999	1.5	0.6667
ZB	–25.51	> 0.9999	3	0.2
PL	–21.99	> 0.9999	0.6	0.6667
PWM3	–36.78	> 0.9999	2.08	0.3
LINOR	–13.68	> 0.9999	0	> 0.9999
CW	–35.05	> 0.9999	0.33	0.7
BW	–40.18	> 0.9999	0.75	0.5
NSL	–5.7	> 0.9999	0.33	0.8
CBL	–17.26	> 0.9999	2.4	0.3333
BB	–21.24	> 0.9999	0.33	0.8
WB	–18.2	> 0.9999	0	> 0.9999
LB	–3.76	> 0.9999	0.33	0.8
MW	–34.97	> 0.9999	–5.4	0.8333
MHm3	–22.31	> 0.9999	–3.5	0.6667
m1–m4	–8.72	> 0.9999	–4.14	0.6333
dp1–m4	–17.29	> 0.9999	–4.76	0.7167
Lm3	–25.39	> 0.9999	–5.76	0.7833
Wm3	–40.99	> 0.9999	–4.07	0.6
dP1–M4	–23.29	> 0.9999	–0.29	0.3833
M1–M4	–17.69	> 0.9999	–4.58	0.6667
LM3	–16.49	> 0.9999	–7.61	0.9167
WM3	–20.18	> 0.9999	–0.33	0.3833

Table 3.—Results of a non-parametric Kruskal–Wallis analysis of variance (ANOVA), calculated from Mosimann's variables, for differences between males and females of *Dromiciops*, with specimens from all studied localities. The number of analyzed specimens is 134, 52 ♀, 75 ♂. Asterisks mark significant differences (if existent) for Bonferroni-corrected values, following Rice (1989). See text for variable abbreviations.

Variables	*H*	*P*-value
TTL	–0.27	> 0.9999
HBL	–0.47	> 0.9999
TL	–1.14	> 0.9999
F	–1.97	> 0.9999
E	3.6	0.0516
W	2.33	0.127
GCL	–26.91	> 0.9999
ZB	–23.89	> 0.9999
PL	–21.43	> 0.9999
PWM3	–35.76	> 0.9999
LINOR	–11.78	> 0.9999
CW	–34.11	> 0.9999
BW	–38.88	> 0.9999
NSL	–5.05	> 0.9999
CBL	–16.41	> 0.9999
BB	–21.96	> 0.9999
WB	–18.44	> 0.9999
LB	–3.4	> 0.9999
MW	–41.81	> 0.9999
MHm3	–26.68	> 0.9999
m1–m4	–13.35	> 0.9999
dp1–m4	–20.91	> 0.9999
Lm3	–29.32	> 0.9999
Wm3	–46.06	> 0.9999
P1–M4	–26.52	> 0.9999
M1–M4	–21.64	> 0.9999
LM3	–25.93	> 0.9999
WM3	–18.32	> 0.9999

Dromiciops are presented in Table 5. Of these, most cranial and dental measurements, with the exception of between bullae (BB), mandibular width (MW) and height at m3 (MHm3), and length of m3 (Lm3), showed low coefficients of variability (*CV*s), implying a small relative dispersion of the studied measurements. These results provide no morphometric support to separate *Dromiciops* into the different species proposed by D'Elía et al. (2016), or the insular and continental arrangement of Thomas (1919), Osgood (1943), and Greer (1965) (i.e., *D. gliroides* and *D. australis*, respectively).

No significant trend was found when the first 2 PCs were regressed with latitude for any set of variables, indicating no evidence for clinal variation (all measurements: n = 49; PC1, r^2 = 0.09, F = 5.86, P = 0.0194; PC2, r^2 = 0.06, F = 4.07, P = 0.0493; external measurements only: n = 99; PC1, r^2 = 0.00, F = 0.73, P = 0.3948; PC2, r^2 = 0.01, F = 1.7, P = 0.1952; craniodental measurements only: n = 60; PC1, r^2 = 0.04, F = 3.62, P = 0.0621; PC2, r^2 = 0.02, F = 2.02, P = 0.1601; and dental measurements only: n = 76; PC1, r^2 = 0.02, F = 2.72, P = 0.1035; PC2, r^2 = 0.00, F = 0.02, P = 0.9025).

What follows is a description of the cranium, mandible, and teeth of *Dromiciops*, and comparisons with several aspects described by D'Elía et al. (2016) as diagnostic for their new species.

General structure of the cranium and mandibles.—The skull of *Dromiciops* is similar in general aspect to that of small didelphids, but the skull is taller, with a shorter rostrum, broad zygomatic arches and large orbits. In ventral view, 3 characteristics are the most conspicuous: 1) completely closed tympanic bullae, which are large and occupy most of the basicranium; 2) large maxillopalatine fenestrae, which occupy half of the palate; and 3) large incisors, small premolars, and molars, especially when compared to similar-sized marsupials.

In dorsal view, nasals are short, not extending beyond the premaxilla anteriorly, narrow in general shape, and without a posterior broadening. They contact the frontals forming an open, but not very broad V. Frontals have a well-marked interorbital constriction located close to the posteriormost extension of the nasal, without lateral processes or crests. Frontal and parietal bones join in a broad, mostly straight line, with lateral projections of the parietals in the dorsoposterior area of the orbit. Parietals contact the interparietal posteriorly, which extends laterally to the sides of the skull. The lambdoidal crest

is absent in all studied specimens, even those with great tooth wear (e.g., CRUB 015, CRUB 011).

