Trabajo

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Morphological evolutionary acquisitions in the specialized genus of lizards *Phymaturus* (Iguania: Liolaemidae). The origin of herbivory and saxicolous mode of life in liolaemid lizards

Fernando Lobo[1], Soledad Valdecantos[1], Gabriela Velázquez[2], Carolina Lobo Terán[3]

[1] IBIGEO (Instituto de Bio y Geociencias del NOA), Salta, Argentina.
[2] FCN (Facultad de Cs. Naturales, Universidad Nacional de Salta), Salta, Argentina
[3] UEL (Unidad Ejecutora Lillo), Tucumán, Argentina.

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ABSTRACT

With few exceptions, there are still not enough studies on the origin of herbivory and the saxicolous mode of life in lizards of the Liolaemidae family, nor on the possible morphological adaptations that may have favored these traits. In the present study, we recorded external measurements and collected data from skeletons representing all major clades of *Liolaemus* and *Phymaturus*, as well as *Ctenoblepharys*. To identify modifications that could explain the different body shapes and their possible relationship with modes of life, we studied seventeen body measurements, the lengths of the bony and inscriptional ribs, and the number of trunk vertebrae. ANOVA and principal component analysis were performed, and the evolution and origin of these characters were analyzed in a metatree of the family. We found that *Phymaturus* and herbivorous species of *Liolaemus* exhibit the largest abdominal volume and body size. Greater abdominal capacity, trunk height, and head height characterize the herbivorous saxicolous clades, which is reasonable for accommodating larger viscera and plant contents, as well as providing a flattened head shape important for using rock crevices as refuges. On average, *Phymaturus* species possess at least two additional vertebrae, and their inscriptional ribs are elongated, contributing to their greater abdominal volume. We also observed pseudo-valvules in the small intestine, which may favor slower movement of plant material along the digestive tract. According to our analysis, herbivory and the saxicolous mode of life were acquired by *Phymaturus* independently within the Liolaemidae family. Our phylogenetic statistics indicate that the body measurements studied have a strong phylogenetic imprint. Thus, in the phylogeny of Liolaemidae, the origin of herbivory and saxicoly can be traced to the ancestors of different lineages (at least eight and seven cases, respectively) and was later inherited by almost all descendants.

Key words: Abdominal Capacity; Intestines; Skeletons; Diet; Saxicoly.

RESUMEN

Con pocas excepciones, aún no existen suficientes estudios sobre el origen de la herbivoría y el modo de vida saxícola en lagartijas de la familia Liolaemidae, ni sobre las posibles adaptaciones morfológicas que pudieron haber favorecido estos rasgos. En el presente estudio, registramos medidas externas y recolectamos datos de esqueletos que representan a todos los clados principales de *Liolaemus* y *Phymaturus*, así como en *Ctenoblepharys*. Para identificar modificaciones que pudieran explicar las diferentes formas corporales y su posible relación con los modos de vida, estudiamos diecisiete medidas corporales, las longitudes de las costillas óseas e inscripcionales, y el número de vértebras del tronco. Se realizaron análisis de ANOVA y de componentes principales, y se analizó la evolución y el origen de estos caracteres en un meta-árbol de la familia. Encontramos que *Phymaturus* y las especies herbívoras de *Liolaemus* exhiben el mayor volumen abdominal y tamaño corporal. Una mayor capacidad abdominal, altura del tronco y altura de la cabeza caracterizan a los clados saxicolas herbívoros, lo cual les permite albergar vísceras y contenido vegetal de mayor tamaño, además de proporcionar una forma de cabeza aplanada, importante para usar las grietas de las rocas como refugio. En promedio, las especies

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Author for correspondence: flobo@unsa.edu.ar

de *Phymaturus* poseen al menos dos vértebras adicionales, y sus costillas inscripcionales son alargadas, lo que contribuye a su mayor volumen abdominal. También observamos pseudo-válvulas en el intestino delgado, lo que podría favorecer un tránsito más lento del material vegetal a lo largo del tracto digestivo. Según nuestro análisis, la herbivoría y el modo de vida saxícola fueron adquiridos por *Phymaturus* de forma independiente dentro de la familia Liolaemidae. Nuestras estadísticas filogenéticas indican que las medidas corporales estudiadas tienen una fuerte impronta de la filogenia. Por lo tanto, en la filogenia de Liolaemidae, el origen de la herbivoría y la saxicolía se pueden rastrear hasta los ancestros de diferentes linajes (al menos ocho y siete casos, respectivamente) y fue heredado posteriormente por casi todos los descendientes.

Palabras claves: Capacidad Abdominal; Intestinos; Esqueletos; Dieta; Saxicolía.

Introduction

Contemporary studies on the relationship between animal morphology and mode of life are based on analyses that consider the group's evolutionary history. The central question is whether the modifications observed in certain organisms constitute adaptations to their mode of life or whether, on the contrary, they have been inherited from a common ancestor. The prediction of an association between form and function is evidenced by the study of morphological traits linked to modes of life in each animal lineage (Feilich and López-Fernández, 2019; Kennedy *et al*., 2020). In recent decades, numerous approaches and methodologies have been developed to analyze eco-morphology in a phylogenetic context, demonstrating the need to always consider the evolutionary relationships of the organisms studied (Felsenstein, 1985; Martins and Hansen, 1997; Freckleton *et al*., 2002; O'Meara, 2012, among others). In reptiles, morphology is closely linked to ecological mode of life (feeding, habitat, locomotion) through adaptive evolution. This often leads to phenomena of evolutionary convergence between distant lineages, although always under the strong influence of phylogenetic history. Among the main factors driving these changes are habitat-specific body shape (e.g., flattened versus slender bodies), mandibular modifications associated with diet, and limb length in relation to locomotion (Pianka 1969, 1986; Losos 1990, 1994; Vitt and Caldwell, 2013).

Several studies have addressed these issues from multiple perspectives. For example, Bauwens *et al.* (1995) analyzed the evolution of running speed in lacertid lizards, relating limb length to locomotor function and microhabitat. Losos (1990, 1994) demonstrated strong links between morphology and microhabitat in *Anolis* lizards, showing that long limbs are associated with open habitats and short limbs with closed habitats. For a comprehensive review of the relationship between form and habitat in reptiles, including the ecomorphological importance of scale structure, see Vitt and Caldwell (2013). Klaczko *et al.* (2016) identified a strong association between the cranial morphology of xenodontine snakes and their dietary preferences, while Hudry and Herrel (2025) showed that head morphological patterns reflect ecological differences: fossorial species have compact heads that widen posteriorly, aquatic species exhibit hydrodynamic profiles, and arboreal species tend to have elongated heads for maneuvering in complex habitats.

These examples illustrate that, although related species often share traits due to phylogenetic inertia, they can diverge rapidly by occupying different ecological niches or converge with distant species in similar habitats.

The present study aims to analyze the general body morphology of a large and representative sample of Liolaemidae species, exploring its relationship with three biological and ecological characteristics that could have influenced their current form: diet, microhabitat/roof preference, and reproductive mode. To fully understand morphological evolution and its link to lifestyle, it is essential to optimize these traits in phylogenetic trees (for example, using parsimony). This approach allows us to elucidate the origin of traits and the sequence of changes that have led to the morphological configuration observed in different lineages. The genus *Phymaturus* includes species of iguana-like lizards distributed mainly in Patagonia, the foothills, the Andean mountain ranges, and the Puna region of Argentina and Chile. They inhabit areas from 200 to 4200 meters above sea level, facing extreme environmental conditions such as large daily temperature ranges, strong winds, high solar radiation, and limited resources. They are characterized by a wide and robust body, relatively short limbs, slow movements, and a marked preference for rocky environments, where they use crevices as refuges (strictly saxicolous) (Fig. 1A). They are viviparous, with small litters of large offspring (Valdecantos *et al*., 2019) (Fig. 1B), and strictly herbivorous, feeding on leaves, fruits, and flowers (Castro *et al*., 2013; Corbalán and Debandi, 2014; Córdoba *et al*., 2015), and possess a well-developed anterior cecum (Figs. 1C and D). In the last 20 years, 41 of the 52 known species have been described, significantly enriching our knowledge of their taxonomy and phylogeny (Lobo and Barrasso, 2021). *Liolaemus*, for its part, is the most diverse genus in the family, with 288 species distributed from Peru to Patagonia (Argentina and Chile). This diversity is reflected in the variety of diets (herbivores, omnivores, insectivores) and in the occupation of different substrates (terrestrial, psammophilous, saxicolous, and even semi-arboreal). *Liolaemus* species can be viviparous or oviparous; viviparity

Figure 1. The genus *Phymaturus* comprises lizards with a very restricted mode of life; they are saxicolous, viviparous, and herbivorous. A) *Phymaturus extrilidus* in a rock crevice in the Sierra de la Invernada mountains, San Juan, Argentina. Photo: R. Espinoza. B) Dissected female of *P. verdugo* (MCN-UNSa 1973, SVL=101,7 mm) with two full developed fetuses (FE). C) *Phymaturus extrilidus* consuming flowers. Photo: R. Espinoza. D) Dissected female of *Phymaturus* sp. (*gualcamayo*) (MCN-UNSa 3538, SVL=93,0 mm) notice the large anterior colon (=*caecum*, ac) fulfilled of plant material.

is associated with adaptation to high-altitude, cold regions or high latitudes (Schulte *et al*., 2000). The evolutionary analysis of the family is now more accessible thanks to numerous cladistic contributions on the phylogeny of both genera (Quinteros, 2013; Lobo *et al*., 2016, 2018; Esquerre *et al*., 2019, 2022; Abdala *et al*., 2020), which allows for a comparative evaluation of the origin and evolution of traits both between genera and within *Phymaturus*.

Compared to most *Liolaemus species*, *Phymaturus* has a noticeably wider body (Figs. 2A and B). While this characteristic has been repeatedly noted in the literature, it had not previously been evaluated through large-scale comparative studies. Preliminary observations of osteological preparations have revealed that the characteristic body width of *Phymaturus* could be due to the elongation of a series of post-xiphysternal ribs with free cartilaginous ends (inscriptional ribs), although these are also present in *Liolaemus*, but arranged differently.

Given that *Phymaturus* combines biological characteristics, preferences, and modes of life (herbivorous, saxicolous, viviparous), it is essential to determine how these factors have shaped their morphology and what their influence has been. It is also relevant to consider whether the origin of these morphological changes preceded and favored the emergence of these modes of life. Were they initially herbivorous, and did this lead to changes that facilitated the other traits? Or was viviparity or a saxicolous mode of life the initial factor?. To address these questions, we must first review the background of each case and its particular problems that have arisen over time; therefore, we will do so in separate sections below, under the following subtitles: viviparity and litter size, saxicoly, herbivory, origin of characters and evolutionary tracking in trees, and morphological aspects studied to date.

Viviparity and litter size

Recent studies examined both, size and shape of body in *Phymaturus* have indicated that these dimensions may respond to certain selective regimes (Reaney *et al*., 2018; González Marín *et al*., 2018, for the *Phymaturus patagonicus* group). However, these studies do not specifically identify which aspect of the mode of life of these animals may be involved (e.g. herbivory, saxicoly), as there are no specific tests that evaluate this. Valdecantos *et al.* (2019) explicitly assessed fecundity and sexual dimorphism, revealing that species exhibiting sexual size dimorphism (female biased SSD) there is a positive relationship between brood size and brood mass with body size and body mass (respectively) of gravid females giving strength to the fecundity advantage hypothesis. Furthermore, the relationship between litter size and mass with body size and mass, respectively, was positive, providing additional support for the fecundity advantage hypothesis. In *Phymaturus*, litter size is reduced (mean 1.9) compared to most *Liolaemus* species, where litter size is generally larger. Pincheira-Donoso and Tregenza (2011) collected data from 72 *Liolaemus* species and found that only 10 species have an average of 2–2.5 offspring, while in the remaining 62 species, litter size varies from 3 to 14.5, with an average of 4.6. This reduction in litter size does not appear to be related to reproductive mode, as only 3 of those 10 *Liolaemus* species are viviparous. One might wonder whether reproductive mode, the number or size of eggs/offspring, is related to the widening of the abdomen and the increase in its capacity. In these viviparous animals, could the possession of a reduced litter size but larger fetuses have been favored by the acquisition of greater abdominal volume? Preliminary evidence suggests, for example, that *L. magellanicus* or *L. vulcanus*, both viviparous, have an average of six offspring but reach a smaller size than *Phymaturus* fetuses. Despite having elongated ribs, their arrangement has not produced the same widening effect. To clarify this, a better understanding of the phylogenetic origin of viviparity in liolaemids, as well as litter size, is needed. This should be addressed within a broader framework involving phylogenetic analysis. Previous studies have found incongruent results regarding the origin and evolution of viviparity (Pincheira Donoso *et al*., 2013; Esquerre *et al*., 2018). The main differences being that in the first case reversals are prohibited and an oviparous origin is forced on the group, in the second case the origin in the liolemids is ambiguous and it is proven that there were numerous reversal events between both modes of parity.

Saxicoly

Previous studies on saxicolous lizards have shown that they often are characterized by having acquired longer limbs and a more flattened head and body (Doughty and Shine, 1995; Vanhooydonck and Van Damme, 1999; Revell *et al*., 2007; Goodman *et al*., 2008). However, it has been indicated that despite being saxicolous species, their use of that environment may not be the same (Revell *et al*., 2007).

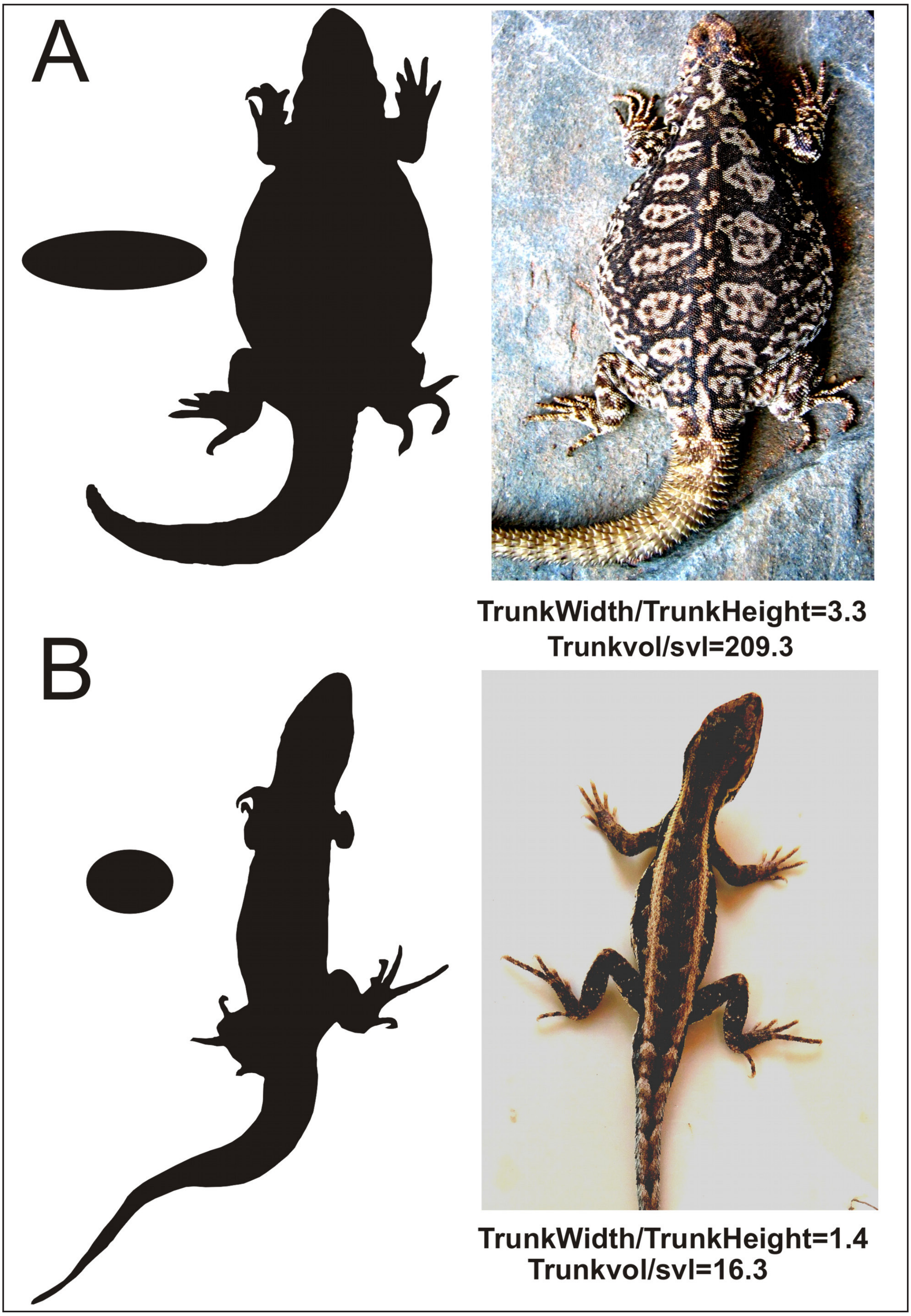


Figure 2. The body shape and trunk volume of a species of the genus *Phymaturus* and a species of *Liolaemus*. A) the strict herbivorous *Phymaturus roigorum* (MCN-UNSa 1962, SVL= 95,2 mm). To the left its body shape with a cross section at mid-trunk indicated. B) the insectivorous *Liolaemus chacoensis* (IBIGEO 6879, SVL= 39,2 mm) one of the smallest species of the genus and the minimal trunk volume/svl index value. The two individuals are shown on the same scale for comparative purposes. Trunk in *Phymaturus roigorum* is almost three times wider than the trunk of *Liolaemus chacoensis*. Trunk volume is calculated using the elliptic cylinder equation following Goodman et al. (2009).