In lateral view, the rostrum is high, and normally not dorsoventrally compressed, as in most small didelphids such as *Thylamys pallidior* or some Australian dasyurid marsupials (e.g., *Antechinus*, *Phascogale*, *Sminthopsis*). The premaxilla contacts the maxilla almost in a straight line, including I5 in lateral view and the shallow paracanine fossa, which is highly variable in length (depending on the specimen's age), and usually larger than canine breadth (e.g., USNM 391772, USNM 536888, LIEB-M-1528). The maxilla contacts the nasal dorsally, has a narrow posterodorsal contact with the frontal and lacrimal, and a posteroventral wedge-like contact with the jugal. The maxilla is perforated by an anteriorly opening infraorbital foramen, situated above P3–M1. The zygomatic arch is slender, strongly inflected ventrally, right before the suture between jugal and squamosal. In the region below the contact with the lacrimal, it has a well-developed shelf where the M. zygomaticus is located (sensu Turnbull 1970). The contact between jugal and squamosal bones is broad, with the jugal forming a thin but long ventral spine, similar to the one found in most didelphids. The postglenoid process is short and slender, the glenoid fossa is broad but shallow. The tympanic bullae are tall and completely enclosed by 3 bones: the ectotympanic laterally, an anterior tympanic process of the alisphenoid, a caudal posterolateral tympanic process of the petrosal, and a rostral mesioventral tympanic process of the petrosal (Sánchez-Villagra and Wible 2002). Bones at the distal end of the skull, including interparietal, supraoccipital, and exoccipital bones, expand posteriorly.

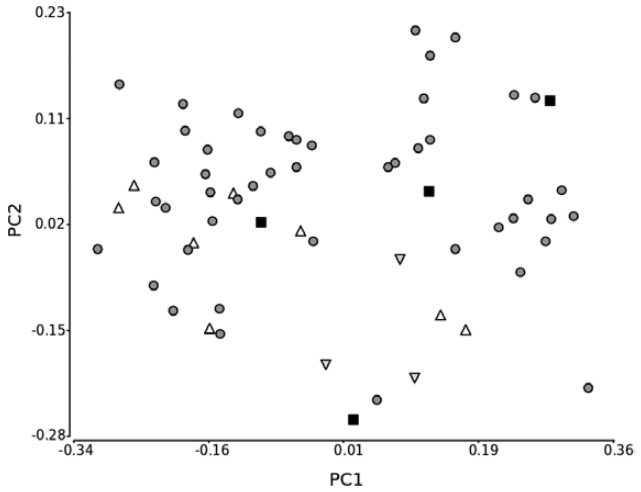

Fig. 2.—Principal component analysis (PCA) of all studied individuals of *Dromiciops* using craniodental measurements, following the groups described by Himes et al. (2010) and D'Elía et al. (2016). Clade A (*Dromiciops bozinovici*): black squares; Clade B (*D. mondaca*): white triangle; Clade C (*D. gliroides*): gray circles. The inverted gray triangles were used for specimens from Chiloé Island, formally assigned by the above authors to Clade C (*D. gliroides*).

In ventral view, the palate has a triangular shape, similar to that of small didelphid and dasyurid marsupials (e.g., *Cryptonanus chacoensis*, *Lestodelphys halli*, *Marmosa constantiae*, *T. pallidior*, *Sminthopsis* spp., *Antechinus* spp.), but rounded instead of pointed. The premaxillary includes all incisors, and has incisive fenestrae of varied size, from very small (e.g., MACN 19142) to large (e.g., MACN 13038, MACN 48.26). These occupy most of the premaxilla, and although variable in size, they extend posteriorly to the anterior edge of the canines. The maxilla contacts the premaxilla almost in a straight line in specimens with small incisive fenestrae, or by small and thin wedge-like contacts in those specimens with larger fenestrae. The maxilla is posteriorly perforated by the maxillopalatine fenestrae, which occupy a large proportion (sometimes close to 50%) of the distal part of these bones. Maxillopalatine fenestrae are separated in the middle area by a medial septum (sensu Giannini et al. 2004), which is not present in some specimens (e.g., CRUB 015) probably due to breakage during preparation. The contact between maxilla and palatine is very narrow, depending mostly on the size of the maxillopalatine fenestrae. The interpterigoid bridge is slender, and is perforated laterally by small posterolateral foramina. The presphenoid is broad, and extends anteriorly contributing to the nasal septum; it has a very prominent keel that extends from the vomer to the basioccipital, separating the primary palate in two. This keel (also known as sphenoid crest sensu Giannini et al. 2004) also holds the soft palate in the medial region, due to the lack of support from the palatine, which is highly perforated by the maxillopalatine fenestrae. The presphenoid contacts the basisphenoid, which is perforated by 2 well-marked carotid foramina, almost at the suture with the basioccipital. Between each carotid foramen and the anteromedial portion of the alisphenoid, the oval foramen opens to the interior of the skull. The contact between basisphenoid and basioccipital is wide, occupies all the area between the bullae, and is located at the major anteromedial extension of the rostral process of the petrosal. The basioccipital occupies most of the basicranium between the auditory bullae; it is laterally perforated by 2 foramina, the yugal and hypoglosal, at the contact with the caudal

Table 4.—Results of the multivariate analysis of variance (MANOVA) with all specimens of *Dromiciops*, performed between the first 5 principal components (PCs) and the classification criteria (clades) of D'Elía et al. (2016) and specimens from Chiloé Island, with craniodental measurements; *n* indicates the number of specimens analyzed per group. The last column shows the groups assigned by the MANOVA; same letter indicates same group.

Clade	PC1	PC2	PC3	PC4	PC5	*n*	Group
A (Northern)	0.09	−0.03	−0.06	−1.00E-03	−0.03	4	A
B (Central)	−0.09	−0.06	0.03	−0.01	2.00E-03	8	A
C (Southern)	4.20E-03	0.02	3.00E-03	4.00E-03	1.50E-03	47	A
Chiloé Island	0.06	−0.15	−0.04	−0.04	0.02	3	A

Table 5.—Average values of external, cranial, and dental measurements of *Dromiciops gliroides*, with specimens from all studied localities. Total number of analyzed specimens (*n*) per category, average ($\bar{X}$), *SD*, maximum (Max) and minimum (Min) measurements, and coefficient of variability (*CV*) are presented. Asterisks mark *CV*s with values lower than 7. See text for variable abbreviations.

Variable	*n*	$\bar{X}$ ± *SD* (Max – Min) *CV*
TTL	117	206.50 ± 16.89 (258.00 – 165.00) 8.18
HBL	113	99.84 ± 11.41 (131.60 – 70.00) 11.43
TL	119	106.53 ± 10.27 (140.00 – 82.00) 9.64
F	116	17.78 ± 1.38 (22.00 – 15.00) 7.77
E	111	16.29 ± 2.18 (20.00 – 8.80) 13.38
W	103	23.75 ± 9.07 (68.00 – 10.00) 38.20
GCL	72	27.95 ± 0.98 (29.85 – 25.00) 3.49*
ZB	75	15.80 ± 0.64 (17.55 – 14.00) 4.05*
PL	74	13.65 ± 0.65 (15.10 – 12.20) 4.72*
PWM3	77	9.14 ± 0.38 (10.13 – 7.90) 4.14*
LINOR	79	4.94 ± 0.22 (5.40 – 4.40) 4.38*
CW	78	5.23 ± 0.30 (6.20 – 4.40) 5.68*
BW	79	12.31 ± 0.41 (13.54 – 11.20) 3.34*
NSL	76	10.41 ± 0.63 (11.70 – 9.10) 6.08*
CBL	71	24.69 ± 1.03 (26.77 – 21.90) 4.16*
BB	77	3.43 ± 0.46 (4.37 – 2.60) 13.55
WB	74	4.15 ± 0.26 (4.70 – 3.50) 6.15*
LB	74	6.93 ± 0.30 (7.70 – 6.25) 4.31*
MW	80	1.01 ± 0.08 (1.30 – 0.80) 8.04
MHm3	80	2.31 ± 0.18 (2.70 – 2.00) 7.64
m1–m4	80	5.70 ± 0.19 (6.10 – 5.10) 3.31*
dp1–m4	80	8.54 ± 0.28 (9.10 – 7.70) 3.29*
Lm3	79	1.40 ± 0.10 (1.63 – 1.20) 7.27
Wm3	79	0.86 ± 0.06 (0.97 – 0.60) 6.82*
dP1–M4	79	7.85 ± 0.28 (8.50 – 6.90) 3.63*
M1–M4	79	5.01 ± 0.21 (5.40 – 4.10) 4.12*
LM3	79	1.45 ± 0.08 (1.63 – 1.10) 5.54*
WM3	79	1.71 ± 0.08 (2.00 – 1.50) 4.83*

process of the petrosal. A detailed description of the tympanic bulla of *Dromiciops* was provided by Segall (1969a, 1969b), due to its unique conformation among living marsupials. There are 4 main osseous components in the bulla: an alisphenoid tympanic process, with anteroventral development as in many didelphids; a petrosal caudal process that posteriorly "closes" the bulla; a medioventrally developed rostral process of the petrosal; and an ectotympanic that laterally closes the bulla. The basioccipital and exoccipital processes completely enclose the bullae in their contact with the basicranium. This pattern that is typical of adults is slightly different in subadults and juveniles, where the ectotympanic limits the acoustic meatus, instead of the alisphenoid and the caudal process of the petrosal (Giannini et al. 2004). Other characteristics of the tympanic bullae were described by Sánchez-Villagra and Wible (2002), and included a broad contact between rostral and caudal processes of the petrosal, and a deep sulcus for the internal carotid artery.

The mandible is slender, with a shallow (not deep) horizontal ramus that shows a straight lower border (not inflected as in most didelphids and small dasyurids), and with a short ascending ramus that forms a clear obtuse angle with the horizontal ramus. The mandibular symphysis is short and subvertically oriented, barely extending posteriorly beyond the root of c1, or to a point between c1–dp1. In lateral view and from posterior to anterior, the mandible is vertically oriented until p3–m1, where its main axis shifts obliquely, generating a shovel-like structure (in dorsal view) when mandibles are joined, surrounded by the small spatulate incisors, canine, and premolar. This can be directly associated to a broad and round muzzle. The mandible has a mental foramen located bellow dp1 or between dp1–dp2, and 1 or more subsidiary foramina anterior and posterior to this one, which can be separated by its larger size and deeper structure. The ascending ramus has a thin anterior border, which originates at mid-height of the horizontal ramus, and forms an obtuse angle with the horizontal ramus. The masseteric fossa is shallow, and similar in overall size to that of other small marsupials, with the exception of highly animalivorous species (e.g., *L. halli*, *Monodelphis* spp., *Sminthospis* spp.—Archer 1981; Martin 2005). The coronoid process is thin and slender, while the mandibular condyle is wide and robust, in proportion with the broad glenoid fossa. The angular process is thin and ventrally inflected ("rod-like" sensu Sánchez-Villagra and Smith 1997).

Dentition.—Dromiciops can be characterized by the following general dental traits: incisors with spatulate crowns and of large size when compared to other teeth; continuous contact (without diastema) between I1 and the rest of the upper incisors; small-sized straight (non-procumbent) canines; and premolars and molars of small overall size in relation to skull size.

All analyzed specimens showed upper incisors with a round cross section at the base (at the alveolus level) and spatulate crowns, which expand posteriorly over the gum, reducing in size from I1 to I5, and with crowns in contact with that of the anterior or posterior tooth or both. The 1st upper incisors are straight like I2–I5, not separated at their base and not medially inflected as in didelphids (e.g., *Didelphis*). Lower incisors are subequal in size, increasing slightly from i1 to i4, with a posterolingually developed crown, which forms a well-marked socket. The 2nd lower incisor (i2) is not staggered, a condition that has been discussed extensively when arguing the taxonomic position of Microbiotheria (see Hershkovitz 1995, 1999, and literature cited therein).

Upper canines are small, straight and not well developed posteriorly, rarely taller than P3 in lateral view. Lower canines are similar to incisors in shape and size, forming a continuous cutting edge with them. They can be separated from them by their broader (anteroposteriorly longer) root, and the development of a small talon, which bears a cusp that disappears by wear. No sexual differences were found between upper or lower canines of males and females.