For example, while many species move and utilize practically vertical rock walls, this behavior may not be the case for *Phymaturus*. The feet are comparatively somewhat shorter relative to the snout vent length than those of species in the Chilean group of *Liolaemus* (unpublished data) of different modes of life (not only saxicolous). Perhaps the traction and general locomotor work on the surface of the rocks and inside the cracks in our case would be reflected more in certain segments of the limb and not in all. Tulli *et al.* (2011) found that arboreal and saxicolous species of liolaemids exhibited greater resistance to mechanical traction effects across all substrates compared to generalists and psammophilous species. These species showed a positive relationship between forelimb dimensions (length of the humerus and length of the claw of finger 5) and the maximum force exerted. The distribution of species in this genus is very restricted in the most of species, to small rocky outcrops of little extension (20-30 km) to a very few that are distributed in a larger range (i.e. *P. palluma*) Lobo *et al.* (2010), Corbalán *et al.* (2011). Often, these outcrops consist of small rocks protruding from the ground, no more than 1.5 to 2 meters high, characterized by cracks of different sizes where *Phymaturus* individuals seek refuge. It is worth asking whether the body of *Phymaturus* is indeed flattened (which would be advantageous for entering their shelters) and to what extent compared to other lineages, to verify the hypothesis of longer limbs and if this body shape originated as an adaptive response to their mode of life. In a group of "flattened" lizards (family Scincidae) with saxicolous mode of life, it was initially postulated that their clutch size would be affected by a depressed body (Goodman *et al.*, 2009), *Phymaturus* in comparison to most *Liolaemus* exhibits a reduced "output" (Boretto and Ibargüengoytía 2006, 2009; Boretto *et al.*, 2007; Valdecantos *et al.*, 2019). It is viviparous and develops one to two large offspring on average (Fig. 1B), is the reduced reproductive output observed in this lineage, relative to other Liolaemidae, associated with the evolution of its distinctive body shape?. First of all, in order to answer this question, it should be known if they are flattened and to what extent (as there is currently no specific study comparing this genus to other related ones), and whether their abdominal volume differs from that of other liolaemids, and if the reduced litter size was either a novelty for *Phymaturus* or if this condition was already present in the ancestor of the family. We also do not know if other saxicolous lineages of *Liolaemus* exhibit morphological characteristics like *Phymaturus*, and if they have responded in their history in the same way.

Herbivory

Atwood *et al.* (2020) demonstrated that trophic level and body size are significant factors influencing extinction risk across all amniote species. Specifically, herbivorous reptiles and large-bodied herbivores consistently exhibit the highest proportions of threatened species. Given that the family Liolaemidae includes an entire genus of herbivores (*Phymaturus*) and several lineages of *Liolaemus* with herbivorous species, it is essential to expand our knowledge about these clades, including the origin of their dietary preferences, morphological characteristics, evolutionary history, and other related topics.

In past contributions, the researchers sought to study the evolution of herbivory in liolaemids, as well as its relationship with body size, length of the digestive tract, and the presence of parasites (Espinoza *et al.*, 2004; O'Grady *et al.*, 2005 and more recently Ocampo *et al.*, 2022); however, some conclusions in those contributions are somewhat contradictory, which warrants a reassessment. In Espinoza *et al.* (2004), it was found that within the Liolaemidae family, herbivory has evolved more frequently than in all other squamate reptiles combined. Furthermore, in contrast to other herbivorous lizards and according to existing theory, most herbivorous liolaemids are small-bodied and live in cold climates. Herbivory is generally believed to evolve only in reptile species that are large-bodied, inhabit hot climates, and maintain high body temperatures. These three well-known "rules" of herbivory are the basis of the physiological constraints that explain the scarcity of herbivorous reptile species. O'Grady *et al.* (2005) compared a variety of digestive tract specializations among different diet categories within the family Liolaemidae (18 *Liolaemus* spp and 3 *Phymaturus* spp) to test the hypothesis that herbivores require greater intestinal complexity to process plant matter, and that herbivory favors the evolution of larger body size. Herbivorous liolaemids were found to be larger relative to their omnivorous and insectivorous counterparts, resulting in larger viscera. The herbivorous species examined in this study lacked the morphological specializations observed in herbivores of the families Iguanidae and Agamidae (see Iverson, 1982). O'Grady *et al.* (2005) found that the length of the small intestine of herbivorous liolaemids was longer than that of others. However, Hoppe *et al.* (2021) found that the large intestine is longer in the case of herbivores. Nevertheless, other modifications, not necessarily as drastic as those observed in iguanids, could be present in herbivorous liolaemids, which deserves a more detailed study (in Lobo *et al.*, 2016, folds were described in the walls of the most posterior end of the large intestine in species of *Phymaturus*).

The first to study the relationship between body size and diet in liolemids were O'Grady *et al.* (2005), although their taxonomic sample was limited in terms of the representation of the different groups (21 species out of 338 species recognized for the family, Abdala *et al.*, 2021). In fact, only a single example of the *montanus* group was included, a clade consisting of more than 60 species inhabiting the puna and cordillera by Abdala *et al.* (2020) (*L. dorbignyi* probably *L. vulcanus*; in O'Grady's study, data on the species used were not indicated). Examples of small-sized herbivores that contradict the herbivory-greater body size hypothesis have been described in subsequent studies, such as Valdecantos *et al.* (2012), who found that *L. poecilochromus* (now *L. kunza*, see Abdala *et al.*, 2021) is mainly herbivorous (>80% plants in the diet; Cooper and Vitt, 2002; Espinoza *et al.*, 2004), which is surprising for several reasons. Firstly, the old "rules" of herbivory for lizards stipulate that herbivores must be large-bodied (Pough, 1973) (*L. kunza* males: 63.5mm, mean SVL females: 62.8 mm).

Herbivorous species of liolaemids seem to be an exception to the "rule" of body size, although within liolaemids herbivorous species according to O'Grady *et al.* (2005) are generally larger than non-herbivorous species. Herbivory would also be present in other small altitude *Liolaemus* species. Olivera Jara and Aguilar (2020) presumably raise to 9 the species of the *L. montanus* group that primarily feed on plants (although only a few works are specific diet investigations, Olivera Jara and Aguilar, 2020; Valdecantos *et al.*, 2012). On the other hand, another aspect not yet studied is that referred to the volume or capacity of the abdominal cavity. Does a greater volume favor the development of larger digestive organs?. The body shape of *Phymaturus* seems to offer greater abdominal capacity (volume) compared to an insectivorous species of *Liolaemus* (Fig. 2), but trunk volume has not been measured until now. Clauss *et al.* (2017) proved that, in mammals, herbivores generally have a larger body cavity volume than carnivores, although they included other tetrapods in the study (including some reptiles), and their conclusions are not decisive for those groups. Hoppe *et al.* (2021) found that the large intestine is longer in the case of herbivores.

Being *Phymaturus* a strict herbivorous animal, one might wonder if this characteristic is evident when we compare it with species of the sister genus *Liolaemus* where omnivory and insectivory predominate, with herbivory occurring only in some lineages. Another character obviously related to diet and not considered in all these studies is dental morphology that would be related to eating habits. Etheridge (1995), Lobo and Abdala (2001) and Lobo *et al.* (2012) studied the morphology of the teeth in *Ctenoblepharys*, *Liolaemus* and *Phymaturus* for systematic or phylogenetic reconstruction purposes only. However, dental morphology has not yet been studied comparatively between herbivores of both genera (*Phymaturus* and *Liolaemus*) to assess the existence of similar adaptations. The studies conducted by Parsons and Cameron (1977) and Iverson (1980, 1982) represent the most important contributions to date, and no similar studies have been conducted on liolaemids.

About the modifications in the digestive tract related to the herbivorous diet in reptiles. In fact, there is a lack of knowledge about the morphology of the digestive tract that should be addressed. In a recent contribution, Ocampo *et al.* (2024) found that herbivorous species have evolved larger heads, shorter hindlimbs, and a small difference between forelimb and hindlimb length, while omnivores and insectivores exhibited smaller heads and longer hindlimbs. Their conclusions were based on a set of seven measurements and the reconstruction of ancestral states. The evolution of diet was carried out using probabilistic methods, finding percentages of probabilities about the origin expressed in pie charts see Fig. 1 from Ocampo *et al.* (2024).

The origin of characters and evolution tracking on trees (and their problems)

The studies published so far have used disparity of criteria when reconstructing ancestral states or analyzing the evolution of these aspects (ML, Bayesian analysis and parsimony) so they are not completely comparable, and in all cases the comparisons with outgroups are restricted to just one or completely null (e.g. Pincheira-Donoso *et al.*, 2013; Esquerre *et al.*, 2018). Hence the need to reevaluate the origin and evolution of these aspects. The limited use of outgroups or the arbitrary use of only one significantly affects the result regardless of the method used, whether probabilistic methods or parsimony (Grant, 2019). Schulte *et al.* (2000) optimized viviparity using parsimony, but with wrong assignment of reproductive modes in outgroups, while Pincheira-Donoso *et al.* (2013) applied a Bayesian analysis of ancestral reconstruction but forced the analysis in the root of Liolaemidae in the oviparous mode without considering the distribution of these characters in the outgroups and those related to Liolaemidae. Esquerre *et al.* (2018) employed Bayesian analyses, utilizing information from a single outgroup, leaving the explanation with a high degree of uncertainty at the basal nodes (indicated by probabilities pie chart at nodes). Regarding herbivory, Espinoza *et al.* (2004) optimized a Liolaemidae tree using maximum likelihood and parsimony for 91 species across three diet categories, while, more recently, Ocampo *et al.* (2022), found results that are not consistent with those of Espinoza *et al.* (2004), employing Bayesian methods and their ancestral reconstructions are uncertain/ambiguous (probability percentages pie charts at nodes) (furthermore, they did not consider the use of multiple outgroups, which can also influence the analyses.). The definition of the diet categories is problematic, as there are few detailed studies of the diet of species involving the analysis of the contents of a large sample of individuals (information is available for only about 10% of species). In several cases, it has been reported that diet can be affected by seasons, ontogeny, and sexual dimorphism. In the case of the saxicolous mode of life, it has not been explicitly studied. Blankers *et al.* (2013) did it for Iguania including representatives of all families, although they used an extremely limited sample of liolaemids (5 spp.).

Morphological aspects studied so far that raise questions

Cei *et al.* (2003) found that females of viviparous *Liolaemus* species have a greater trunk length than those of oviparous species, although the effect of phylogeny was not evaluated at that time. O'Grady *et al.* (2005) indicated that, in their sample of liolaemids, the small intestine is longer in herbivores. However, the results of this work are not entirely conclusive and exhibit some contradictions with other studies. Hoppe *et al.* (2021), studying the length of intestines in reptiles and mammals, found that the large intestine is longer in herbivores. Previous studies on *Liolaemus* did not find any relationship between morphology and habitat use, but they did find correlations between morphology and escape behavior (Jaksic and Núñez, 1979; Jaksic *et al.*, 1980; Schulte *et al.*, 2004; Pincheira-Donoso *et al.*, 2009). Tulli *et al.* (2011) found a positive relationship between grip strength and forelimb length in saxicolous and arboreal species. Additionally, Tulli *et al.* (2012) studied the effects of different substrates on the locomotor performance of various species, finding that most morphological characters would be restricted by phylogeny, considering the morphology of liolaemids as highly conservative. Toyama (2017) analyzed morphology relationships with habitat use in Tropidurinae, incorporating a sample of liolaemids and relating them to genera of Tropiduridae following Pyron (2013). However, it is currently known that the relationships of this family are different (Burbrink *et al.*, 2020), and their results are not very significant for the liolaemids. Regarding some morphological relationships and habitat use, he finds similar results to those found previously (longer forelimbs, narrower bodies in arboreal, Sinervo and Losos, 1991; Kohlsdorf *et al.*, 2004; length of toes and nails greater in arboreal species than in terrestrial ones, Ribas *et al.*, 2004; Tulli *et al.*, 2009). For saxicolous species, Revell *et al.* (2007) and Toyama (2017) find flattened heads and bodies, and long extremities. Anyway, Revell *et al.* (2007) indicated that for some taxa, this rule would not apply, possibly due to different uses of the same habitat.

In the present contribution, our aim was to analyze the origins of viviparity, herbivory, and the saxicolous mode of life in liolaemid lizards, as well as the possible morphological changes related to these characteristics. Since during the evolution of the group the three aspects have interacted in some way simultaneously and not independently of each other, although we do not know which has prevailed over the others or to what extent, it is inevitable to study them together. For example, a hypothesis to illustrate this problem could state that "in *Phymaturus* a greater abdominal volume allowed having larger viscera for the herbivorous diet, thereby facilitating the development of larger offspring, but this greater volume and size was conditioned by the saxicolous mode of life, using cracks as shelters for which more flattened bodies were needed". However, to confirm this hypothesis, we must first study the morphologies of the different lineages, relating them to their modes of life within the context of their phylogenetic history. What came first, viviparity, herbivory, or the saxicolous mode of life? Which morphological characters were influenced in each case? In summary, as a general hypothesis, it is considered that the mode of birth, diet, and the use of preferred habitat are reflected in specific body measurements (such as head, trunk, and extremities) that will be the result from the interaction of the three aspects of the mode of life mentioned, without one prevailing over another. Characters not influenced by mode of life are surely due to phylogenetic inheritance.

The first step needed to study the origin and evolution of any feature and to advance any kind of interpretation is to optimize it in a phylogenetic tree. To have a broad look at these issues indicated above, we decided to study these data applying both conventional statistics (ANOVA, PCA) and tests where the phylogenetic relationships of the analyzed species are considered. We also consider it important to specify our considerations about the categories assigned to species regarding diet and mode of life before studying their evolution.

Materials and methods

Character mapping

The optimization of characters was performed solely for the purpose of establishing their origin and changes at the root of the liolaemids and the nodes of *Phymaturus* and *Liolaemus,* as well as their two large clades. The optimization of the three characters, herbivory, viviparity and saxicolous use of habitat were performed using TNT Goloboff *et al.* (2008) on a meta tree (315 spp.) based on the last topologies of *Phymaturus*, *Liolaemus,* and their major clades compiled by Quinteros (2021), and following also (in part) Portelli and Quinteros (2018), Lobo (2001, 2005), Abdala (2007), Abdala *et al.* (2020), Lobo *et al.*, (2012, 2016, 2018), Lobo and Barrasso (2021) and Esquerre *et al.* (2019, 2022). This metatree and the complete optimizations can be seen in the supplementary files S1-S3. That metatree is also shown in Fig. 8. Since many of the relationships within the terminal clades of *Liolaemus* remain unresolved, as well as the existence of alternative hypotheses, we only focus on the origin of these characters at the basal nodes. We employed maximum parsimony as criterion (preferred because provides rejectable hypothesis with decisive assignations to ancestral nodes instead of probability pie assignations to nodes as other methods do). Additionally, we utilized all pleurodont families as outgroups (based in the last hypothesis of Squamate phylogenetic relationships available in literature, Reeder *et al.* 2015, Burbrink *et al.* 2020). Squamate relationships for outgroup optimizations were made considering Reeder *et al.* (2015) (combined hypothesis of molecules and morphological information), the use of Burbrink *et al.* (2020) (molecular only analysis) didn´t change conclusions in our analysis because the peculiar distribution of the three characters, which are rare in most other families (Fig. 1). We consider it important to include a large sample of outgroups in the analysis, unlike in previous studies (i.e. Pincheira Donoso *et al.*, 2013, Esquerre *et al.*, 2018), because the limited use of outgroups or the arbitrary use of only one significantly affects the result regardless of the method used, whether probabilistic methods or parsimony (Grant, 2019).

Necessary clarifications to be made before the analysis of the diet in liolaemids

Because there exist only a very limited number of contributions to the diet of liolaemids, it is quite difficult, or at least somewhat risky, to estimate or generalize about its evolution and rates of changes, transitions etc. (as in Ocampo *et al.*, 2022). In fact, only 37 articles (see Appendix 1) have been published with detailed diet analysis of 32 species (in a total of more than 330 spp of Liolaemidae, Abdala *et al.*, 2021). Most diet assignments to species come from occasional observations of feces, the dissection of one or a few individuals, behavioral observations made in the field, or are taken from the original taxonomic descriptions, which introduce a commentary on the natural history of animals. None of these assignments consider the existence of ontogenetic variation, seasonal variation, and even sexual dimorphism related to diet, that are only detected after the study/examination of a numerous series of individuals, of both sexes, ages and samples taken in different seasons (Rocha 1998, 2000; Valdecantos *et al.*, 2012; Semhan *et al.*, 2016, among others). With the purpose of providing comparable results with previous studies, we considered that the current classification of the three categories of diet used for liolaemids in the literature: herbivorous, omnivorous, insectivorous, but for mapping character evolution we preferred in the present study a more conservative analysis considering just herbivorous versus non-herbivorous.

Different ways of considering a lizard to be saxicolous

With respect to the definition of saxicolous, it is important to make some distinctions, i.e. species of the *Liolaemus elongatus* clade are traditionally considered to be saxicolous in their vast majority (Cei, 1986), but for example *Liolaemus ceii* in Lonco Luan (Neuquén province, Argentina) can be seen on rocks, but they always take refuge under holes located under the same rocks they use for basking, it is not the same as a *Liolaemus heliodermis* in Tucumán that always takes refuge in cracks (like *Phymaturus*) (Robles and Halloy, 2011). Lizards have different reasons for carrying on their activities over rocks, sunbathing, social communication, hunting prey (in case of insectivorous species), mating etc., having their preferred refuges in rock crevices or not, which one of these activities can affect morphologies during their evolution?. The species that we find on the rocks could be differentiated by 1) exclusive use of cracks as shelter (*Phymaturus*, some spp. of the subclade of *Liolaemus capillitas*, some spp. of the clade of *Liolaemus dorbignyi*) 2) use of cracks in the rocks as well as hollows and caves in the earth or under rocks as shelter (majority of spp. of the *Liolaemus elongatus* clade, some spp. of the *Liolaemus dorbignyi* clade, some spp. of the *Liolaemus nigroviridis* clade), and 3) use of hollows and caves in the ground as refuge (most of *Liolaemus* spp. that are indicated many times as saxicolous). We think that making the differentiation of saxicolous modes of life would be more informative about their evolution and morphological adaptations (if there exist). However, this knowledge is null along liolaemid literature, and we are unable to conduct analyses with a new criterion. We optimized the saxicolous mode of life occurrence following the traditional and actual literature for assigning this feature to each species. But for the PCA analysis combining diet and lifestyles versus morphological characters we did make a difference, as is explained below.

Anatomical observations

All specimens studied are listed in Appendix 1. We studied 322 skeletons of 61 spp of *Liolaemus*, *Ctenoblepharys*, 29 spp of *Phymaturus,* and 73 skeletons of pleurodont outgroups. Data were obtained from cleared and stained specimens prepared following Wassersug (1979), which are deposited at MCN-UNSa and IBIGEO herpetological collections, and from RX images taken by Richard Etheridge, currently stored at IBIGEO library.

To compare whether the number of trunk vertebrae between the genera *Liolaemus* and *Phymaturus* is statistically significant, a Wilcoxon test was performed (the distribution was not normal, according to the Shapiro-Wilks test). To compare whether the length of the inscriptional ribs between *Liolaemus* and *Phymaturus* is statistically significant a T-test was performed (the distribution was normal according to the Shapiro-Wilks test).

Additionally, we dissected and studied the digestive tract of 54 *Phymaturus* and 49 *Liolaemus* specimens, six and eight species respectively. For everyone, the sex was recorded, and the snout-vent length (SVL) was taken. The observation and analysis of the digestive tract were also carried out using a longitudinal section of the same (dissection) to determine the presence/absence of folds, valves and/or sphincters (following Parsons and Cameron, 1977; Iverson, 1982; Srichairat *et al.*, 2018). Detailed observations of the interior of the tract were performed using a binocular magnifying glass. The different morphological characteristics of the internal mucosa were photographed using a digital camera coupled to an Olympus stereoscopic magnifying glass, as well as a Nikkon Coolpix B B500 compact camera with macro settings for submerged material.

Body measurements and statistical comparisons

External measurements were made based on alcohol-preserved specimens deposited in the following herpetological collections: MCN-UNSa (Museo de Ciencias Naturales de la Universidad Nacional de Salta, Argentina), IBIGEO (Instituto de Bio y Geociencias del NOA, Salta, Argentina) and FML (Herpetological collection of Fundación Miguel Lillo, Tucuman, Argentina). External morphology data were collected from a sample comprising 123 spp of *Liolaemus* (n= 882) and 33 spp of *Phymaturus* (n=309), in addition to *Ctenoblepharys adspersa* (n=5). Measurements taken to estimate trunk volume of species included trunk length, trunk width, and trunk height (measured at mid-trunk), and the ellipsoidal cylinder formula was applied (following Goodman *et al.*, 2009) ($V=\Pi Rrh$) (R = half the width of the trunk measured at half its trunk length, r = half the height at half its trunk length, and h = interlimb length). According to Goodman *et al.* (2009), applying this formula yields similar results to those obtained using water displacement (Archimedes principle). The advantage of using that formula is the collection of individual measurements that are analyzed for other purposes (i.e., trunk height for revealing the potential flattened shape of bodies of saxicolous species). Also, we measured: height, width, and length of the head; hand, length and width of radio-ulna, humerus; thigh and tibia, and foot length (from ankle to the tip of the IVth toe).

To have a broad look at these issues indicated above, we decided to study the morphology of liolaemids using both conventional statistical methods and phylogenetic tests. For comparisons of body measurements, we utilized INFOSTAT software (Di Rienzo *et al.*, 2012) for all statistical analyses. The analyzed characters represent morphometric variations, including trunk length (tl), trunk width (tw), trunk height (th), head height (hh), head width (hw), head length (hl), femur length (fe), femur width (few), tibia length (ti), tibia width (tiw), foot length (fo), hand length (ha), humerus length (hu), humerus width (huw), radius length (ra), radius width (raw), and trunk volume (tv). Since the trunk cavity contains the viscera, and this could make a difference for herbivores, we decided to measure the volume of the trunk. Given species variability in body size, which can affect all morphometric measurements, we conducted a regression for these characters using SVL as the independent variable, and the residuals were used for ANOVA and PCA. We performed an ANOVA (analysis of variance), followed by Fisher's LSD (Least Significant Difference) test for multiple comparisons to analyze external morphology; we used the conventional categories of herbivorous, omnivorous, and insectivorous (being cautious in our interpretations due to the lack of information in the literature as we detailed above). We use non-parametric tests when the data does not follow a normal distribution (Kruskal-Wallis). Comparisons by mode of life are made discriminating between species classified as: "psammophilous", "strict psammophilous", "terrestrial", "saxicolous" and "strict saxicolous". We performed two different PCA analyzes (variance-covariance matrix), one comparing the lineages of *Liolaemus* and *Phymaturus* for the morphometric variables. The second analysis was based on known combinations of diet and lifestyle assigned to the species sample included in this study (these were: strict saxicolous-insectivorous, strict saxicolous-omnivorous, strict saxicolous-herbivorous, terrestrial-insectivorous, saxicolous-insectivorous, saxicolous-omnivorous, saxicolous-herbivorous, terrestrial-omnivorous, terrestrial-herbivorous, strict psammophilous-insectivorous, strict psammophilous-omnivorous, psammophilous insectivorous, psammophilous omnivorous, psammophilous herbivorous, pseudo-arboricolous-omnivorous). This combination is made considering that both biological aspects evolved together, and their interaction may have affected morphological aspects of the animals to different degrees. Strict saxicolous species were distinguished from saxicolous species based on the former exclusively requiring cracks in rocks as shelter, whereas the latter can utilize other types of shelters. Strict psammophilous species dive into dunes and have restricted use of the environment, while psammophilous species have a wider range of environmental utilization and do not exhibit specialized burrowing behavior in sand (see Halloy *et al.*, 1998), described differences in behavior between members of the *L. wiegmannii* group and the *L. fitzingerii* complex. To evaluate the degree of independence/dependence of these morphological characters on the phylogenetic history of the group, we performed a phylogenetic ANOVA (Garland *et al.*, 1993) using the residuals of regression of log10 transformed characters with Log10svl as the regressor variable. Because the distribution of habitat preference was not normal, the Kruskal-Wallis test was performed. Statistical significance in the phylogenetic ANOVA was assessed using a permutation test with 1,000 permutations. P-values for post-hoc comparisons were adjusted using the Holm method (Holm, 1979) to account for multiple testing. We also calculated the lambda paramether of phylogenetic signal (Pagel, 1999). These tests were performed in R 4.3.0 (R Core Team, 2023) applying the "phytools" (Revell, 2012) and "ape" (Paradis and Schliep, 2019) packages.

Results

1-Origin and evolution of viviparity, herbivory, and saxicolous mode of life.

Viviparity (Fig. 3A and Fig. S1) occurs in only two families of pleurodontans: Phrynosomatidae and Liolaemidae. Zuñiga-Vega *et al.* (2016) reported five instances of the origin of viviparity in Phrynosomatidae (within *Phrynosoma* and *Sceloporus*), with oviparity being the ancestral parity mode of this family. In Liolaemidae, the common ancestor of *Liolaemus* and *Phymaturus* is recovered as viviparous. Within *Liolaemus* further changes to oviparity (13 times) are found 2 times in the *alticolor-bibroni* group, and eleven in the *nigroviridis*, *lemniscatus*, *gravenhorsti*, *nigromaculatus*, *tenuis*, *punmahuida*, *kriegi*, *monticola*, *capillitas* and *petrophilus* groups and in the subgenus *Eulaemus* in the *boulengeri* group. Terminal re-acquisitions of viviparity seem to be more restricted, occurring only 6 times, once in the *nigroviridis* group, 3 times in the *alticolor-bibroni* group, and twice in *Eulaemus* (*L. xanthoviridis* and the *ornatus* clade). The size of the litter was also optimized; most pleurodonts have an average litter size of 4.8–5.8. There was a reduction in litter number among pleurodonts, at the node of leiosaurids and liolaemids, to 3.7–4.7. Subsequently, there was a further reduction for the ancestral node of *Liolaemus* and *Phymaturus* (1–2.5 eggs or offspring). Within *Liolaemus,* the number increased in certain lineages. In summary, both viviparity and reduced litter size are primitive and did not represent anything new in *Phymaturus*.

Within pleurodontans the herbivorous diet arises twice: in Iguanidae and in liolaemids (Fig. 3B). This occurs independently in *Phymaturus* and at least 18 times within *Liolaemus (kriegi ceii* group, *lineomaculatus* group, 9 times within the *montanus* group, 4 times in the *boulengeri* group*, L. araucaniensis, punmahuida* group, and *nigromaculatus* group) (Fig. S2). Saxicoly in Pleurodonta arose several times: Iguanidae, Tropiduridae, Phrynosomatidae, Opluridae and Liolaemidae (Fig. 3C and Fig. S3). Iguanas are arboreal or terrestrial, except for *Sauromalus*; the root of Iguanidae is non–saxicolous. Blankers *et al.* (2013) found in their optimization of saxicoly the non-saxicolous mode of life as the ancestral state for Tropiduridae; because *Microlophus* and several species of *Stenocercus* and *Tropidurus* are saxicolous and relationships among genera are not very well resolved currently, we prefer to assign a more conservative ambiguous state for the family root. Within the family Phrynosomatidae, a saxicolous mode of life, occurred in *Petrosaurus* and several species of *Sceloporus*. We follow Blankers *et al.* (2013) that assign at the root of the family a non–saxicolous state. In Opluridae, *Chalarodon madagascariensis* is terrestrial, while *Oplurus* consists of both arboreal and a saxicolous clade. The root of this family is non–saxicolous. In liolaemids, the saxicolous mode of life occurred in *Phymaturus*, while the ancestor of *Liolaemus* was non–saxicolous. Within *Liolaemus,* saxicolous mode of life arises at least 13 times; this includes seven times in the subgenus *Eulaemus* (*L. kolengh*, *L. robertoi*, *L. orientalis*, *L. chlorostictus, L. dorbignyi, L. jamesi* and *L. qalaywa* species or species groups) and six times in *Liolaemus* sensu stricto (within the *alticolor-bibroni*, *nigromaculatus*, *elongatus*, *nigroviridis*, and the *altissimus* groups once, and in *L. nitidus*) (Fig. S3).

2-Body shape and trunk volume

The characteristic body shape of *Phymaturus,* which sets it apart from other liolaemids, is clearly given by the shape of its trunk, they are wider. When examining a cross-section of the middle of the trunk, the cutting surface is an oval, with its long axis greater than the vertical one. In fact, the width of the trunk is more than three times its height (Fig. 2), while in most *Liolaemus* and *Ctenoblepharys* this relationship is much less pronounced. It is known from previous studies that herbivorous animals tend to reach greater sizes than those that are not (see, for example, Espinoza *et al.*, 2004). The most common explanation is that this would allow them to contain larger viscera to better process plant–origin food.

In Figure 4, we present the distribution of the trunk volume to SVL ratio across 156 species of *Phymaturus*, *Ctenoblepharys adspersa* and *Liolaemus*. As evident, the *Phymaturus* species in this sample are located at the far left of the graph, exhibiting the largest volumes of the trunk, especially the species of the *palluma* group, surpassing even the *patagonicus* group (Fig. 4). Our estimations of trunk volume indicate that *Phymaturus,* with a few species of *Liolaemus* (*kriegi* and *montanus* groups), have the highest values of trunk volume/SVL. Figure 4 illustrates that *Phymaturus* display 2–10 times greater trunk volumes than insectivorous *Liolaemus* species. Below a trunk volume/SVL =100, only 7 out of 112 species are herbivorous. Above this value, 87% are herbivorous (with only 6 *Liolaemus* omnivorous species); there are no insectivorous species surpassing trunk volume/SVL= 100.

In Figure 4B, we show the number of herbivorous species across different lineages. All species within the *palluma* and *patagonicus* groups of *Phymaturus* exhibit herbivory, along with the species of the *Liolaemus kriegi* subclade (5 spp) (after our own dissections of *L. buergeri*, *L. kriegi*, and *L. ceii*, and the report for *L. tregenzai* and *L. zabalai* of Pincheira-Donoso and Scolaro, 2007 and Troncoso Palacios *et al.*, 2015). Herbivory occurred at a low frequency

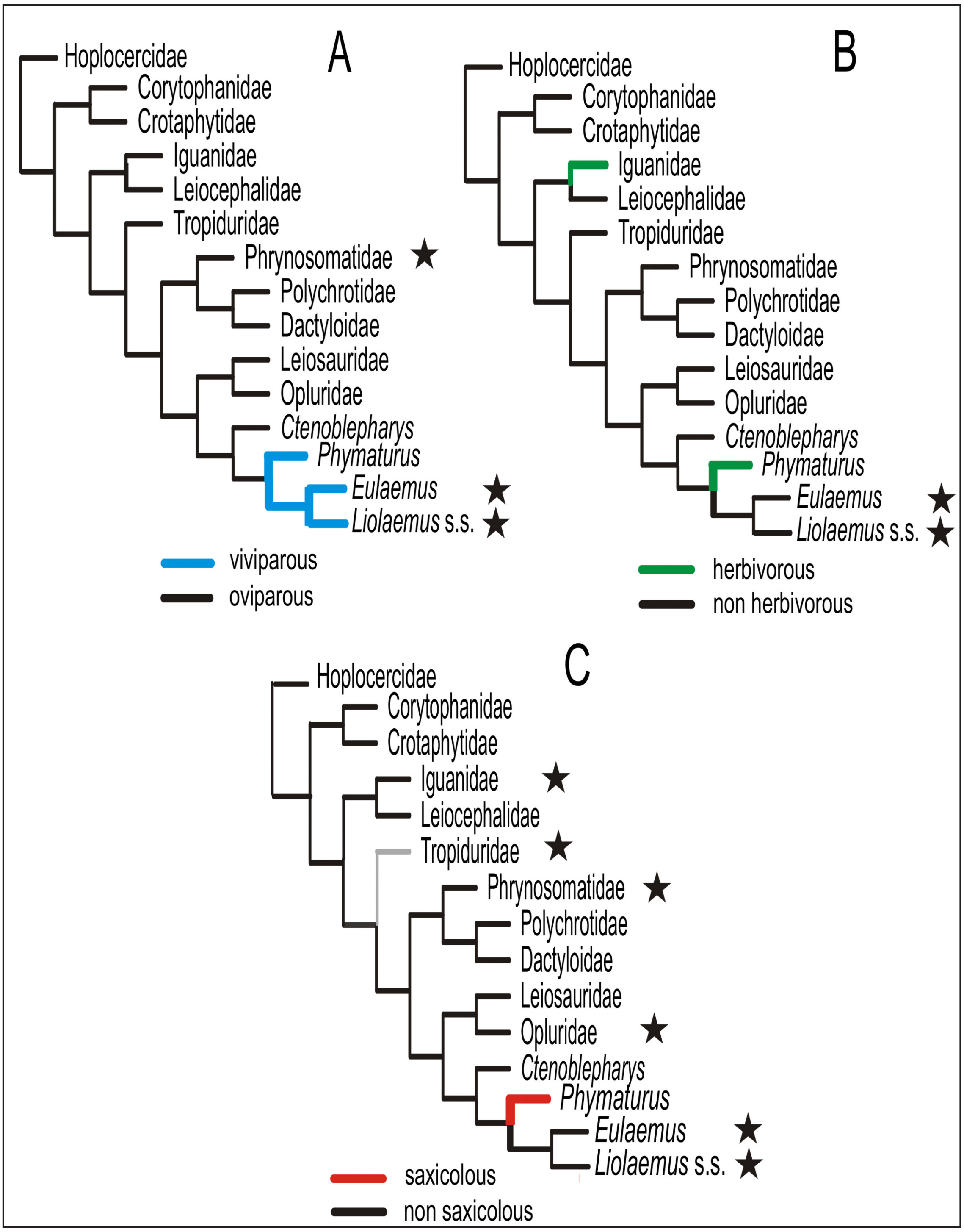


Figure 3. Liolaemid genera and their pleurodont relatives. Optimizations were made on the tree topology of squamates recovered by Reeder et al. (2015) based on an analysis of total evidence. A) Viviparity was acquired in the ancestor of *Liolaemus* and *Phymaturus* and was lost numerous times during evolution (within both subgenera of *Liolaemus*). With the star we indicate the origin of viviparity within Phrynosomatidae (within *Phrynosoma* and *Sceloporus* at least five times according to Zuñiga-Vega et al., 2016), oviparity being the ancestral parity mode of this family. B) Herbivory evolved twice, in Iguanidae and in *Phymaturus*, the basal condition for *Liolaemus* is non herbivorous, different lineages within both subgenera of *Liolaemus* got the condition independently (indicated by stars). C) The saxicolous mode of life occurred several times within pleurodonts (indicated with a star), within Iguanidae (*Sauromalus*) Phrynosomatidae (*Petrosaurus* and spp. of *Sceloporus*), Tropiduridae (*Microlophus* and spp. of *Stenocercus* and *Tropidurus*), Opluridae (saxicolous species of *Oplurus*) and Liolaemidae (*Phymaturus* and at least 11 eleven times within *Liolaemus*, the basal condition for *Liolaemus* is non saxicolous). In Liolaemidae *Phymaturus* and several lineages of *Liolaemus* are saxicolous. For more detail and discussion see in the text.

within the larger clades: *L. montanus* (69 spp), *L. elongatus-petrophilus* (30 spp), and *L. boulengeri* (74 spp) groups. Two species within the small *L. lineomaculatus* group (7 spp) are herbivorous, while two are omnivorous, and the diet of the remaining three remain unknown (Abdala *et al*., 2021).