Upper premolars are fairly homogeneous both in lateral and occlusal views, albeit increasing in size from dP1 to P3. Certain variation was observed in dP1 size and position, sometimes with a diastema between C1–dP1, dP1–dP2, or in both directions (i.e., anterior and posterior diastema). This diastema showed the following patterns and proportions among the analyzed sample: 1) C1 D̲ dP1 D̲ dP2–M4 (77%); 2) C1 D̲ dP1 D̲ dP2 D̲ dP3–M4 (20%); 3) C1 D̲ dP1–M4 (3%). Lower premolars are small, with their main cusp anterolabially displaced,

a talon that increases in size from dP1 to P3, and a poorly developed but clearly distinguishable lingual cingula. The first 2 premolars are subequal in size in lateral view (e.g., MACN 19142), or with the dP1 larger than dP2 (e.g., MACN 13038) in both lateral and occlusal view. The 3rd premolar is always the largest and tallest, although its main cusp is rarely higher than the protocone of the any of the molars. Lower premolars also showed diastemas, with the following patterns and proportions within the analyzed sample: 1) C1 D̲ dP1 D̲ dP2–M4 (58%); 2) C1 D̲ dP1 D̲ dP2 D̲ P3–M4 (23%); 3) C1 D̲ dP1–M4 (3%); (d) without diastema (16%).

The 3 first upper molars are subequal in size, both in their labiolingual and anteroposterior extension. M4 is clearly different and reduced, which is rarely larger than the size of a premolar. All molars are characterized by a straight centrocrista and a reduced stylar shelf, which is almost at the same level as the trigon basin. The ectoflexus, although shallow, increases in depth from M1 to M3. Also, the parastylar region broadens and becomes larger from M1 to M3, with an extension of the preparacrista length, and a reduction of the metastylar region with a reduction in postmetacrista length. The protocone is in line with the paracone, becomes more bulbous from M1 to M2, and shows a progressive increase in length of the postprotocrista. Upper molars have no cingula, as previously described by Reig (1955) and Goin (2003). Lower molars show a similar pattern to the upper ones, with an increase in size from m1 to m3, and a clearly reduced m4. Little difference was found between the depth of the trigonid and talonid basins. The talonid is longer and broader (larger overall) than the trigonid, which becomes smaller from m1 to m3. The hypoconid is notably displaced labially, the paraconid is reduced and subequal in size to the entoconid, the hypoconulid is labially displaced and not "twinned" to the entoconid.

Analyses of the variability and variation of morphologic characters as described above provide no support to separate *Dromiciops* into the species proposed by D'Elía et al. (2016), or insular and continental forms.

The only replaced deciduous teeth in *Dromiciops* are dP3/dp3, as in other marsupials. The upper deciduous premolar is ⅔ smaller than M1, but similar in shape and general structure. The lower deciduous premolar is also similar to the preceding molar (i.e., m1), with less developed cusps and reduced in size to nearly 50% of m1 size.

Dental anomalies for this species were described by Martin (2007), and despite an increase in the number of analyzed specimens from 91 to 135 since that publication, the percentage of specimens with anomalies has slightly been modified from 9% to 8%. Anomalies in *Dromiciops* have been recorded in 2 main categories: missing or supernumerary teeth, and morphologic anomalies in the crown of molars and premolars (see Martin and Chemisquy 2016).

Discussion

The large number of specimens analyzed herein provided a good opportunity to examine intraspecific variability and putative interspecific variation throughout most of the geographic range of *Dromiciops*. The variability in morphometric measurement values suggests a conspecific sample, with clearly overlapping measurements among the samples throughout the studied variables (see Table 5; Fig. 2; Supplementary Data SD5–SD7).

The ANOVA for sexual dimorphism, individually or with pooled localities, showed no significant differences (Tables 1–3). This lack of sexual dimorphism was documented for *Dromiciops* before, albeit with smaller sample sizes (e.g., Hershkovitz 1999; Martin 2008; Astúa 2010). Sexual size and shape dimorphism was documented by Astúa (2010) for some other small New World marsupials, whereas morphometric analyses in *Lestoros inca*, *Rhyncholestes raphanurus*, *L. halli*, and several species of *Thylamys* showed no sexual size dimorphism (Martin 2005, 2008, 2013). Most of these species live in extreme environments that lack significant seasonal variation or can fluctuate drastically during short periods of time (e.g., *L. inca*, *R. raphanurus*, *L. halli*), or are at the edges of environmental gradients at a continental scale (e.g., *T. pallidior*). Larger *CV*s were found in external measurements, with most craniodental measurements having lower values (Table 5), a trend that appears to be a natural consequence of resource allocation during growth or development, in which parts of an organism are more functionally constrained than others (e.g., chewing mechanics in an insect-feeding marsupial will be less variable than body weight or head-body size). Also, a smaller variability in linear dimensions of the skull and teeth (be them individual or as a morphofunctional system) shows that several studied characters will be more constant when compared within a single-species sample. This provides little support to distinguish between continental and island forms of *Dromiciops*, or to distinguish the species proposed by D'Elía et al. (2016), with overlapping individuals throughout the morphometric space (Fig. 2; Supplementary Data SD5). Even when analyzing dental measurements, which hold the smallest *CV*s, individuals from the largest continental samples (i.e., La Picada and southern Chile) represented the extremes of the morphospace, containing all other specimens (Supplementary Data SD7). D'Elía et al. (2016) used geometric morphometrics to separate the 3 species they recognized, a methodology that was not used in this study. To account for shape changes, I used Mosimann's variables (Mosimann 1970), as described above. Results did not provide indication of differences among the studied samples. The MANOVAs performed using all measurements (Supplementary Data SD8), external (Supplementary Data SD9), craniodental (Table 4), and only dental measurements (Supplementary Data SD10) also revealed morphometric overlap among samples analyzed.