3-Changes on *Phymaturus* anatomy

After studying the skeleton of 322 individuals of *Phymaturus*, *Liolaemus* and *Ctenoblepharys*, (Figs. 5 and 6) we found three important characteristics to mention. Analysis of the trunk skeleton in liolaemids revealed that the inscriptional ribs are more elongated in *Phymaturus,* averaging 50.3% (SD= 0.06; n=54; 28 spp) of the total rib length; whereas in *Liolaemus,* this measurement reaches only 26.2% (SD= 0.09; n= 69; 26 spp) (Figs. 5A and B). Consequently, the elongation of the inscriptional ribs, and not the bone portion, contributes to the increased trunk width observed in *Phymaturus*. Indeed, the difference between the lengths of the inscriptional ribs of *Liolaemus* and *Phymaturus* is statistically significant (T test, p< 0.0001). However, the position of the postxiphysternal ribs in *Phymaturus* differs, being situated at a lower angle relative to the anteroposterior axis of the vertebral column compared to the other genera (Fig. 5B). This elongation of the ribs, added to their more perpendicular location than in *Liolaemus*, gives the typical silhouette of a widened body observed in species of this genus, as depicted in Figure 2. At the same time, we observed that, on average, the genus *Phymaturus* possesses more trunk vertebrae compared to *Liolaemus* and *Ctenoblepharys*, as well as most other pleurodonts (Fig. 5C), (mean= 26.32; versus 24.19 of *Liolaemus* and 25 of *Ctenoblepharys*). Running the Wilcoxon test, we found that the differences between *Liolaemus* and *Phymaturus* genera in the number of trunk vertebrae are significant (p< 0.0001).The combination of having more vertebrae in the trunk and longer inscriptional ribs has facilitated an increase in the volume or resulting capacity of the trunk in *Phymaturus*, making it possible to carry larger viscera, which is important in relation to its strictly herbivorous diet. Our review of 64 digestive tracts across 9 species of *Liolaemus* and 6 of *Phymaturus* has allowed us to appreciate interesting characteristics in the internal relief of the digestive tract. The small intestine in *Phymaturus* species of the *palluma* group has sections with smooth walls forming dilated chambers separated by 1–3 pseudo–valves (Fig. 6). In *Liolaemus*, the walls feature conspicuous longitudinal folds along most of their length, lacking chambers (except in herbivorous forms, which can exhibit pseudo–valves contrary to insectivorous species). These pseudo–valves were found in individuals of herbivorous species of *Liolaemus*: *L. buergeri*, *L. kriegi*, *L. albiceps*, and *L. kunza* representing different lineages of the genus. In the case of *Liolaemus kunza*, every individual exhibits these pseudo–valves; their diet was studied by Valdecantos *et al.* (2012), which includes lizards of small size and with reduced trunk volume, unlike the large size observed in most herbivorous species (Fig. 4). The anterior colon has smooth internal walls in most of the species studied, both in *Liolaemus* and *Phymaturus*. It may present small transverse or oblique folds, but not in the entire sample of individuals; they were found in three species of *Phymaturus* (*P. palluma*, *P. indistinctus*, and *P. yachanana*) and two of *Liolaemus* (*L. buergeri* and *L. tulkas*). Other differences found in the morphology of the digestive tract include the middle region of the stomach, where most species of *Phymaturus* (except *P. aguanegra* and *P. zapalensis*) have longitudinal folds, while in most *Liolaemus* species it lacks folds (except for the herbivorous *L. kriegi* and *L. buergeri*). The pyloric region is externally differentiated from the rest of the stomach; it is more tubular and elongated in shape in *Phymaturus*, while being short and inconspicuous in *Liolaemus*. The duodenal bulb is conspicuous in *Liolaemus* species but indefinite in *Phymaturus*. Measurements and proportions of the different sections of the digestive tract and their analysis are part of another ongoing research.

4-Head, trunk and limb measurements, phylogenetic signal

Our observations indicate that herbivorous species are larger (ANOVA, F=656.49, P <0.0001) than omnivores or insectivorous species. Herbivores (average adult svl: 85.4 mm) were 14.7% larger than omnivores species (73.8 mm) and omnivores were 19% larger than insectivores (59.5 mm). In Table 1, we found that the measurements showing significant differences in the ANOVA regarding herbivory are tl (trunk length), tw (trunk width), head length (hl), foot length (fo), humerus length and width (hu an huw), and tv (trunk volume). Herbivores exhibit greater trunk length (tl) and trunk width (tw) compared to omnivores and insectivores. Head height (hh) is lower in herbivores than in the other two groups. Head length (hl) is higher in insectivores than in omnivores, and in turn, omnivores have higher head length than herbivores. Additionally, in herbivores, the foot (fo) is shorter than in omnivores and insectivores. Both humerus length (hu) and width (huw) are greater in herbivores compared to omnivores and insectivores. The trunk volume of an

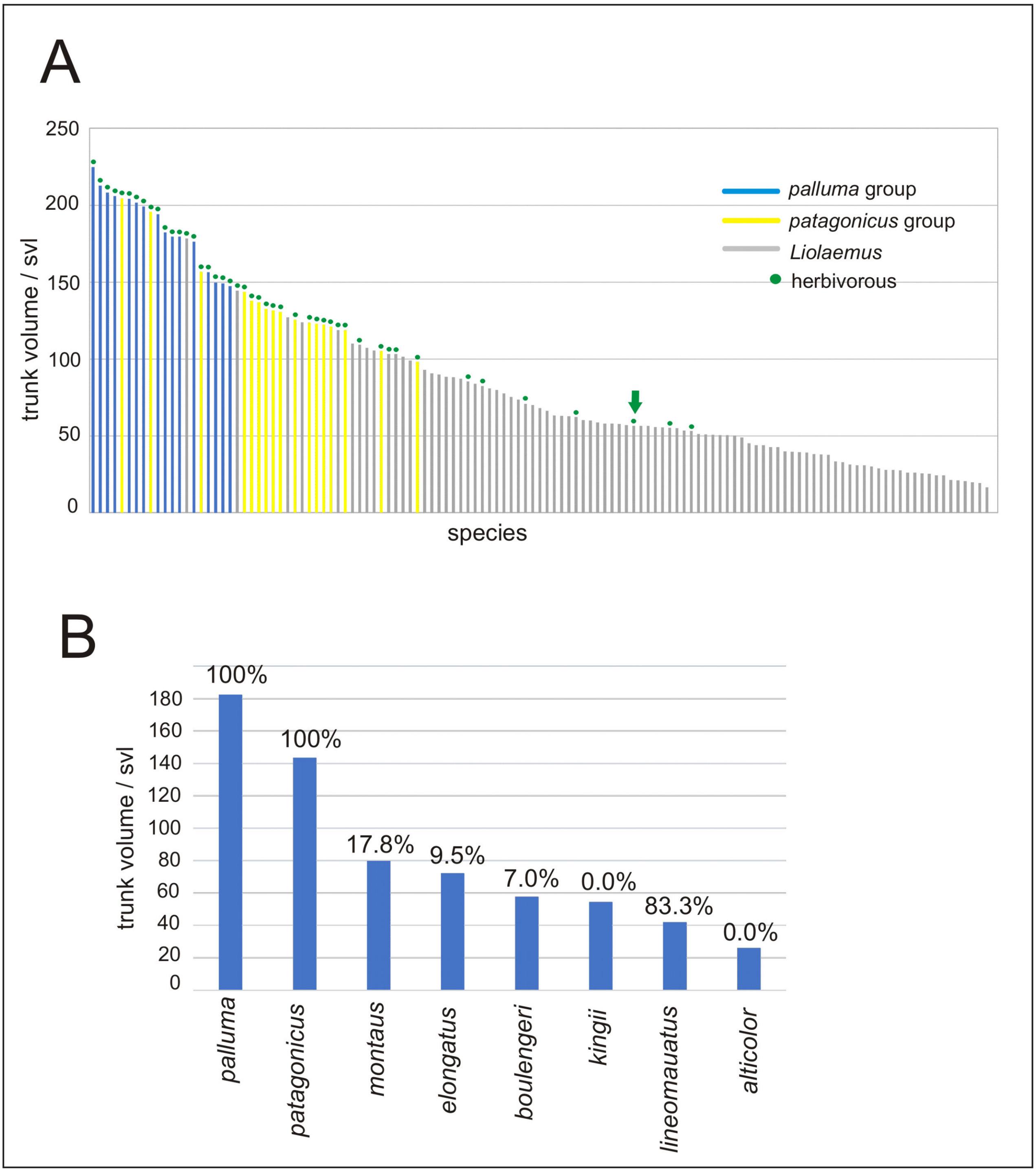
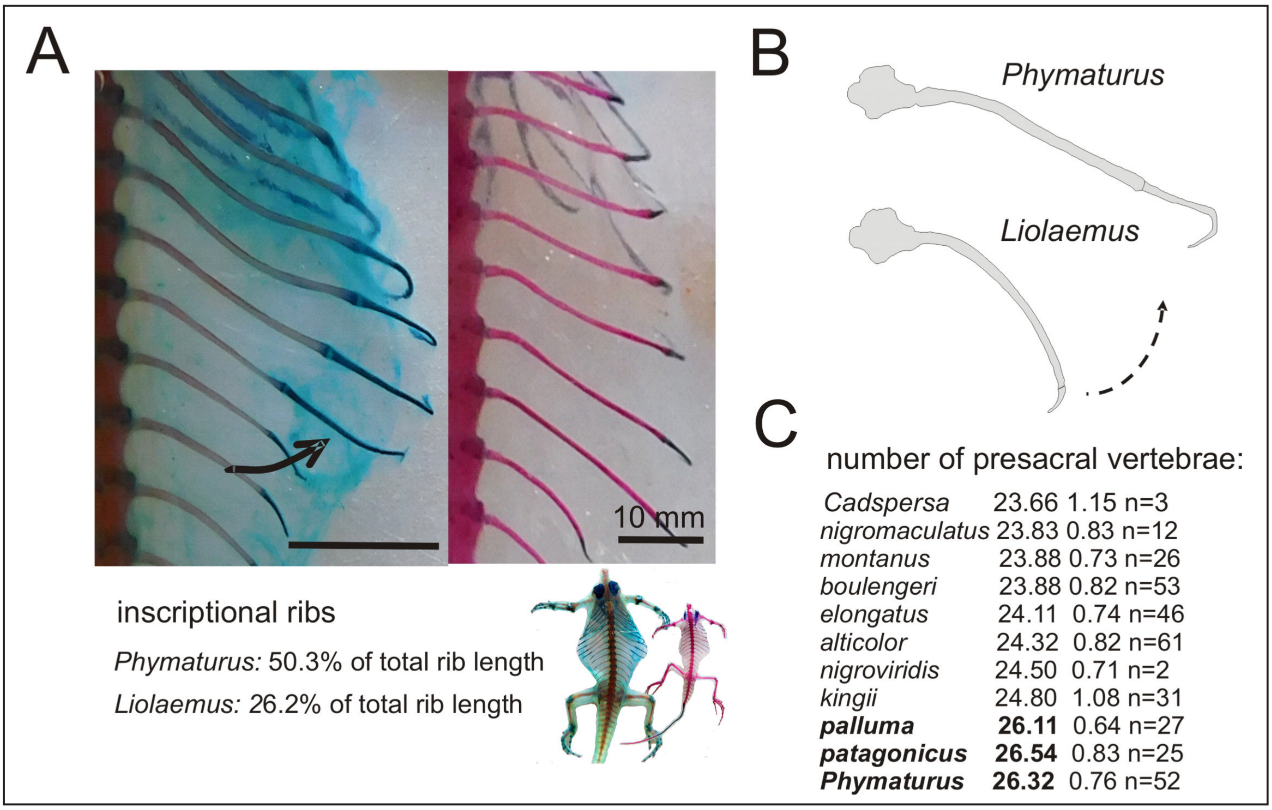


Figure 4. Herbivory in liolaemids and its relationship with trunk volume and body size. A) The distribution of trunk volume/svl index along the studied sample (156 spp.) showing the enlarged trunk capacity found in *Phymaturus* and some species of *Liolaemus* (values are the trunk volume/svl index). In blue *P. palluma* group species of *Phymaturus*, in yellow species of the *P. patagonicus* group, in gray are indicated *Liolaemus* species. Green dots indicate herbivory. Below trunk volume/SVL =100 only 7 species among 112 are herbivorous. Above this value 87% are herbivorous (only 6 *Liolaemus* omnivorous species), there are no insectivorous species above 100. B) percentage of herbivorous species within main clades of *Phymaturus* and *Liolaemus*. The arrow indicates the position of *Liolaemus kunza*, with low trunk volume/svl but with pseudo-valves in the small intestine as in most *Phymaturus*.

herbivore is 80.1% greater than that of an insectivore and 57.4% greater than that of an omnivore. The differences between them are more conspicuous than those indicated by SVL. As we mentioned above, the correlation between an herbivorous diet and trunk volume is somewhat greater than that found between herbivory and SVL. Changes in some of the dimensions comprising the volume (length, width, or height of the trunk) have significant consequences, as observed in tl and tw (Table 1).

Regarding saxicoly, the measures considered in the literature include head and trunk depression and longer hindlimbs according to Toyama (2017), Revell *et al.* (2007), among others. Comparisons made among different habitat uses reveal significant differences in trunk length, height, and width (tl, th, tw), head height and length (hh, hl), femur length and width (fe, few), foot, hand, and humerus length (fo, ha, hu), radius length and width and trunk volume (ra, raw, tv). The trunk length is greater in strict terrestrial saxicoles, while the trunk width is greater in strict saxicoles and strict psammophilous. The trunk height is higher in strict psammophilous. In strict saxicoles, the head height is lower than in all the other groups. Additionally, the head length is shorter in strict saxicoles. Foot length in strict and terrestrial saxicoles is shorter than in psammophilous. The length of the humerus is greater in strict saxicoles than in saxicoles and terrestrials. Furthermore, in the strict saxicoles, the forearm is wider than in saxicoles. The comparisons made between the modes of life (Table 1) reveal several differences between the species classified as strict saxicolous and the saxicolous, demonstrating that a too general definition of saxicolous, which includes all the species, is wrong or uninformative.

The results of the phylogenetic ANOVA indicate the non-independence of these morphologies from the phylogenetic history, with the P–values obtained being higher than those of the conventional ANOVA. There is a strong influence of phylogeny on morphologies; in fact, out of the 17 variables



Cadspersa	23.66	1.15	n=3
nigromaculatus	23.83	0.83	n=12
montanus	23.88	0.73	n=26
boulengeri	23.88	0.82	n=53
elongatus	24.11	0.74	n=46
alticolor	24.32	0.82	n=61
nigroviridis	24.50	0.71	n=2
kingii	24.80	1.08	n=31
palluma	**26.11**	0.64	n=27
patagonicus	**26.54**	0.83	n=25
Phymaturus	**26.32**	0.76	n=52

Figure 5. Skeletal innovations acquired by lizards of the genus *Phymaturus* that favored achieving a greater trunk volume. A) Cleared and stained skeletons of *Phymaturus cacivioi* (larger) and *Liolaemus quilmes*. Posxiphisternal ribs of *Phymaturus* and *Liolaemus*. There is no significant difference between the bony sections of both genera but in *Phymaturus* their cartilaginous free ending (inscriptional ribs) is longer and curved at its tip. B) In *Liolaemus* the terminal cartilage is shorter and ventrally curved. In *Phymaturus* are articulated in a lower degree respect to vertebral column. C) In *Phymaturus* there is on average one pair more presacral vertebrae than in *Liolaemus* which explain differences in trunk length. Even when *Phymaturus* exhibit a more flattened body than most *Liolaemus*, its larger capacity of trunk needed for is strict herbivory is ensured by the other two dimensions (length and width).

studied, only four present phylogenetic signals below 50%, these are trunk height (th), humerus and radius width (hw and raw), and trunk volume (tv) (see Table 1).

In Figure 7A (Table 2), our PCA of body measurements versus major liolaemid lineages revealed that trunk length and trunk width contribute to the morphological differentiation of the *Phymaturus palluma* group, *P. patagonicus* group, and the *Liolaemus lineomaculatus* group. In the first two cases, all *Phymaturus* are strict herbivores, while most species of the *lineomaculatus* group are reported as herbivorous. When we perform a PCA combining habitat preference and diet (Fig. 7B, Table 2), we found that the strict saxicoly and herbivorous species (including *Phymaturus* species and a few of *Liolaemus*) are better explained by measurements of the trunk, mainly: tv (trunk volume), tl (trunk length), tw (trunk width) and th (trunk height). But also, hh (head height), tiw (tibia width), and huw (humerus width). All analyses were performed considering residuals to avoid the effect of SVL differences. Measurements directly related to herbivory, recovered in the first analysis, along with trunk height, which have direct explanation on their strict saxicolous mode of life (utilizing rock crevices exclusively as refuge). Trunk volume is built by all three dimensions, but trunk width and trunk length are more related.

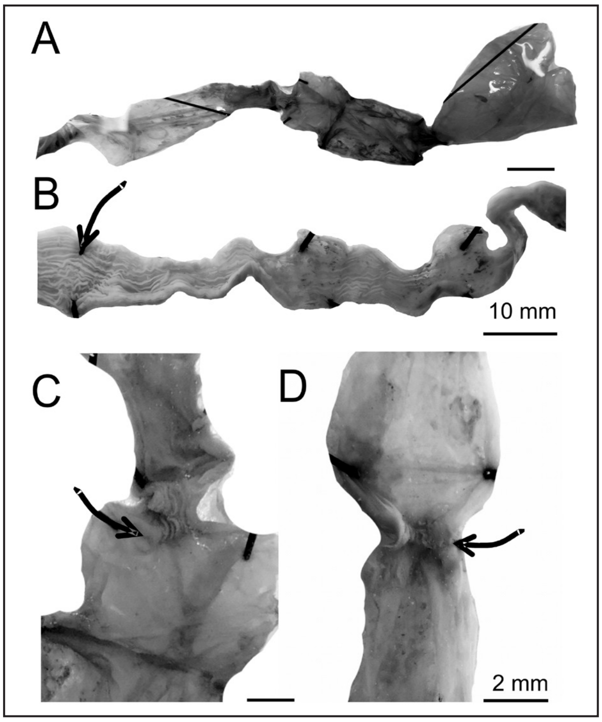


Figure 6. Modifications inside the digestive tract of *liolaemids*. Internal relief of the small intestine of A) small intestine of *Phymaturus aguanegra* (MCN 982, SVL=92.9 mm) showing its smooth walls; B) *Liolaemus mapuche* (MCN-UNSa 4803, SVL= 68.2 mm) the arrow indicates longitudinal folds typically present in insectivorous *Liolaemus*; C) *Phymaturus aguanegra* MCN 982 and D) *Liolaemus kunza* (MCN 1788, SVL= 63.1mm) with an arrow indicating the position of a pseudo-valve.

When we make comparisons between clades, we can make some interesting observations. In our study, although no significant differences were found (Table 3), there is a trend. The head and trunk are rather depressed in both groups of *Phymaturus* (Table 3), and the forelimbs are relatively long compared to the other clades. However, in the case of the hindlimbs, they are different between the *P. patagonicus* and *P. palluma* groups (there are significant differences between them in the length of the tibia and foot). In the first case, they are elongated, while in the *P. palluma* group, they are rather short. Greater trunk volume can be achieved in herbivores, but in a different way; in the *Liolaemus lineomaculatus* clade and in *Phymaturus*, it is achieved by increasing the length and width of the trunk, both have a rather depressed trunk. However, in the *L. kriegi* clade, the greatest volume is achieved by increasing the width and height of the trunk, but not the length of the trunk (Table 3).

Discussion

Given that *Phymaturus* exhibits a combination of biological characteristics, preferences, and mode of life (herbivorous, saxicolous, viviparous), and considering that we were unsure whether any of these traits were new in the origin of *Phymaturus* and if they had any effect on the current morphology of the group, we analyzed their origin and occurrence in the genus. According to our results, viviparity and reduced litter size are primitive characters already present in the ancestor of *Phymaturus* and *Liolaemus* together, whereas herbivory and saxicoly being novel in *Phymaturus* (Fig. 3). Below, we discuss the results obtained in relation to each of these three characteristics.

On liolaemid herbivory

Our comparisons among the three classical categories reveal that herbivores are 14.7% larger than omnivores, while omnivores are 19% larger than insectivores (O'Grady *et al.*, 2015, found herbivores to be 33% larger than omnivores, while omnivores were 18% larger than insectivores). Comparisons made in the present study found a smaller difference between

Table 1. ANOVA results obtained after comparisons across 157 Liolaemid species for seventeen measurements for diet and Kruskal-Wallis test for habitat preference (in this case the distribution was not normal). Different capital letters following mean ± standard error between species indicate a significant difference. Characters that showed significant differences are indicated in bold. For each case, the phylogenetic ANOVA was calculated using a permutation test with 1,000 permutations. P-values for post-hoc comparisons were adjusted using the Holm method. The phylogenetic signal (lambda index of Pagel, 1999) is also indicated for all characters. Abbreviations: Her= herbivore, Omn= omnivorous, Ins= insectivorous, Psa= psammophilous, Strict psa= strict psammophilous, Sax= saxicolous, Strict sax= strict saxicolous, Ter= terrestrial, tl= trunk length, tw= trunk width, th= trunk height, tv= trunk volume, hh= head height, hw= head width, hl= head length, fe= femur length, few= femur width, ti= tibia length, tiw= tibia width, fo= foot length, ha= hand length, hu= humerus length, huw= humerus width, ra= radius length, raw= radius width.

	Her	**Omn**	**Ins**	**P value**	**Phylo Anova**	**Psa**	**Strict psa**	**Sax**	**Strict sax**	**Ter**	**Test: Kruskal W**	**Phylo Anova**	**Phylo signalλ**
tl	B	A	A	**<0.0001**	0.568	AB	AB	A	B	B	**0.0199**	0.967	0.700523
tw	B	A	A	**<0.0001**	0.525	A	B	A	B	AB	**0.0001**	0.715	0.781915
th	-	-	-	-	-	AB	B	A	A	A	**0.0040**	0.904	**0.251346**
hh	A	B	A	**0.0001**	0.603	BC	C	AB	A	BC	**0.0001**	0.765	0.621969
hw	-	-	-	-	-	-	-	-	-	-	-	-	0.85829
hl	A	B	B	**<0.0001**	0.434	AB	B	B	A	AB	**0.0208**	0.936	0.895781
fe	-	-	-	-	-	AB	AB	A	B	A	**0.0026**	0.929	0.820286
few	-	-	-	-	-	BC	C	A	B	AB	**0.0084**	0.949	0.62415
ti	-	-	-	-	-	B	AB	A	A	A	**0.0444**	0.935	0.914291
tiw	-	-	-	-	-	-	-	-	-	-	-	-	0.589477
fo	A	B	AB	**0.0125**	0.825	B	AB	AB	A	A	**0.0176**	0.928	0.8212
ha	-	-	-	-	-	-	-	-	-	-	-	-	0.824825
hu	B	A	AB	**0.0005**	0.663	AB	AB	A	B	A	**0.0002**	0.783	0.726085
huw	AB	B	A	**0.0255**	0.875	-	-	-	-	-	-	-	**0.436747**
ra	-	-	-	-	-	AB	B	AB	B	A	**0.0060**	0.905	0.872795
raw	-	-	-	-	-	B	B	A	B	AB	**0.0134**	0.944	**0.358359**
tv	B	A	A	**0.0001**	0.629	AB	C	A	B	B	**0.0025**	0.874	**0.463064**

herbivores and omnivores than O'Grady *et al.* (2015). This difference may be due to the different sample sizes studied (135 spp versus 21). An important distinction between the herbivory of *Phymaturus* and *Liolaemus* is that in the former it is strict, with only vegetable content found, while in *Liolaemus* there is always a percentage of material of animal origin (insects). In only two cases, some insect remnants were reported in the gut of *Phymaturus* (in *P. zapalensis* Boretto and Ibargüengoytía, 2018; *P.* sp. related to *P. yachanana*, Obregón Streitenberger *et al.*, 2018), but it has not been proven at this time if they are a frequent item (not accidental) of their diet. Not much discovery has been made since Espinoza *et al.* (2004) regarding the evolution of herbivory in liolaemids. Ocampo *et al.* (2022, 2024) conducted an ancestral reconstruction of dietary diversification throughout the Liolaemidae evolutionary history, shown in pie charts at nodes representing posterior probabilities of each diet class. Even though they suggested an insectivorous origin (Ocampo *et al.*, 2022), their optimizations are not decisive (because the method performed). In their analysis, they found that herbivory exhibited a higher rate of diversification than insectivory and omnivory. It's possible that their result was influenced by *Phymaturus* radiation, consisting of 52 species, all inheriting herbivory from their ancestor. Within *Liolaemus,* herbivory is rare (see their own Fig. 1), as reported for 30 out of 288 species of *Liolaemus* according to Abdala *et al.* (2021). In Ocampo *et al.* (2024), the most likely ancestor of Liolaemidae was found to be omnivorous. We traced the evolution of herbivorous versus non–herbivorous species, avoiding more precise optimizations. However, due to the limited number of contributions on the diet of liolaemids (full diet studies only focused on 32 out of more than 330 spp. of liolaemids, see list of diet literature in Appendix1), assigning a specific diet type to species is somewhat risky. Most diet assignments to species come from

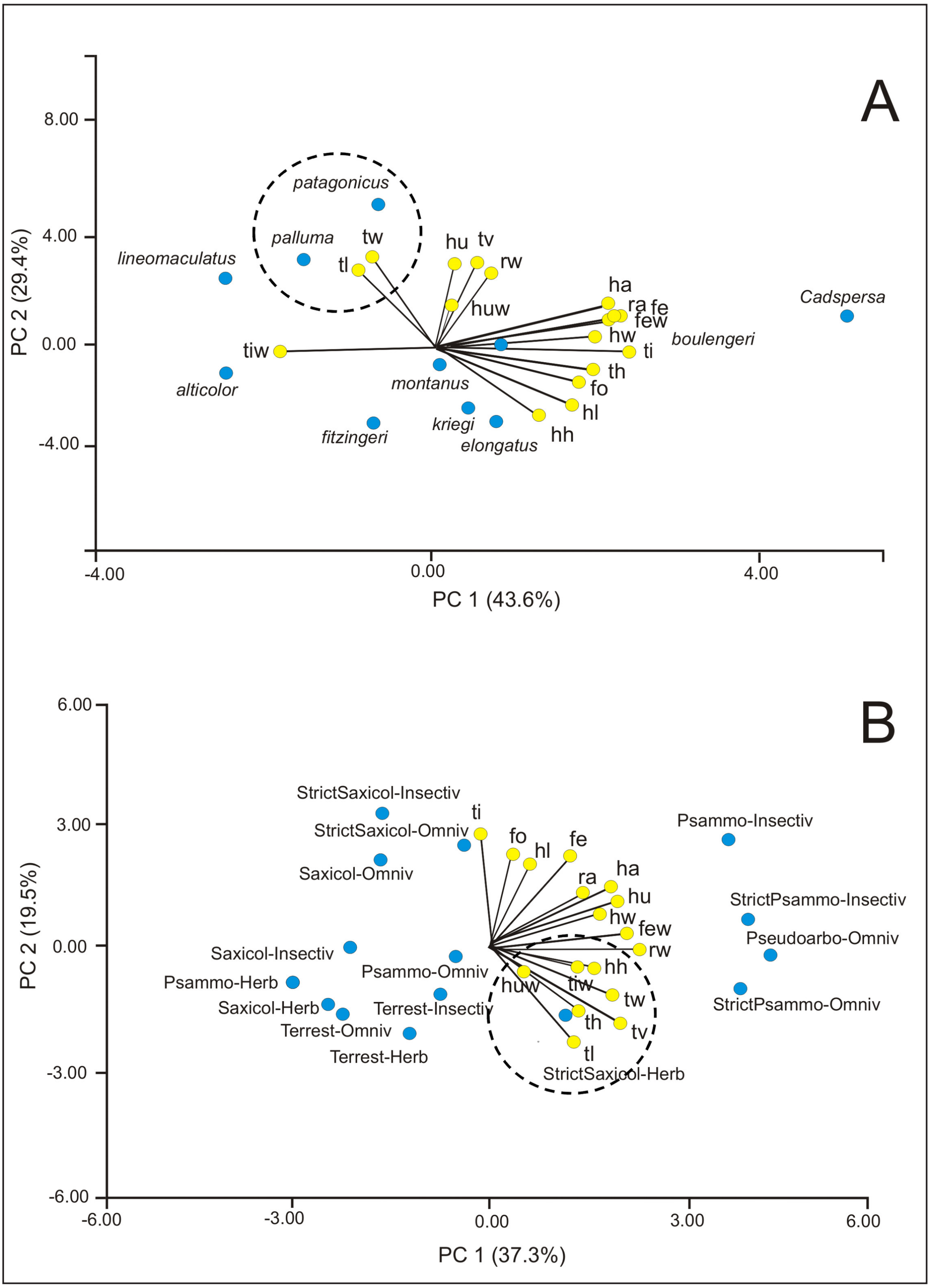


Figure 7. Spatial relationship of the studied body measurements and their relationship with groups of *Phymaturus* species and other Liolaemids and modes of life. A) PCA of Clades / body measurements: PCA1 vs PCA2 represents 73% of information. The *palluma* and *patagonicus* species groups of *Phymaturus* informed by tl (trunk length) and tw (trunk width). B) PCA of diet-habitat preference / body measurements: PCA1 vs PCA2 represent 56.8% of information. The combination strict saxicolous-herbivorous (all *Phymaturus* and few species of *Liolaemus*) is informed mainly by trunk dimensions: tv (trunk volume), tl (trunk length), tw (trunk width) and th (trunk height). But also, hh (head height), tiw (tibia width) and huw (humerus width). All analyses performed considering residuals to avoid the effect of SVL differences.

occasional observations of feces, dissections of one or a few individuals, behavioral observations made in the field, or are taken from the original taxonomic descriptions, which include commentary on the natural history of animals. None of these assignments consider the existence of ontogenetic variation, seasonal variation, and even sexual dimorphism related to diet, which are only detected after studying/examining a numerous series of individuals, of both sexes, ages, and samples taken in different seasons (Rocha 1998, 2000; Valdecantos *et al*., 2012; Semhan *et al*., 2016, among others, see full diet literature of Liolaemidae in Appendix 1). Only 12 *Liolaemus* diet studies (out of 37 published) addressed any of these aspects (ontogenetic variation, sexual dimorphism, and seasonal variation) of a genus of 288 species. Due to the fragmentary nature of the information, we considered it inappropriate to estimate or generalize, calculate rates of changes and transitions considering the three state-categories (insectivorous, omnivorous, herbivorous) (as Ocampo *et al*., 2022 did). Instead, we preferred, in certain cases, a more conservative approach, emphasizing comparisons between herbivores and non-herbivores.

Ocampo *et al.* (2024) found that herbivorous species have evolved larger heads, shorter hindlimbs, and a minimal difference between forelimb and hindlimb length, whereas omnivores and insectivores displayed smaller heads and longer hindlimbs. However, comparing these findings with ours becomes difficult since, in our case, 16 measurements versus 7 (Table 1) were taken (including the three related to the trunk) also estimating the trunk volume. Our results support that in the case of herbivores, they have greater length and width of the trunk than in non-herbivores (contrary to Ocampo *et al*., 2024). We demonstrate that in the case of *Phymaturus,* this is explained by the addition of two presacral vertebrae and the elongation of the inscriptional ribs (Fig. 5). We found (contrary to Ocampo *et al*., 2024) that heads are smaller (we found significant differences in head height and head length). The length of the head is shorter (shorter snout), consistent with previous studies on a broader scale in squamates by Vitt *et al.* (2003). In insectivorous species, the snout tends to be longer; see also Metzger and Herrel (2005). This is related to the need for a more elongated snout and its ability to capture prey. Ocampo *et al.* (2024) found that the total length of hind limbs is shorter in herbivores, our individual measurements of the limb segments show us that the difference lies in the feet (which are shorter in herbivores), with no differences in femurs and tibias.

In the context of pleurodontan clades, the occurrence of herbivory is rare, much like viviparity, as we previously highlighted (Fig. 3B). Unlike *Phymaturus*, where herbivory and saxicolous habitat preference are strictly combined, which was a clear novelty in the origin of the genus (Fig. 3), within *Liolaemus* this combination is exceptional. Only 3 species belonging to the subgenus *Eulaemus* are known to be herbivorous and saxicolous simultaneously (*L. chlorostictus*, *L. orientalis*, *L. aymararum*), compared to 20 other herbivorous species that are not saxicolous. Within the *Liolaemus* sensu stricto subgenus, the *L. kriegi* group (*L. buergeri*, *L. zabalai*, *L. ceii*) and *L. tregenzai* are herbivorous and saxicolous at the same time versus two other herbivorous–only species. Herbivory is generally quite exceptional in the *Liolaemus* sensu stricto subgenus. Independent changes have occurred along independent lineages. In fact, we show that a greater trunk volume can be achieved in herbivores, but in a different way. In the *L. lineomaculatus* clade and in *Phymaturus*, this is accomplished by increasing the length and width of the trunk. Both have a rather depressed trunk. However, in the *L. kriegi* clade, the greatest volume is achieved by increasing the width and height of the trunk, but not its length (Table 3).

Saxicolous mode of life

In the *palluma* group of *Phymaturus,* the hind limbs are shorter compared to those in the *patagonicus* group (and these latter ones do not present significant differences with *Liolaemus* clades). Perhaps this is linked to the fact that the species in the *P. palluma* group are slightly larger, have a greater volume of the trunk (heavier), and the fact of having shorter limbs and a lower center of mass ensures better balance on inclined surfaces. Climbers should have rather strong and short limbs to maintain their center of gravity closer to the substrate, along with trunks that are flatter and closer to the surface (Van Damme *et al*., 1997). *Phymaturus* species from both groups have longer forelimbs compared to most *Liolaemus* species (Table 3). According to Tulli *et al.* (2011), the challenge presented by rocky environment for lizards is solved with longer forelimbs, taller nails, and a shorter distance between limbs. These adaptations contribute to improved clinging performance in these animals. Our results agree with this last statement, except for "shorter distance between

Table 2. Principal component scores based on 17 continuous characters (measurements). The values shown correspond in the upper case to the PCA displayed in Figure 7A, in the lower case to the PCA displayed in Figure 7B.
Values above 0.30 were arbitrarily considered here (in bold) for description of results and discussion purposes. Species vary in body size, and this can affect all morphometric measurements; hence, a regression was performed for these characters using SVL as the independent variable, and the residuals were used for the PCA.