Previous morphologic assessments of *Dromiciops* were done by Hershkovitz (1999) and Martin (2008). This study expands on those previous analyses, and also shows that intersample variation (in the sense described above) of morphologic characters (e.g., Marshall 1978; D'Elía et al. 2016) was not recovered consistently, probably due to a larger number of studied specimens and a broader range of localities analyzed. The lack of discrete variation among samples for several characters, in

which the variability shown overlapped between specimens from different samples, provided no support to discriminate the 3 species of *Dromiciops* proposed by D'Elía et al. (2016). Because the analyses described herein were not originally delineated to test these recently described species, some characters were not analyzed in detail. To test how some of these characters (e.g., rostrum, pterygoid breadth, basioccipital breadth at petrosal level, jaw row molar height) account for intraspecific variability and interspecific variation, several morphometric variables were analyzed. For other discrete characters (e.g., incisive foramina, palatine fenestra, masseteric fossa), a detailed description of the variability within characters and their variation among samples, along with character-state frequency, is presented when possible. The following numbers correspond to the characters described by D'Elía et al. (2016: table 3): 1) Skull lateral profile: the lateral skull profile of *Dromiciops*, as in several small marsupials, varies from mostly rounded to flattened throughout the individual's ontogeny, a pattern observed during this study but also documented by Giannini et al. (2004). The use of alleged differences in lateral profile without detailed information on specimen age is misleading. Apart from this, the recent study of Valladares-Gómez et al. (2017) using geographic morphometrics provides no support for the assumption of variation between samples in skull lateral profile. 2) Rostrum: the shape of the rostrum was described as narrow, short, and tapering for *D. gliroides*; narrower, large, and tapering for *D. mondaca*, and thickened, short, and truncate for *D. bozinovici*. To test this hypothesis of narrowing rostrum, Mosimann's variables for palate width at canines (CW) was subtracted from palate width at M3 (PWM3), and plotted against palate length (PL). This provided a morphometric indication of how the rostrum changes in shape, using a larger sample than that used by D'Elía et al. (2016). In this analysis, specimens with a narrower and shorter rostrum should appear at the lower left side of the graph, while those with a thickened (i.e., broad) and larger rostrum should appear toward the upper right side of the graph. When analyzed in this context, measurements clearly show an unordered specimen distribution, with those assigned to *D. gliroides* showing the highest variability (Fig. 3). This provides no support to the use of this character as diagnostic. 3) Lateral edges of the rostrum: this is a very difficult character to classify and distinguish, especially since the maxillary bone is broad and straight toward the toothrow and curves dorsally toward the nasals. 4) Incisive foramina: a great deal of variability was found in this character in the studied sample, which was also described as highly variable by Marshall (1978), Giannini et al. (2004), and Martin (2008). As described above, very small (e.g., MACN 19142) and very large (MACN 13038, MACN 48.26) fenestrae were found in specimens of *D. gliroides*, showing large variability in this character and providing little support to consider it as diagnostic. 5) Palatine fenestra: this character was described by D'Elía et al. (2016) as square for *D. gliroides* and *D. mondaca*, and posteriorly rounded for *D. bozinovici*. Contrary to that, I found 12 specimens of *D. gliroides* (e.g., USNM 391772, LIEB-M-1528) that have rounded and narrowing palatine fenestra (a character used as diagnostic for *D. bozinovici*), and high variability in this character. 6) Palatine fenestra: the posteriormost extension and overall development of palatine fenestrae has been studied for several small-sized marsupials, revealing it as highly variable (e.g., Archer 1981; Tate 1933; Martin 2005, 2013). The larger number of specimens analyzed in this study does not support geographic variation in the shape and size of palatine fenestrae. In the studied sample, several specimens of *D. gliroides* (e.g., USNM 391772, LIEB-M-1528) showed the pattern supposedly diagnostic for *D. bozinovici*. The same was observed for the posteriormost extension of these fenestrae, with most specimens exhibiting extended fenestrae, reaching the posteriormost point of M4. 7) Posterolateral palate foramina: this character was described as open and rounded for *D. gliroides*, but at least 15 specimens of the sample from La Picada (southern Chile) and other specimens from localities throughout the species range showed small and narrow palatine foramina, a character assigned to *D. bozinovici* (the northern clade described by D'Elía et al. 2016). 8) Pterygoid breadth: in contrast to D'Elía et al. (2016), I found the relation of pterygoid breadth with incisor breadth to be highly variable and not diagnostic. Breadth of the palate at the canines (roughly the same linear measurement as outer incisor breadth, since canines in *Dromiciops* are poorly developed) is a highly variable measurement (Table 5). 9) Transverse canal foramen: the transverse canal foramen was coded by D'Elía et al. (2016) as deep or shallow. This character was found to be highly variable (i.e., present-absent) in didelphids and other marsupials (Archer 1976; Sánchez-Villagra and Wible 2002; Voss and Jansa 2003), with individuals of the same species showing contrasting differences (i.e., present in some, absent in others), and variability described for individuals of the same species but of different age. The same pattern was documented by Sánchez-Villagra and Wible (2002) who specifically coded this character for *Dromiciops* as polymorphic, thus implying variability between shallow or deep, and rendering this character as ambiguous. 10) Carotid canal opening: as with most foramina in the crania of marsupials, those of the basicranium are variable in shape and size. Unfortunately, the distinction between oblique and flattened canal opening is difficult to understand, and D'Elía et al. (2016) provide no description of how this character was codified or interpreted. 11) Alisphenoid tympanic process: the relative size of the tympanic processes of both alisphenoid and petrosal bones is difficult to distinguish unambiguously, especially due to a continuous range of intermediate morphologies within specimens. Segall (1969) mentions the alisphenoid contributing "about one-third of the bulla," whereas Giannini et al. (2004) mention that both the tympanic process of the alisphenoid and the caudal process of the petrosal grow over the ectotympanic throughout ontogeny. The latter shows that the bulla in *Dromiciops*, especially its alisphenoid portion, will continue to grow during the individual's life. 12) Basioccipital breadth at the petrosal level: this was calculated as the between bullae (BB) measurement herein defined in "Materials and Methods" and Fig. 1. When analyzed throughout the studied sample (n = 77), specimens from *D.*