PCA Clades/measurements					**PCA Diet-mode of life/measurements**				
(Figure 7A)					(Figure 7B)				
measurements	pc1	pc2	pc3	pc4	measurements	pc1	pc2	pc3	pc4
RDUO LOG10tl	-0.14	**0.35**	-0.07	-0.22	RDUO LOG10tl	0.21	**-0.37**	-0.14	-0.27
RDUO LOG10tw	-0.12	**0.41**	-0.05	0.10	RDUO LOG10tw	**0.30**	-0.18	-0.24	0.28
RDUO LOG10th	0.28	-0.10	-0.09	0.23	RDUO LOG10th	0.21	-0.23	0.38	0.02
RDUO LOG10hh	0.19	**-0.31**	-0.23	0.28	RDUO LOG10hh	0.08	-0.08	0.52	-0.10
RDUO LOG10hw	0.29	0.06	-0.40	0.15	RDUO LOG10hw	0.23	0.19	0.20	0.48
RDUO LOG10hl	0.25	-0.25	-0.19	0.08	RDUO LOG10hl	0.09	**0.31**	0.29	0.45
RDUO LOG10fe	**0.32**	0.13	0.27	-0.14	RDUO LOG10fe	0.21	**0.37**	-0.25	0.09
RDUO LOG10few	**0.32**	0.14	0.21	0.06	RDUO LOG10few	**0.33**	0.05	0.03	-0.18
RDUO LOG10ti	**0.35**	-0.01	0.20	0.02	RDUO LOG10ti	- 0.03	**0.43**	0.15	-0.29
RDUO LOG10tiw	-0.28	-0.01	0.30	0.38	RDUO LOG10tiw	0.21	-0.08	0.25	-0.24
RDUO LOG10fo	0.26	-0.15	0.45	0.04	RDUO LOG10fo	0.05	**0.35**	0.24	-0.26
RDUO LOG10ha	**0.32**	0.19	2.0E	-0.21	RDUO LOG10ha	0.29	0.23	-0.20	-0.03
RDUO LOG10hu	0.03	**0.37**	0.30	0.02	RDUO LOG10hu	0.27	0.12	-0.32	0.05
RDUO LOG10huw	0.02	0.18	0.13	0.69	RDUO LOG10huw	0.26	-0.08	0.17	0.12
RDUO LOG10ra	**0.34**	0.14	-0.02	-0.19	RDUO LOG10ra	**0.31**	0.17	-0.06	-0.36
RDUO LOG10raw	0.10	**0.33**	-0.40	0.07	RDUO LOG10raw	**0.37**	-0.01	-0.04	-0.09
RDUO LOG10vol	0.07	**0.38**	-0.13	0.22	RDUO LOG10vol	**0.32**	**-0.30**	0.07	0.11

limbs” aspect. In the present contribution, we show that trunk length in *Phymaturus* exceeds that of all other *Liolaemus* lineages. The combination of longer and wider trunks in these herbivores animals has allowed them to increase their abdominal capacity. Toyama (2017, Fig. 2) illustrated in a PCA analysis of different variables that *Phymaturus* separates from other genera, with the width of the abdomen and the length of the trunk being the related characteristics. This fact (more evident changes of the trunk dimensions) would be evidence that herbivory has predominated over their saxicolous mode of life. This is evident in their trunk measurements, which deviate more from those expected for a life on rocks (even though we found significant differences, they are not flatter than terrestrial or psammophilous species; see Table 1). However, the saxicoly did manifest itself in a measurement of the head; in fact, the height of the head is lower than in all other categories. The longer forelimbs appear to be the most important evidence regarding saxicolous life (as previously found by Tulli *et al.*, 2011). Longer forelimbs would provide greater adhesion force to the substrate, primarily due to the longer forelimbs (Tulli *et al.*, 2011) (see humerus, radius and hand length in Table 1 and Table 3). In this work, we found that the length of the hindlimbs differs between both clades of *Phymaturus* (Table 3), being longer in the *P. patagonicus* group and more in accordance with what would be expected for a saxicolous clade. Tulli *et al.* (2016) found a correlation between muscle-tendinous morphology and habitat use; strict saxicolous lizards tend to exhibit wider flexor digitorum longus aponeurosis (they studied two species of the *P. patagonicus* group). However, species of the *L. kriegi* clade, although saxicolous, do not strictly use cracks as shelter (they can take refuge in holes under rocks as well) as the *Phymaturus* species do; for them the height of the trunk is not a limitation. Species of the *L. lineomaculatus* group, such as *L. kolengh,* sometimes take refuge under slabs equivalent to cracks in the preferred environments of *Phymaturus*. Strict psammophilous exhibit smaller trunk volume than all other categories; according to Halloy *et al.* (1998), these are the unique liolaemids that exhibit specialized diving behavior in sand dunes, and a larger trunk volume could mean being an obstacle to this.

The phylogenetic distribution of herbivory and saxicoly

The results of the phylogenetic ANOVA indicate the non-independence of these morphologies from the phylogenetic history, with the P–values obtained being higher than those of the conventional ANOVA. These results may appear contradictory to those found with traditional statistics; however, we believe that they complement them. If we observe the distribution of herbivory and saxicoly (and the related morphology) in the phylogenetic tree, we notice that herbivory and strict saxicoly were acquired at the origin of *Phymaturus* (Fig. 8). Subsequently, this genus underwent important

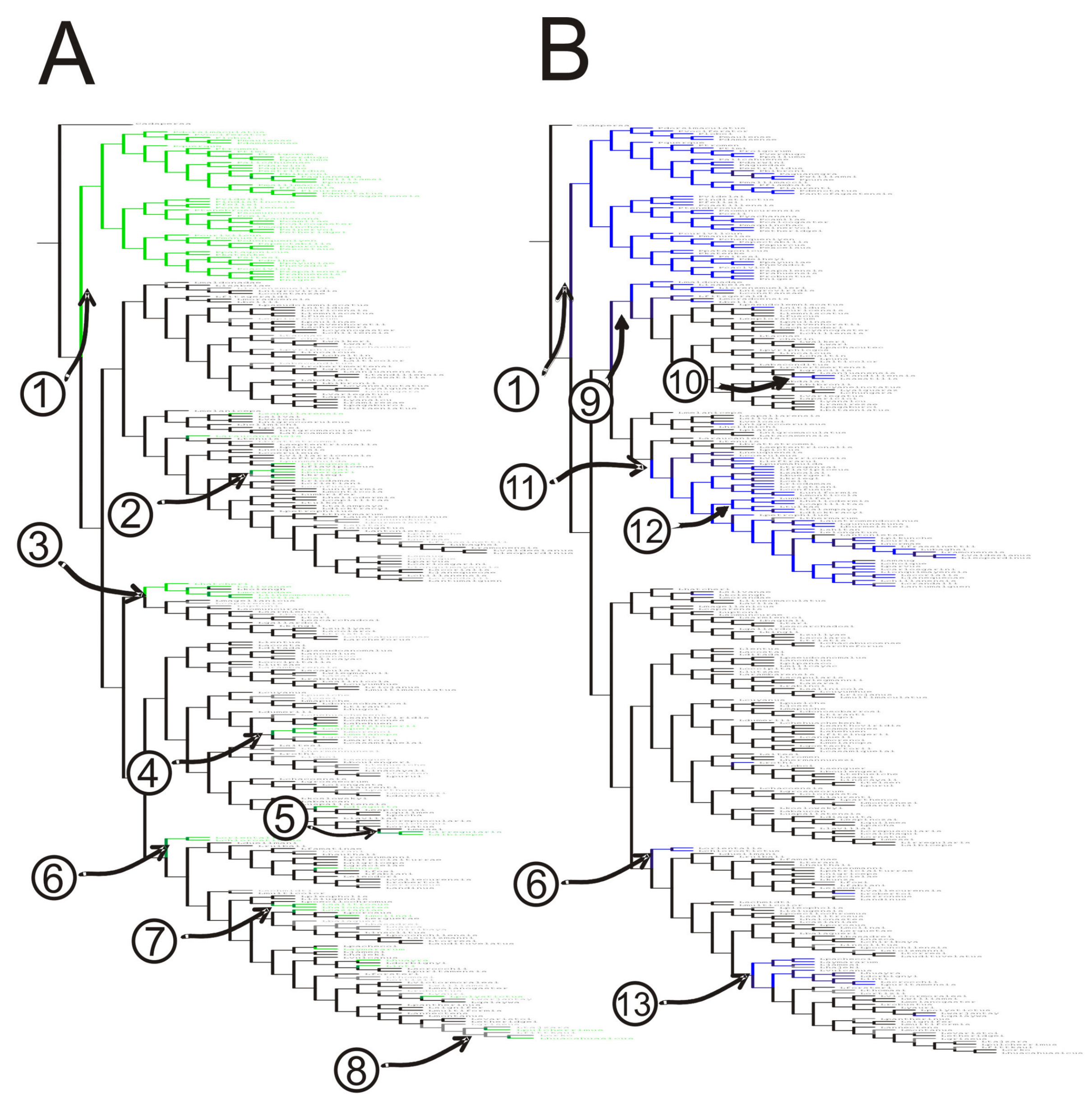


Figure 8. The persistence of modes of life in different lineages of Liolaemidliolaemids: the occurrence of herbivory (A) and saxicoly (B). Arrows indicate the lineages where herbivory or saxicoly were originally acquired (ancestor) and this characteristic remained conserved in all its descendant species. Therefore, it is expected that these characteristics and their associated morphology will be found in phylogenetic tests as due to a phylogenetic effect. 1- *Phymaturus* (herbivorous and strict saxicolous) 2- *Liolaemus kriegi* subclade (herbivorous), 3- *L. lineomaculatus* clade? Group? (herbivorous), 4- *L. fitzingerii* complex (herbivorous/omnivorous), 5- *L. albiceps-L. irregularis* (herbivorous), 6- *L. orientalis- L. chlorostictus* (herbivorous and strict saxicolous) 7- *L. cazianiae* (herbivorous), 8- *L. pulcherrimus* (herbivorous) 9- *L. nigroviridis* and *L. belli* subclades (saxicolous),10- *L. saxatilis-tandiliensis* (saxicolous), 11- *L. elongatus-petrophilus* group (saxicolous) ,12- *L. capillitas* subclade (strict saxicolous) 13- *L. dorbignyi* and *L. jamesi* subclades (strict saxicolous).

Table 3. ANOVA results obtained after comparisons across ten liolaemid lineages. The raw (actual) values for each case are presented, as they may be useful to other researchers (but not the residuals). Since differences were found in SVL between the analyzed species, the residuals of the regression of each measurement character versus SVL were used to remove the possible effects of size across analyses. Data are given in millimeters, except for tv, which is given in milliliters. Different capital letters following the mean ± standard error between species indicate a significant difference ($p < 0.05$). For each lineage, the sample size is indicated above, with the number of species recorded per lineage shown below. The *Liolaemus fitzingeri* complex is nested within the *boulengeri* group and the *Liolaemus kriegi* subclade nested within the *elongatus-petrophilus* group, were analyzed separated because are omnivorous or herbivorous lineages different from the rest of species of the groups they belong. Abbreviations: the same as Table 1. The *Phymaturus patagonicus* and *palluma* species groups are highlighted to show their morphology in comparison with *Liolaemus* and *Ctenoblepharys* lineages. *Phymaturus* species groups share similar head and trunk height (somewhat depressed) and the longest forelimbs among Liolaemid lizards. Hindlimbs exhibit differences (foot and tibia are longer in the *patagonicus* group).

	elongatus **n=162** **14**	***kriegi*** **n=423**	***montanus*** **n=171** **19**	***Cadspersa*** **n=51**	***fitzingerii*** **n=334**	***boulengeri*** **n=284** **28**	***alticolor*** **n=138** **15**	***lineomaculatus*** **n=222**	***patagonicus*** **n=167** **18**	***palluma*** **n=124** **13**	**Test**	**P**
tl	33.47+-5.96 A	47.3+-3.96 A	36.98+-5.59 AB	31.83+-2.22 ABC	38.96+-6.49 ABC	30.39+-7.12 ABC	25.22+-3.06 BCD	30.87+-6.74 BCD	44.29+-4.55 CD	52.62+-5.97 D	F=35.39	<0.0001
tw	19.50+-3.93 ABC	28.20+-2.72 BC	22.50+-4.79 C	15.93+-3.38 ABC	21.25+-2.96 A	16.17+-4.05 BC	11.43+-1.99 BC	18.42+-1.58 D	33.89+-2.84 D	38.61+-3.93 D	F=74.64	<0.0001
th	9.47+-2.20 AB	13.93+-3.82 CD	10.12+-1.90 ABC	10.32+-2.00 D	10.03+-2.95 BCD	8.43+-2.30 BCD	6.26+-2.83 A	7.26+-3.08 AB	9.71+-2.60 AB	10.90+-2.20 AB	F=17.60	<0.0001
hh	7.86+-0.92 BC	9.68+-1.52 D	8.48+-1.67 CD	7.75+-1.48 D	8.70+-2.31 CD	7.09+-1.56 CD	5.20+-0.87 AB	5.74+-0.05 AB	7.62+-0.73 A	8.68+-0.92 AB	F=68.49	<0.0001
hw	12.74+-1.76 BC	15.26+-3.03 C	13.72+-2.87 C	12.53+-2.13 D	12.16+-2.13 A	10.35+-2.15 C	7.71+-1.04 A	9.38+-0.49 C	13.88+-1.10 AB	16.65+-1.76 BC	F=32.39	<0.0001
hl	16.34+-1.72 CD	18.62+-3.02 CD	16.16+-2.64 C	14.90+-1.87 D	15.70+-1.69 B	13.24+-2.28 C	10.72+-1.23 AB	11.39+-0.46 AB	15.08+-0.79 A	17.53+-1.72 B	F=102.01	<0.0001
fe	12.91+-2.18 C	15.17+-2.11 AB	12.77+-2.58 BC	12.56+-1.33 D	12.84+-0.51 AB	10.15+-2.33 BC	7.93+-1.33 AB	8.18+-0.14 A	15.86+-1.59 C	16.88+-2.18 ABC	F=23.25	<0.0001
few	6.33+-1.21 AB	7.40+-1.40 AB	6.58+-1.81 AB	6.14+-0.85 C	7.32+-1.75 AB	5.16+-1.40 BC	3.60+-0.63 A	4.08+-0.39 AB	8.19+-0.87 BC	9.05+-1.21 AB	F=16.28	<0.0001
ti	14.50+-1.71 D	18.50+-3.29 BC	14.12+-2.62 BCD	15.25+-1.61 E	15.59+-3.01 CD	12.16+-2.55 CD	9.06+-1.04 A	9.36+-1.19 AB	13.31+-1.22 CD	17.04+-1.71 AB	F=56.52	<0.0001
tiw	4.27+-0.69 BC	5.40+-0.93 BC	4.22+-0.88 BC	2.69+-0.28 A	4.94+-1.23 BC	3.68+-1.04 BC	2.58+-0.54 B	2.88+-0.32 BC	5.44+-0.72 C	5.64+-0.69 BC	F=14.92	<0.0001
fo	21.70+-2.89 E	25.70+-4.84 CD	20.38+-2.87 ABCD	19.99+-2.05 E	24.10+-2.27 DE	18.11+-3.35 DE	14.49+-1.65 ABC	14.14+-0.95 AB	24.05+-1.19 DE	23.45+-2.89 A	F=44.74	<0.0001
ha	12.58+-1.67 BC	13.85+-1.99 AB	12.12+-2.18 ABC	14.62+-1.54 D	13.04+-1.03 A	9.82+-1.75 ABC	8.45+-1.10 AB	8.64+-0.25 ABC	15.23+-1.06 C	16.25+-1.67 ABC	F=20.81	<0.0001

hu	10.52+-1.32 BCD	12.52+-2.09 ABC	10.42+-1.85 BCD	9.01+-1.08 BCD	11.78+-0.61 A	8.59+-1.42 CD	6.88+-0.97 ABC	7.44+-0.92 ABC	13.89+-1.06 E	15.58+-1.32 DE	F=43.26	<0.0001
huw	4.07+-0.97 ABCD	5.48+-1.41 ABC	4.89+-1.09 D	3.48+-0.60 ABCD	4.80+-0.68 ABCD	3.52+-1.12 CD	2.33+-0.34 A	2.72+-0.15 BCD	5.71+-0.80 BCD	6.36+-0.97 ABCD	F=20.75	<0.0001
ra	8.50+-1.20 BC	9.86+-1.83 ABC	8.95+-1.86 ABC	10.48+-1.11 D	9.82+-1.54 AB	6.99+-1.37 ABC	5.37+-1.03 AB	6.55+-1.20 ABC	10.87+-0.95 C	11.77+-1.20 BC	F=20.78	<0.0001
raw	3.75+-0.74 AB	5.47+-1.46 ABC	4.14+-1.02 BCD	3.64+-0.39 DE	3.84+-0.99 A	3.25+-0.83 BCD	2.28+-0.56 AB	3.21+-0.50 E	5.21+-0.68 CDE	5.80+-0.74 CDE	F=18.46	<0.0001
tv	5462.37+-2603.95 AB	15119.60+-6398.69 CD	7009.87+-3300.43A BCD	4215.05+-1673.94 CD	7007.84+-3787.20 ABC	3779.16+-2761.25 BCD	1531.39+-1053.95 ABC	3482.74+-2372.91 D	11431.49+-3624.37 D	17269.31+-3823.02 D	F=25.83	<0.0001

diversification in Argentina and Chile, and all its descendants retained these same characteristics. That is why both the phylogenetic ANOVA and the lambda index suggest that these characters would be explained by phylogeny (common ancestry). We can say that the same principle applies for the origin of saxicoly in the *Liolaemus elongatus* clade and all the species it encompasses inheriting those characteristics (Fig. 8), where the strict saxicoly of species in the *L. capillitas* subclade occurred in their ancestor and was inherited by all its descendants (*L. heliodermis*, *L. capillitas*, *L. umbrifer*, *L. tulkas*, *L. fiambala* and *L. galactostictos*). The same can be said for the herbivorous *Liolaemus kriegi* subclade. Therefore, conventional ANOVA describes the novelties of those diets and modes of life at the origin of these different clades, which were conserved in subsequent diversifications (Fig. 8).

Skeletal novelties in *Phymaturus*

In the broader context of squamate reptiles, according to Bergmann and Irschick (2011), a higher number of vertebrae has been reached by several lineages, mainly including Serpentes, Amphisbaenia, Pygopodidae, and some lineages of Scincidae and Anguidae. Bergmann and Irschick (2011) have shown that increased rates of evolution in vertebral numbers have coincided with increased rates and disparity in body shape evolution. But at the same time, they also found that the evolution of many vertebrae has not inhibited body shape or taxonomic diversification, and they concluded that increased vertebral number is not a key innovation. Small changes vertebral number can indeed contribute to achieving a particular body shape configuration in cooperation with other anatomical changes as we explain below. Bergmann and Irschick (2011) findings demonstrate that lineage attributes, such as the relaxation of constraints on vertebral number, can facilitate the evolution of novel body shapes. However, they also remarked that various factors are responsible for body shape and taxonomic diversification. We agree with this latter statement. For instance, a higher number of vertebrae has facilitated, for example, the acquisition of a snake-like body shape multiple times, especially in those lineages adapted to a fossorial mode of life. But, in our case, *Phymaturus* increased (but moderately) their vertebral number, this, combined with a widened body due to the disposition of their postxiphysternal ribs and elongation of the inscriptional ribs (Fig. 5), favored a general increase in their trunk volume (needed for their strict herbivorous diet).

Most iguanids possess 24 presacral vertebrae (including the atlas and axis), with a range spanning from 21 to 26. Hoffstetter and Gasc (1969) tabulated presacral vertebral numbers for most lizard families, noting a modal number of 26 in gekkotan and scincomorphan, and 29 in anguimorphan, with even higher numbers in snake body shape clades. Romer (1956) previously considered the primitive condition to be the one found in rhynchocephalian 23–25. Etheridge and De Queiroz (1988) also regarded these numbers as primitive in their analyses of iguanian lineages relationships. Considering the current relationships of squamate lineages, within Toxicophora, we had a clade conserving primitive condition (pleurodonts), with a modal number of 24. In this context, in a clade highly conservative, *Phymaturus* increased a little bit just the needed to increase abdominal volume. Within the pleurodonts, only Polychrotidae have been found to possess 26 to 27 presacral vertebrae, as in *Phymaturus*.

Digestive tract novelties in *Phymaturus*

The occurrence of pseudo–valves in the small intestine, which is convergent with herbivorous species of *Liolaemus*, could have meant a specific strategy to slow down the transit of food along the tract. To date, these structures have not been found in other lizards, perhaps they went unnoticed in previous studies. In the case of small species (such as *L. kunza*) which lack a significant trunk volume to contain larger viscera (Fig. 4) and do not have marked partitions in the cecum like iguanids, this might have led them to develop a different strategy. The occurrence of these pseudo–valves (Fig. 6D) in the small intestine to facilitate optimal transit and digestion of plant material. The caecum shows smooth walls in most species of *Phymaturus* and *Liolaemus*, with only a few exceptions showing oblique and transverse folds, but never developing very conspicuous partitions like those described for iguanids (Iverson 1980, 1982). In most species of *Phymaturus* (except *P. aguanegra* and *P. zapalensis*), the middle region of the stomach has longitudinal folds, while in most *Liolaemus* species it lacks folds (except the herbivorous *L. kriegi* and *L. buergeri*). The pyloric region is differentiated, it is tubular and elongated in shape in *Phymaturus*, while being short and inconspicuous in *Liolaemus*. The duodenal bulb is conspicuous in *Liolaemus* species, but indefinite in

Phymaturus. However, the functional implications of these last two structures remain unknown.

Comments on the origin and evolution of viviparity

Our parsimony reconstructions provide a decisive assignment (unambiguous) along a Liolaemidae tree. The use of all pleurodont families as outgroups reveals that viviparity is rare (only occurring within Phrynosomatids and in the ancestor of *Liolaemus-Phymaturus*, with later changes inside *Liolaemus* (Fig. 3, see also Fig. S1). This hypothesis differs from previous studies in two aspects: the use of multiple outgroups, a parsimony analysis, and the use of an updated topology of Liolaemidae. Schulte *et al.* (2000) were the first authors to study the origin and evolution of viviparity in *Liolaemus*. They performed a parsimony analysis based on 60 species of *Liolaemus*, two *Phymaturus* species, and three outgroups. Depending on whether they considered viviparity as reversible or irreversible, different interpretations were made regarding the tree: six gains of viviparity or a combination of three gains and three losses of viviparity within *Liolaemus*. Their study was pioneering in suggesting the correspondence between the occurrence of viviparity and high elevations of the Andes at areas located at high latitude (then cold climate). However, their conclusions were not decisive, which provoked later studies to address the same topic. Pincheira-Donoso *et al.* (2013), influenced by previous authors who stated that for squamates in general, viviparity is regarded as predominantly irreversible, and that oviparity is unlikely to re-evolve (they cited Lee and Shine, 1998; Shine and Lee, 1999; and Shine, 2005), conducted their analyses in consistency with this criterion. They performed likelihood reconstructions of character evolution with Mesquite v.2.01 (Maddison and Maddison, 2011) and applied phylogenetic methods to evaluate the transitions between oviparity and viviparity in *Liolaemus* topology. Pincheira *et al.* (2013) remarked that the unidirectional oviparity–viviparity evolutionary transition was found in their analyses to be most likely among competing hypotheses. But their results are clearly influenced by the methods they applied, as reported in the methods section: "*For these two irreversible models of trait evolution to exhibit both character states in the tips, a tree root fixed to character state 0 (i.e. oviparity) is required. Therefore, we fixed the tree root to an oviparous state, using a modified version of the Diverse package of Mesquite (v.2.01) developed by R.G. FitzJohn (Goldberg & Igic, 2008).*" So, what are the chances that they will find a transition from viviparity to oviparity more frequently? By not using outgroups and fixing the ancestral state and then applying a method to analyze the oviparous-viviparous transition, we ensure that our results are consistent regardless of the model used. Schulte *et al.* (2000) remarked that different studies have addressed the issue of the reversibility of parity mode in squamate reptiles and agree that there is no strong evidence exists for the irreversibility of viviparity (Benabib *et al.*, 1997; Lee and Doughty, 1997; Lee and Shine, 1998). More recently, Esquerre *et al.* (2018) analyzed the evolution of parity mode in Liolaemidae applying a Bayesian MCMC routine. They considered only one outgroup, and their results fell into a significant degree of uncertainty regarding the ancestral condition for liolaemids. Esquerre *et al.* (2018) analysis provided a pie charts representation of probabilities for both parity modes for each node of the tree, so the nature of their analysis avoids contributing any decisive hypothesis of ancestry. Any future study that modifies the assignment of parity mode to any terminal taxa or update the tree topology, or employs different outgroups, will always represent probabilities of both parity modes at each node. Consequently, these hypotheses become un-rejectable, offering no alternatives of new discoveries. Their assignment of transitions between parity modes along the tree was based on a qualitative assessment of node state likelihoods, inferring transitions when the likelihood of a node's state exhibited a different, most likely state than its ancestor. A positive result of this study was demonstrated that viviparity is reversible, and the transition viviparity to oviparity occurred several times during *Liolaemus* diversification, in opposition to the hypothesis of Pincheira *et al.* (2013). Parsimony optimizations provide rejectable hypotheses and dissipate uncertainties on ancestral reconstructions. Our optimization brings a full hypothesis for all nodes of the tree that are refutable; animals are either oviparous or viviparous, not 30% of oviparous and 70% viviparous at the same time, the same is for all internal branches of the tree. The evolutionary explanation for liolaemids is recovered here with the simplest path: the novelty of viviparity occurred in the ancestor of *Liolaemus-Phymaturus* (different to Schulte *et al.*, 2000; Pincheira *et al.*, 2013; Esquerre *et al.*, 2018) and reverted several times to oviparous (as in Esquerré *et al.*, 2018). Here we recovered a hypothesis of evolution of parity mode in liolaemids, implying 13 transitions from viviparous to oviparous and only 6 transitions from oviparous to viviparous (Fig. S1). Retake viviparity in more terminal clades was rare or more unlikely. Esquerré *et al.* (2019) recovered 8 transitions from oviparity to viviparity and 7 from viviparity to oviparity.

Conclusions

Viviparity was the ancestral condition for the *Phymaturus-Liolaemus* node, along with reduced litter size. The novelties in the origin of *Phymaturus* were the herbivorous diet and the saxicolous life with exclusive use of crevices as shelter. Our phylogenetic statistics (phylogenetic ANOVA and lambda test of phylogenetic signal) indicate a strong phylogenetic imprint on the body measurements studied. All lineages showing characters with significance regarding diet and mode of life would have acquired them early, with all their descendants inheriting them (Fig. 8).

Phymaturus, with respect to the large clades of *Liolaemus*, differed mainly in the width of the abdomen and length of the trunk, which helped to considerably expand its abdominal capacity. This expansion is important for its herbivorous diet and, secondarily, it favored the development of large fetuses, the accumulation of fat more than in the tail, and the defensive behavior of "inflating" in the cracks. In *Phymaturus* the head is larger than *Liolaemus* but is smaller in relation to the body. Its snout is shorter unlike what occurs in most omnivorous and insectivorous *Liolaemus*. The herbivory generated the necessary changes such as greater abdominal volume to contain larger viscera due to herbivory, expressed in greater trunk length and width. Secondarily, this would have allowed these animals to develop larger fetuses (with reduced litter numbers ancestral for both *Phymaturus* and *Liolaemus*; see Fig. S1) and to contain larger fat deposits, more in the abdominal region rather than the tail (the reverse in *Liolaemus*, Paz, 2017), and possibly the ability to inflate inside the cracks (behavior not yet tested or studied in these animals) (like what has been described for *Uromastyx* and *Sauromalus*, Deban *et al.*,1994, Cooper *et al.*, 2000). In the *palluma* group of *Phymaturus*, the modifications were a little more extreme compared to the *P. patagonicus* group, including larger volumes of the trunk and somewhat larger body sizes, resulting in heavier individuals with shorter hind limbs (perhaps thus obtaining a lower center of mass, see Ting *et al.*, 1994; Clemente *et al.*, 2008; Foster *et al.*, 2018). Longer posterior extremities are more related to better runners in saxicolous species (Revell *et al.*, 2007), maybe the use of habitat is a little different between species of the *P. patagonicus* (longer hindlimbs) and *P. palluma* groups. In *Phymaturus,* as in other saxicolous liolaemids, the adherence force of forelimbs was proved by Tulli *et al.* (2011) their fore limbs are longer, we recovered same result. Longer forelimbs would provide greater adhesion force to the substrate, mainly due to their longer forelimbs (Tulli *et al.*, 2011). According to Tulli *et al.* (2016), there exists a correlation between muscle-tendinous morphology and habitat use, suggesting that strict saxicolous lizards tend to exhibit wider flexor digitorum longus aponeurosis, which might be explained by the higher resistance imposed by clinging to rocks. We add this greater grip force by the forelimbs as an anti-predatory mechanism, as described by Cooper *et al.* (2000) for other lizards, to prevent their extraction from crevices. *Phymaturus* species, when they try to avoid being extracted from the cracks, go as deeply as possible into the cracks, pressing their bodies against the crevice roof and extending their legs to exert pressure against it. The disposition of the spiny tails against the predator adds another strategy (Cooper *et al.*, 2000, Ramm *et al.*, 2020). The genus *Phymaturus* exhibit a series of exclusive features that differentiate them from the other two liolaemid genera: the monotypic *Ctenoblepharys* and the highly diverse *Liolaemus* (circa 288 spp.). These characteristics could be related to their diet and lifestyle. The teeth of *Phymaturus* have been described as tricuspid, with their crowns rounded, the central one being larger than the other two (Etheridge, 1995), which is convergent with members of the *Liolaemus fitzingerii* group (Lobo and Abdala 2001, 2002; Abdala, 2007). Additionally, the acquisition of pseudovalves in the small intestine, which we think serves to slow down the transit of plant material along the tract (Fig. 6). The anterior colon (= intestinal cecum) is particularly developed, see Fig. 1B (statistical validation is still needed, as the measurements and proportions of the different sections of the digestive tract of liolaemids are the subject of another study currently in progress). Greater trunk length and abdomen width generating abdominal capacity several times greater than most *Liolaemus* (evidenced in the length of inscriptional ribs and the number of presacral vertebrae). Short hind limbs in the *P. palluma* group are the largest and most voluminous species (lower center of body mass for life on slopes). Differences between the lengths of the hind limbs of the *palluma* and *patagonicus* groups of *Phymaturus* (Table 3) could represent a different use of the environment between the two species groups.

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Supplementary files

Supplementary materials cited in this article are available upon request from FL. Figure S1: Optimization of viviparity in the Liolaemidae tree and clutch/litter size. Figure S2: Optimization of Herbivory. Figure S3: Optimization of saxicoly.

Appendix I

Materials

Acronyms. CMNH: Carnegie Museum of Natural History, Pittsburgh, United States; IBA: Instituto de Biología Animal, Mendoza, Argentina; IBIGEO: Instituto de Bio y Geociencias del NOA, Salta, Argentina; FML: Fundación Miguel Lillo, Tucumán, Argentina; LACM: Los Ángeles County Museum, Los Ángeles, United States; MCN–UNSa: Museo de Ciencias Naturales de la Universidad Nacional de Salta, Salta, Argentina; MNHN: Museo Nacional de Historia Natural, Santiago, Chile; MVZ: Museum of Vertebrate Zoology, Berkeley, United States; SDSU: San Diego State University, San Diego, United States. AMNH (American Museum of Natural History, New York, United States), MCZ (Museum of Comparative Zoology, Harvard University, United States), SDSU (San Diego State University), USNM Unites States Natural Museum, Smithsonian Institution, Washington, United Sates), CAS (California Academy of Sciences, San Francisco, United States) UNSJ (Universidad Nacional de San Juan, San Juan, Argentina). Deposited at IBIGEO: fbc Felix B. Cruz collection, ptf Pamela T. Fierro collection. Pt "proyecto *Tupinambis*" materials.

Preserved in alcohol:

Ctenoblepharys adspersa (5): FML 3781, 368; LACM 94145–46. *Phymaturus aguanegra* (10): MCN–UNSa 970–72, 974,976, 979, 981–82, 990, 994. *Phymaturus antofagastensis* (7): MCN–UNSa 309–310, 1432–33, 1436, IBIGEO 7218–19. *Phymaturus castillensis* (11): IBA 869–1, 869–2, MCN–UNSa 3961–64, 3967, 3969, 3975–76, 3978. *Phymaturus ceii* (10): MCN–UNSa 910, 912–15, IBIGEO 6223–27. *Phymaturus chenqueniyen* (8): IBIGEO 6184–86, 6197–00. *Phymaturus damasense* (9): MNHN 1630–33, 1640, 1642, 1645, 3503. *Phymaturus delheyi* (8): MCN–UNSa 4970–74, 4980–81, 4932. *Phymaturus denotatus* (12): MCN–UNSa 3161, 3176, 3181, 3183, 3186, IBIGEO 5206, 5211, 5213–14, 5217, 5222–23. *Phymaturus dorsimaculatus* (12): MCN–UNSa 1581, 3727–29, 3733–36, 3738–40, 3779. *Phymaturus etheridgei* (6): MCN–UNSa 3109–13, 4308. *Phymaturus excelsus* (13): MCN–UNSa 1582–90, 1385–88. *Phymaturus extrilidus* (12): MCN–UNSa 2664, 2669, 2671, 2710–12, 2714–15, 2725–26, 2735, 2737. *Phymaturus felixi* (9): MCN–UNSa 1279–82, 3979–80, 3983, 3988, 3991. *Phymaturus fiambala* (12): IBIGEO 5757–60, 5762–68, 5774. *Phymaturus indistinctus* (11): MCN–UNSa 667, 682–684, 685, 1274, 1277, 3943–45, 3955. *Phymaturus katenke* (7): IBIGEO 6165–69, 6171–72. *Phymaturus laurenti* (14): MCN–UNSa 306, 313, 316, 324, 325, 1910–11, 1919, 2849, 2851, IBIGEO 5131–33, 5135. *Phymaturus mallimaccii* (7): IBIGEO 5987–92, 6031. *Phymaturus nevadoi* (10): 3647, 3652–57, 3659–3661. *Phymaturus palluma* (8): MCN–UNSa 3130–31, 3612–13, 3619–22. *Phymaturus patagonicus* (10): IBA 789–1, 789–2, 789–3, 789–4, 789–5, 789–6, 789–7, SDSU 1980, MCN–UNSa 1284, 1286. *Phymaturus payuniae* (12): MCN–UNSa 2878–79, 3648–49, 3651, 3665–66, 3668–72. *Phymaturus punae* (5): MCN–UNSa 3116, 3118–19, 3589–90. *Phymaturus querque* (12): MCN–UNSa 3854–57,3860–63, 3865, 4876–77, 4899. *Phymaturus rahuensis* (5): IBIGEO 5539–42, 5576. *Phymaturus sitesi* (13): MCN–UNSa 4757–4761, 4765–69, 4771, 4792–93. *Phymaturus spurcus* (7): MCN–UNSa 1239–40, 1244, 1246–48, 1596. *Phymaturus tenebrosus* (8): MCN–UNSa 1270, 1273,3934, IBIGEO 5588–89, 5591–92, 5594. *Phymaturus verdugo* (7): MCN–UNSa 1958, 1960–61, 1973–75, 1977. *Phymaturus videlai* (5): MCN–UNSa 4203–07. *Phymaturus williamsi* (7): MCN–UNSa 2808–11, 2815,2821, 3262. *Phymaturus yachanana* (9): 4314, 4319–20, 3272, 3274, 3276, 3278, 3280–81. *Phymaturus zapalensis* (10): MCN–UNSa 3844–49, 3851–53, IBIGEO 6251. *Liolaemus abdalai* (13): MCN–UNSa 2735, 2740, 2742–50, fbc 1102–03. *Liolaemus albiceps* (12): ptf 1,3,5,7,10, 12–13, 16, 18, 20, 22, m. *Liolaemus austromendocinus* (14): MCN–UNSa 3698, 3702,3706,3708–11, 2022, 2027–29, 604, 606, 608. *Liolaemus bibroni* (7): MCN–UNSa 763, 768–70, 772, pmc291. *Liolaemus boulengeri* (4): MCN–UNSa 3367, IBIGEO 6122, 6130, 6181. *Liolaemus buergeri* (10): MCN–UNSa 2023–24, 3783–84, 3814, 3828–29, 3882–84. *Liolaemus canqueli* (8): MCN–UNSa 288, 1289–95. *Liolaemus capillitas* (8): IBIGEO 5835–37, FML 2029 (4 indiv.). *Liolaemus cazianiae* (10): MCN–UNSa 2521–22, 2528, 2530, 2537, 2539–40, 2553, 2555, 2568. *Liolaemus ceii* (15): MCN–UNSa 3746, 3750, 3753, 3768–70, 4912–13, 4915, 4918, 4931, 5543–46. *Liolaemus chacoensis* (7): PT 2575–77, 2782, 2784–86. *Liolaemus chaltin* (11): MCN–UNSa 2221, 2225, 2229–31, 2924, IBIGEO 6691–93, 6758, 6761. *Liolaemus chlorostictus* (9): IBIGEO 5452, MCN–UNSa 2499, 2502–03, 3476–80. *Liolaemus coeruleus* (12): 3723–26, 3793–99, 3801. *Liolaemus cuyanus* (5): MCN–UNSa 800–806. IBIGEO 5084. *Liolaemus cyanogaster* (4): CMNH 133118, 133733, MVZ 188724–25. *Liolaemus darwinii* (16): MCN–UNSa 4783–84, 4843–47, 4852–53, 4856–62. *Liolaemus dorbignyi* (5): MCN–UNSa 2119–21, 2132, 2136. *Liolaemus elongatus* (35): IBIGEO 7220–25. MCN–UNSa 780, 1236, 1322, 1325, 1343–44, 1389–92, 3811, 3956–57, 4005, 4209–11, 4213, 4766, 4775, 4782, 4785, 4787, 4900, 4914, 4921, 4986, 5001–02. *Liolaemus escarchadosi* (10): 1519–23, 1529–30, 1533, 1535–36. *Liolaemus espinozai* (6): MCN–UNSa 212–214, 3168–70. *Liolaemus famatinae* (5): IBIGEO 6014–18. *Liolaemus fiambala* (13): MCN–UNSa 2134–35, IBIGEO 5720–24, 5726, 5729–30, 5736–38. *Liolaemus fitzgeraldi* (3): MCN–UNSa 2595, 2597–98. *Liolaemus galactostictos* (13): FML 1794. *Liolaemus gracilis* (6): MCN–UNSa 4820, 4849, 4851, 4854, 4864, 5684. *Liolaemus halonastes* (9): 2523, 2527,2556, 2558, 2560–61, 2565–67. *Liolaemus heliodermi*s (9): MCN–UNSa 3998–99, IBIGEO 5363–66, 6023–25. *Liolaemus inacayali* (9): MCN–UNSa 1226–28, IBIGEO 7235–3940. *Liolaemus irregularis* (17): MCN–UNSa 2242, 2251, 2255, 2279, 2285, 2294–95, 2300, 2308, 2312, 2315, 2760, 2767, 2783–85, 2787. *Liolaemus josei* (5): MCN–UNSa 3696–97, 3699, 3700, IBIGEO 7234. *Liolaemus kingii* (15): 6114–16, 6118–21, 6123–29, 6131. *Liolaemus kriegi* (17): MCN–UNSa 690, 1219–20, 3324,3366, 3868–69, 4328, 4890–93, IBIGEO 6153, 6192, 6194, 7079–80. *Liolaemus kolengh* (14): IBIGEO 5864–68, 5872–77, 5945, 5947–48. *Liolaemus koslowskyi* (15): pt3937,3939, fbc 084, MCN–UNSa 1397–98,1406–07,1409, 1411–15, 3292–93. *Liolaemus kunza* (12): 1839–40, 1860, 1936, 2014,2057–58, 2074,4376–78, 4380. *Liolaemus lavillai* (7): IBIGEO 5602–04, 5606–08, 5618. *Liolaemus lineomaculatus* (8): FML 1797 (3), 2118, 2731, 3356, 10098–99. *Liolaemus loboi* (7): 4551–57. *Liolaemus lutzae* (6): FML 1287. *Liolaemus magellanicus* (5): MCN–UNSa 855,859, 867–68, 872. *Liolaemus mapuche* (13): MCN–UNSa 4825–27,4830–34, 4836,4848–51. *Liolaemus martorii* (6): IBIGEO 6823–6828. *Liolaemus melanops* (5): MCN–UNSa 1297, 1300–01, 1305. *Liolaemus messii* (11):