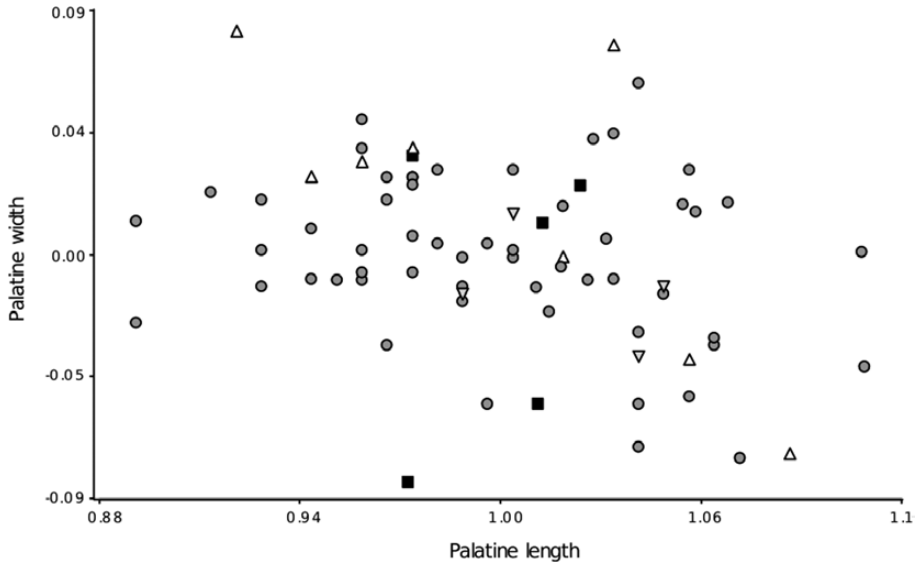

Fig. 3.—Biplot of Mosimann's variables for palate length (PL) versus the result of palate width at canines (CW) subtracted from palate width at M3 (PWM3), following the groups described by Himes et al. (2010) and D'Elía et al. (2016). Clade A (*Dromiciops bozinovici*): black squares; Clade B (*D. mondaca*): white triangle; Clade C (*D. gliroides*): gray circles. The inverted gray triangles were used for specimens from Chiloé Island, formally assigned by the above authors to Clade C (*D. gliroides*).

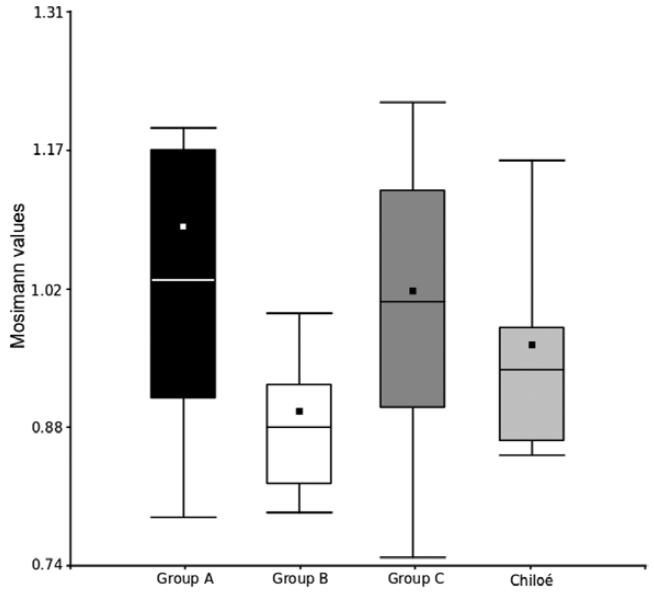

Fig. 4.—Box and whisker plots of Mosimann's between bullae (BB) measurements of all specimens following the groups described by Himes et al. (2010) and D'Elía et al. (2016). Group A (*Dromiciops bozinovici*), Group B (*D. mondaca*), Group C (*D. gliroides*), and Chiloé for specimens from Chiloé Island, formally assigned by the above authors to Clade C (*D. gliroides*).

gliroides (sensu D'Elía et al. 2016) showed the highest variability with values that include all the other individuals (Fig. 4). The discrimination power of this measurement was evaluated following Barbour et al. (1996), where each box plot representing a sample area or clade (sensu Himes et al. 2008; D'Elía et al. 2016, and adding Chiloé as a different sample) was evaluated against the others. This shows that all measurements lie within the values of the 1st and 3rd quartile of the largest sample (Clade C of Himes et al. 2008; representing *D. gliroides* in D'Elía et al. 2016). Also, BB has the highest *CV* among craniodental measurements (Table 5), revealing that this area of the skull is highly variable, even in adults. 13) Occipital condyle: although described as different, this is not observable in the figures presented by D'Elía et al. (2016). It is difficult to observe the well-developed occipital condyle in *D. gliroides* and *D. bozinovici*, compared to the slightly developed occipital condyle in *D. mondaca* (i.e., posteriorly, to the sides, ventrally). This character is ambiguous insofar as it is almost impossible to codify given the information presented. 14) Paracanine fossa length: the diastemas between I5, C, and dP1 are documented in the appropriate section of this study (see above). Giannini et al. (2004) provided the following comment about the diastemas they found: "In adults, there are enlarged diastemata between I5 and C and among the upper and lower premolars, ...therefore the spacing among several teeth modestly increases with age in response to the continuing growth of the supporting bone." These diastemas were found to be highly variable (as described above), and their presence and size are probably related to each individual's development, not to a characteristic pattern within a species. This is another highly variable character that appears ambiguous when looking at larger series of specimens. 15) Upper canines length: this character is highly variable and does not take into account tooth wear and age. Marsupial canines have been found to erupt and grow throughout life (Jones 2003; Chemisquy and Prevosti 2014); therefore, canines are susceptible to change within each individual's growth, and wear derived from different types of ingested food. Other measurements like canine length or width, or their combination in canine basal area, would have been better for comparisons within and between samples, but were not used. 16) Frontal bones: unfortunately, this character was not analyzed herein, and little information is provided by D'Elía et al. (2016) to show how the described variation is not part of intraspecific variability (i.e.,

there are no frequency tables). Characters 17 (jugal root of zygomatic arch), 18 (zygomatic process of squamosal), and 19 (alisphenoid tympanic process height) are all characters that could have been measured with geometric morphometric analysis. The description of the jugal root of the zygomatic arch is ambiguous and not very clear. It is confusingly described as "under premaxillary-maxillary-nasal joint" in *D. gliroides* and *D. mondaca*. If the authors are referring to the anteriormost extension of the jugal, I found no specimen in the studied sample to have that bone extending to a point below the premaxillary-maxillary-nasal contact. This would imply the jugal extending far anteriorly over the infraorbital foramen. The other 2 characters also are highly variable and difficult to codify or measure. 20) Jaw row molar height: unfortunately, D'Elía et al. (2016) do not mention where this measurement was taken, making comparisons between their samples and the information presented herein almost impossible. The mandible of *Dromiciops* has a vertical orientation where molars occlude, but has an anteriorly oblique orientation, from its incisors to the 1st premolars. This modification generates an anterior shovel-like structure when mandibles are joined, which is surrounded by the incisors, canine, and premolars. Modifications of this structure will occur during development, as described by Giannini et al. (2004). Both the width and height of the species' mandible were highly variable, presenting high intraspecific variability as shown in *CV* values (Table 5). All other measurements referring to mandibular characters described by D'Elía et al. (2016), i.e., 21) retromolar fossa breadth, 22) masseteric fossa, 23) lunar notch, 24) condylar process, and 25) angular process are modified during individual growth as described by Giannini et al. (2004). Among them, mandibles essentially change by increasing in robustness, growing toward their posterior end, which results in extending posteriorly past the last molar and deepening ventrally, expanding in the masseteric fossa and coronoid area, and showing the same amount of variability that D'Elía et al. (2016) used as diagnostic. Giannini et al. (2004) also described ontogenetic change in the condyle, postglenoid process, and angular process, characteristics also found to be variable in didelphids and caenolestids (see also Sánchez-Villagra and Smith 1997; Abdala et al. 2001; Flores et al. 2003; Martin 2008, 2013). The information presented in the section above shows some discrepancies with the characters used by D'Elía et al. (2016) and their descriptions. Several features of shape, size, and general form selected in the study of morphologic characters are related to development, ossification patterns, and ultimately to energy intake and requirements for them to be formed. These characteristics and especially their associated variability should be taken into account when used in a taxonomic context. Similar patterns of variability were documented in other New World marsupials (Gardner 1973; Wible 2003; Martin 2005, 2008, 2013). For example, Gardner (1973) recorded variable ossification patterns in *Didelphis* spp. and attributed them to growing differences caused by individual and environmental constraints (i.e., food availability, food intake and processing, food quality, balance between reproductive states, and several other ecological and physiological factors). Variability in the number of mental foramina, mandibular height, supraorbital ridges, palatine fenestrae and their patterns, and extension and depth of the glenoid fossa were described for *L. halli*, *L. inca*, *Monodelphis* spp., and *Thylamys* spp. (Wible 2003; Martin 2005, 2008, 2013). As with all variation and variability, the information presented above shows how complex some anatomical characteristics can be, especially when they are affected by growth, ossification, selective bone deposition, and the like. Also, several studies have shown that small samples of analyzed specimens tend to underrate variability (even genetic), by not showing the amount of change within a population (Yablokov 1974; Simpson et al. 2003; Zachos et al. 2013). All these features should be taken into account when describing the morphological characteristics of a species, and especially when using them as diagnostic for new entities.

As for the genetic differences found by Himes et al. (2008), and discussed by D'Elía et al. (2016), Nilsson et al. (2003) pointed out that cytochrome *b* (*Cytb*) gene differences in *Dromiciops* (which they also found ca. 11%) are "not an extreme value for intraspecific marsupial *Cytb* variation," as was previously described by Da Silva and Patton (1998). Apart from this, genetic analyses of mitochondrial genes and their use in phylogenetics have been questioned due to their high sensitivity to population processes (e.g., random genetic drift) and other limitations (e.g., introgretion hybridization, sex bias—Hailer et al. 2012; Zachos et al. 2013). As for these *Cytb* differences, should they correlate with observed morphological characters to be of interest? Can changes in several or a few base pairs be taken into consideration as variability? The information presented herein shows we should be cautious in delimiting species when genetic variation is unaccompanied by morphological differences. As pointed out by Yablokov (1974), an evaluation of the variability within characters of a species provides unique evolutionary information for a taxon, and specific magnitudes of change can be detected (see also Simpson et al. 2003). If a taxon shows this kind of genetic variability, but this is not correlated by observed morphologic and morphometric differences, one can think of the taxon as an expanding entity, in a taxonomic (and even geographic) sense. For *Dromiciops*, this could imply that the species is beginning to diversify after a distributional (and genetic) contraction in geographic range, a fact that can be easily explained by the latest climatic changes (i.e., after the last glaciation). The south of Chile and Argentina between ca. 37°S and 55°S experienced glaciations along the Andes during the Pleistocene, which covered most of the central and southern portions of the area occupied today by *Dromiciops*, including most of Chiloé Island (Villagrán et al. 1997; Moreno and León 2003). During the Holocene, the area experienced rapid climatic changes on several occasions, alternating between wetter and drier periods (Mayewski et al. 2004). All these climatic fluctuations affected vegetation through expansions and reductions in area, fragmentation and isolation of the different forest types (Villagrán et al. 1997; Heusser et al. 1999), with a direct effect on the ecology of *Dromiciops* and other species of the Southern Temperate Rainforests ecosystem.

Despite its uniqueness as the sole living representative of an entire order, the population structure of *Dromiciops*, as well as intrapopulation variability and geographic variation in ecologic and behavioral traits such as feeding preferences and reproductive cycles, has not been studied. These traits could indicate incipient diversification, and also are important for the conservation of *Dromiciops* as a single evolutionary significant unit (sensu Ryder 1986; Moritz 1994), where geographic and non-geographic morphologic, morphometric, and genetic differences need to be interpreted in the context of the total variability and variation within the species.

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Supplementary Data

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

Supplementary Data SD1.—Variable contributions and eigenvalues of the first 2 axes in a principal component (PC) analysis of all measurements (i.e., external and craniodental) from *Dromiciops*.

Supplementary Data SD2.—Variable contributions and eigenvalues of the first 2 axes in a principal component (PC) analysis of all external measurements (excluding weight) from *Dromiciops*.

Supplementary Data SD3.—Variable contributions and eigenvalues of the first 2 axes in a principal component (PC) analysis of craniodental measurements from *Dromiciops*.

Supplementary Data SD4.—Variable contributions and eigenvalues of the first 2 axes in a principal component (PC) analysis of dental measurements from *Dromiciops*.

Supplementary Data SD5.—PCA of all studied individuals of *Dromiciops* using all measurements (i.e., external and craniodental), following the groups described by Himes et al. (2010) and D'Elía et al. (2016). Clade A (*Dromiciops bozinovici*): black squares; Clade B (*D. mondaca*): white triangle; Clade C (*D. gliroides*): gray circles. The inverted gray triangles were used for specimens from Chiloé Island, formally assigned by the above authors to Clade C (*D. gliroides*).

Supplementary Data SD6.—PCA of all studied individuals of *Dromiciops* using external measurements, following the groups described by Himes et al. (2010) and D'Elía et al. (2016). Clade A (*Dromiciops bozinovici*): black squares; Clade B (*D. mondaca*): white triangle; Clade C (*D. gliroides*): gray circles. The inverted gray triangles were used for specimens from Chiloé Island, formally assigned by the above authors to Clade C (*D. gliroides*).

Supplementary Data SD7.—PCA of all studied individuals of *Dromiciops* using only dental measurements, following the groups described by Himes et al. (2010) and D'Elía et al. (2016). Clade A (*Dromiciops bozinovici*): black squares; Clade B (*D. mondaca*): white triangle; Clade C (*D. gliroides*): gray circles. The inverted gray triangles were used for specimens from Chiloé Island, formally assigned by the above authors to Clade C (*D. gliroides*).

Supplementary Data SD8.—Results of the MANOVA with all specimens of *Dromiciops*, performed between the first 5 principal components (PCs) and the classification criteria (clades) of D'Elía et al. (2016) and specimens from Chiloé Island, with all measurements (i.e., external and craniodental); *n* indicates the number of specimens analyzed per group. The last column shows the groups assigned by the MANOVA analysis; same letter indicates same group.

Supplementary Data SD9.—Results of the MANOVA with all specimens of *Dromiciops*, performed between the first 3 principal components (PCs) and the classification criteria (clades) of D'Elía et al. (2016) and specimens from Chiloé Island, only with external measurements; *n* indicates the number of specimens analyzed per group. The last column shows the groups assigned by the MANOVA analysis; same letter indicates same group.

Supplementary Data SD10.—Results of the MANOVA with all specimens of *Dromiciops*, performed between the first 5 principal components (PCs) and the classification criteria (clades) of D'Elía et al. (2016) and specimens from Chiloé Island, only with dental measurements; *n* indicates the number of specimens analyzed per group. The last column shows the groups assigned by the MANOVA analysis; same letter indicates same group.

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Appendix I

List of specimens of *Dromiciops gliroides* studied and provenance; Country, Province, Locality, and specimen number and collection (in parentheses).

Argentina.—Neuquén province; Cerro Chapelco (MLP 8.IV.02.11); Villa La Angostura (CRUB-M-198); Beatriz (BMNH 19.1.1.46, BMNH 19.1.1.47). Río Negro province; Parque Municipal Llao-Llao (CML 1869, CRUB-M-04, CRUB-M-011, CRUB-M-013); Isla Victoria (MACN 48.26, MLP 6.XI.41.4, MACN 13038, MACN 19142–MACN 19145); Colonia Suiza (CRUB-M-15–CRUB-M-17); Ladera Sur Cerro Otto, Villa Arelauquen (CRUB-M-019); San Carlos de Bariloche (CRUB-M-023, CRUB-M-154); Av. Bustillo Km 13 (CRUB-M-197); Av. Bustillo Km 14 (CRUB-M-199); Bariloche, western Río Negro (BMNH 28.5.7.1). **Chile.**—Concepción province, Concepción (AMNH 92147, AMNH 97746, AMNH 238022). Cautín province; Temuco, Parque Cerro Nielol (USNM 536887–USNM 536889). Valdivia province; Comuna La Unión, Catamutún (UACH 691–UACH 693, UACH 682); Comuna de Valdivia (UACH 671–UACH 681); Fundo San Martín (UACH 683–UACH 690, UACH 1059, UACH 1737, UACH 3130, UACH 4324–UACH 4325); Fundo Santa Rosa (UACH 1731–UACH 1734, UACH 3131); Rupanco, Piedras Negras (UACH 1056–UACH 1058, UACH 1735). Arauco province; Comuna Curanilahue (UACH 1053–UACH 1054). Osorno province; La Picada, Puerto Octay (UACH 2144–UACH 2157, UACH 2159, UACH 2160, UACH 2163–UACH 2166, FMNH 127448, FMNH 127450–FMNH 127451, FMNH 127454–FMNH 127455, FMNH 127457–FMNH 127464, FMNH 129806–FMNH 129810, FMNH 134556). Palena province; Contao, 19.7 Km north of Río Negro y 26.7 Km south of Contao (FMNH 129812–FMNH 129813); Río Negro, 12.4 Km northeast (FMNH 134624). Chiloé province; Ancud (LIEB-M-1521); Cucao (UACH 6996, UACH 6999); Huite (Holotype, BMNH 92.5.9.3); Palomar, Fundo El Venado (UACH 6998–UACH 7000).