IBIGEO 6694–04. *Liolaemus morenoi* (14): FML 17020–28, 22206–10. *Liolaemus multicolor* (10): IBIGEO 6728–37. *Liolaemus multimaculatus* (14): FML 1596. *Liolaemus neuquensis* (7): FML 3548, 7846–48, 9457, 22343–44. *Liolaemus nigriceps* (15): FML 1632(4), 24717–27. *Liolaemus olongasta* (8): FML 2669(4), MCN–UNSa 3328–30, IBIGEO 6057. *Liolaemus orientalis* (13): FML 2036. *Liolaemus ornatus* (12): MCN–UNSa 3595–00, IBIGEO 6722–27. *Liolaemus pacha* (13): FML 2399(6), 3094(7). *Liolaemus pachecoi* (10): FML 28835–40, 28891–92, 28894, 28898. *Liolaemus pagaburoi* (14): MCN–UNSa 472, 477–80, 620–627, 629. *Liolaemus parvus* (10): IBIGEO 6085–90, 6092, 6108–10. *Liolaemus patriciaiturrae* (9): FML 1189(2), 28730, 25949–54. *Liolaemus petrophilus* (9): pt 4841, 4846, MCN–UNSa 787, 1352, 4325, IBIGEO 6150–52, 6257–58. *Liolaemus pictus* (9): FML 1780(5), 7772–75. *Liolaemus pleopholis* (3): FML 26020–22. *Liolaemus porosus* (9): FML 1649(3), 1650(6). *Liolaemus pseudoanomalus* (8): FML 2087(5), 19011–12, 19015. *Liolaemus pulcherrimus* (9): 18238–45, 18247. *Liolaemus puna* (9): MCN–UNSa 2496–97, 2514–16, 3203–04, 3239–40. *Liolaemus puritamensis* (9): FML 983, 985, 18150, 28955–58, 29065–66. *Liolaemus pyriphlogos* (12): FML 1463. *Liolaemus quilmes* (15): FML 2445(4), 2451(6), 2291(5). *Liolaemus ramirezae* (6): MCN–UNSa 468, 519, 524, 2576–77, 2579. *Liolaemus robertmertensi* (13): FML 1308(3), 1488(7), 1847(3). *Liolaemus rosenmanni* (14): FML 29212–14,25936–39,25943–44, 25947–48, 25955–57. *Liolaemus rothi* (11): FML 1037, 10071–72, 17060, 17118–22, 23789–90. *Liolaemus ruibali* (15): IBIGEO 5271–78, 5280–84, 5286, 5289. *Liolaemus sagei* (6): FML 1637(4), 21536, 22426. *Liolaemus salinicola* (14): FML 1912(7), 16782–86, 16788–89. *Liolaemus sanjuanensis* (10): UNSJ 736,738–39, 740, 742–43, 746, 748–49, 766. *Liolaemus sarmientoi* (12): MCN–UNSa 1496, 1500, 1502, 1504–05, 1507–13. *Liolaemus saxatilis* (5): MCN–UNSa 903–05, IBIGEO 6782–83. *Liolaemus scapularis* (16): IBIGEO 5089–99, 5101–05. *Liolaemus scrocchii* (7): MCN–UNSa 2136–38, 4046, IBIGEO 5341–43. *Liolaemus shehuen* (6): 4321–24, 4326, 4330. *Liolaemus talampaya* (6): MCN–UNSa 2031–36. *Liolaemus tandiliensis* (13): MCN–UNSa 1604–16. *Liolaemus tromen* (6): MCN–UNSa 3780–82, 3812–13, 3830. *Liolaemus tulkas* (10): IBIGEO 5804–12, 5814. *Liolaemus umbrifer* (7): IBIGEO 5227–32, 5234. *Liolaemus vulcanus* (9): IBIGEO 5120–22, 5125–27, 5129, 5168–69. *Liolaemus wiegmannii* (12): MCN–UNSa 3139, 3151, 4742–48, IBIGEO 5839–41. *Liolaemus yanalcu* (12): MCN–UNSa 535–36,705, 726, 729, 955–56, 1038–39, 1635, 2237–38. *Liolaemus zullyae* (15): IBIGEO 5931–44.

Skeletons studied from Richard Etheridge´s RX plates collection (each RX plate is called CASE).

CASE L8R *Urostrophus torquatus* CAS 85234–36. *Urostrophus torquatus* CAS 85237. *Anolis* sp. MCZ 85247. CASE L 9R *Liolaemus lutzae* CAS 96881–82. CASELO9R *Plica umbra* CAS 95142, 93241–42. *Morunasaurus groi* CAS 98001. CASE L 10 R *Liolaemus multiformis multiformis* CAS 80903–04, 809042, 80901. *Liolaemus tenuis* CAS 85240, 85249, 85238, 84717. *Stenocercus humeralis* CAS 94112. *Stenocercus humeralis* CAS 94111. CASE L 11 R *Liolaemus chiliensis* CAS 85233.*Tropidurus duncanensis* CAS 12206. *Tropidurus duncanensis* CAS 12200–02. CASE L 12 R *Liolaemus occipitalis* CAS 87093–94. *Liolaemus fuscus* CAS 84747–49. CASE L19R *Liolaemus pictus* CAS 85241, 85243–44, 85246–251, 84719. CASE L 66 R *Liolaemus chiliensis* 85233, *Liolaemus fuscus* 84747. CASE77 *Anolis mirus* 1910.7.11.5 *Leiocephalus apurimata* 62253. *Leiocephalus macropus koopmanni* 55541type. *Leiocephalus fimbriatus* 61226. *Leiocephalus personatus vinculum* 61059–60. CASE L–108–R *Liolaemus alticolor* MCZ 7287. *Liolaemus a. altissimus* MCZ 30611, 38612–13. *Liolaemus hatcheri* MCZ 11828. *Liolaemus schroederi* MCZ 51948–49. *Stenocerus juninensis* MCZ 45820–21. *Stenocerus nigromaculatus* MCZ 1797545820. CASE 110: *Phymaturus palluma* MCZ 2033. CASE L110 *Tropidurus praeornatus* MCZ 33582.*Tropidurus praeornatus* MCZ 33581. *Urocentron flaviceps* MCZ 37270. *Enyalius* sp. CAS9 6826. CASE 111 *Phymaturus patagonicus* MCZ 14914–15. *Stenocercus chrysopygus* MCZ 45833. *Stenocercus chrysopygus* MCZ 8073. *Stenocercus chrysopygus* MCZ 45835. *Diplolaemus bibroni* MCZ 14918–19. *Stenocercus chrysopygus* MCZ 45834. CASE 120 *Pristidactylus scapulatus* MCZ 33584. *Liolaemus elongatus* MCZ 14929–30, 14927. *Enyalioides heterolepis* MCZ 39911. *Enyalioides heterolepis* MCZ 24959. / SDSCCOLL *Enyalius pictus*. *Urocentron* sp. MCZ 12440MA. CASE 123 *Liolaemus lenzi* MCZ 7264. *Liolaemus wiegmannii* MCZ 57402–03, 61219–20. *Liolaemus chacoensis* MCZ 86603–04, 49520–21. *Liolaemus fuscus* MCZ 38622, 38624–26. *Liolaemus signifer* MCZ 86598–01. CASE 125 *Liolaemus schroederi* MCZ 65404. *Liolaemus fitzingeri* MCZ 15901–02. *Liolaemus villaricensis* MCZ 86310–12. *Liolaemus monticola* MCZ 21212–13. *Liolaemus boulengeri* MCZ 14939, 149397. CASE 126 *Liolaemus bisignatus* MCZ 7270 1–4, *Liolaemus lineomaculatus* MCZ 11819–22, *Liolaemus cyanogaster* MCZ 2051, 2051, 2051, *Liolaemus chiliensis* MCZ 19979, 19985. CASE 127 *Liolaemus kingii* MCZ 11839–40, 11837. *Liolaemus lutzae* MCZ 79136–37, 79139–40. *Liolaemus walkeri* MCZ 45816–18, 45813, 45813. *Ctenoblepharys adspersa* MCZ 70228. /SDSC COLL *Pristidactylus torquatus* SDSU. CASE 128 *Liolaemus darwini* MCZ 86620–27, 866291. CASEL128 *Tropidurus torquatus* MCZ 66943.*Tropidurus torquatus* MCZ 80879. CASE 135 *Enyalioides praestabilis* USNM7797. *Enyalioides praestabilis* USNM 7798. *Enyalioides praestabilis* USNM7796. CASE 136 *Liolaemus altissimus altissimus* USNM 1463133–34. *Liolaemus wiegmannii* USNM 70477, 70473–74, 70481. *Liolaemus fitzgeraldi* USNM38937, *Liolaemus tenuis* USNM 5518 (7). CASE 137 *Liolaemus kingii* USNM 36918–23. *Liolaemus lineomaculatus* USNM 36985, 36893–94, 36901, 36896–99. CASE 138 *Liolaemus elongatus* USNM 13954–57. *Liolaemus fitzingeri* USNM 36934–38. CASE 143 Gifts *Liolaemus multiformis* SDSU, SDSU SDSU, SDSU… *Tropidurus boicardi* CASE143 *Tropidurus boicardi*. CASE143 *Tropidurus boicardi*. CASE144 *Tropidurus boicardi*. CASE144 *Tropidurus boicardi* CASE144 *Tropidurus boicardi* CASE144 *Tropidurus boicardi*. *Liolaemus pictus* (6 uncatalogued). CASEL148 *Urocentron flaviceps* AMNH 56409. *Stenocercus azureus* AMNH 17013. *Stenocercus azureus* AMNH 37558. *Stenocercus azureus* AMNH 37559. *Stenocercus azureus* AMNH 37557. *Stenocercus ornatissimus* AMNH 27136–37. *Stenocercus ornatissimus* AMNH 28783. *Urocentron flaviceps* AMNH 57206–08. CASE 156 *Liolaemus lineomaculatus* AMNH 17010, *Liolaemus bibroni* AMNH 80051, *Liolaemus lemniscatus* AMNH 88325, *Liolaemus wiegmannii* AMNH 64806, 12009. *Liolaemus gravenhorsti* AMNH80054–55, *Liolaemus simonsi* AMNH 13491, 13496–98. *Liolaemus* *magellanicus* AMNH 80043–45, *Liolaemus cyanogaster* AMNH 38065–67. CASE157 *Liolaemus fitzingeri* AMNH 80047–49. *Liolaemus chiliensis* AMNH 80052–53. *Liolaemus alticolor* AMNH 79935–39, 38068–70. *Urocentron* sp. MCZ 84247. CASE 158 *Liolaemus niti*dus AMNH 37810–11, 37523, 37808, 37804, 37571–72. CASE 159 *Liolaemus platei* AMNH 37574–75, 37377–78, 37579, 37587–88, 37581. CASE124 *Liolaemus nitidus* MCZ 65402. *Liolaemus nigroviridis* MCZ 86303. *Liolaemus tenuis* MCZ 65401, 65485. *Ctenoblepharys adspersa* MCZ 70228. *Liolaemus lemniscatus* MCZ 21214, 65398. *Liolaemus magellanicus* MCZ 67910–11. *Liolaemus goetschi* MCZ 51950. CASE160 *Enyalioides praestabilis* AMNH 37554–55. CASE170 *Plica umbra* MCZ 101799,101748. CASE173 (no collection data) *Stenocercus doellojuradoi* CASE173 *Stenocercus scapularis*. CASE 173 R (no collection data) *Liolaemus schroederi*. *Liolaemus nigroviridis*. *Liolaemus ornatus* (2). *Liolaemus fitzingeri*. *Liolaemus darwini*. *Liolaemus jamesi*. *Liolaemus bibroni*. *Liolaemus magellanicus*.

Cleared and stained specimens:

Phymaturus aguanegra MCN–UNSa 965–69, 984–85. *Phymaturus cacivioi* MCN–UNSa 3901, 3936, 3903. *Phymaturus calcogaster* MCN 4302–03. *Phymaturus castillensis* MCN–UNSa 3977. *Phymaturus ceii* MCN–UNSa 908–09. *Phymaturus damasense* MCN–UNSa 1643. *Phymaturus delheyi* MCN–UNSa 4976. *Phymaturus denotatus* MCN–UNSa 319, 321. *Phymaturus dorsimaculatus* MCN–UNSa 921, 923, 1577–78. *Phymaturus etheridgei* MCN–UNSa 4306. *Phymaturus excelsus* MCN–UNSa 922. *Phymaturus extrilidus* MCN–UNSa 2665, 2713. *Phymaturus felixi* MCN–UNSa 3990. *Phymaturus indistinctus* MCN1481–82. *Phymaturus laurenti* MCN–UNSa 318, 326. *Phymaturus nevadoi* MCN–UNSa 3658. *Phymaturus niger* IBIGEO 5578, 5568. *Phymaturus palluma* MCN–UNSa 3639. *Phymaturus patagonicus* MCN–UNSa 1285. *Phymaturus payuniae* MCN–UNSa 3673. *Phymaturus querque* MCN–UNSa 3858. *Phymaturus roigorum* MCN–UNSa 2113, 2115. *Phymaturus sitesi* MCN–UNSa 4763. *Phymaturus spurcus* MCN–UNSa 1249. *Phymaturus tenebrosus* MCN–UNSa 1489, 1491. *Phymaturus williamsi* MCN–UNSa 2813, 2817. *Phymaturus yachanana* IBIGEO 7226. *Phymaturus zapalensis* MCN–UNSa 1485–86, 3850. *Liolaemus kolengh* MCN–UNSa 579. *Liolaemus kriegi* MCN–UNSa 1218. *Liolaemus ceii* IBIGEO 6671–72. *Liolaemus austromendocinus* FML 3422–3. *Liolaemus petrophilus* MCN–UNSa 1347. *Liolaemus elongatus* MCN–UNSa 4609. *Liolaemus capillitas* FML 1229–21. *Liolaemus vulcanus* MCN–UNSa 1863, IBIGEO 5119. *Liolaemus ruibali* FML 02574–1, MCN–UNSa 3132. *Liolaemus multicolor* MCN–UNSa 1463,1444. *Liolaemus quilmes* MCN–UNSa 3524–25, 3528. *Liolaemus koslowskyi* MCN–UNSa 573– 574, 576. *Liolaemus albiceps* MCN–UNSa 402, 453, 2585, 457,1452. *Liolaemus irregularis* MCN–UNSa 2446. *Liolaemus ornatus* MCN–UNSa 3547. *Liolaemus lavillai* MCN–UNSa 2686, 4351. *Liolaemus scapularis* MCN–UNSa 283, 253. *Liolaemus inacayali* MCN–UNSa 498. *Liolaemus pseudoanomalus* MCN–UNSa 526. *Liolaemus chaltin* MCN–UNSa 235, 2238, 2222, 2226, 2223. *Liolaemus abdalai* MCN–UNSa 493. *Liolaemus bibroni* MCN–UNSa 491. *Liolaemus sanjuanensis* UNSJ 737,747, 7341. *Liolaemus nigroviridis* MCN–UNSa 569–70, 572.

Digestive tracts studied:

Phymaturus aguanegra MCN–UNSa 970–74, 976–83, 986–87, 989–91, 993–95. *Phymaturus dorsimaculatus* MCN–UNSa 1581, 3729–3736, 3779. *Phymaturus indistinctus* MCN–UNSa 682, 684–85, 687, 1274,1277. *Phymaturus* cf. *palluma* MCN–UNSa 2111–12, 3623–25, 3516. *Phymaturus* cf. *yachanana* MCN–UNSa 3272, 3274, 3276, 3280, 3282, 3277–79. *Phymaturus zapalensis* MCN–UNSa 3844–49; 3851–53. *Liolaemus albiceps* MCN–UNSa 423, 4569–70, IBIGEO 6280, 6284–85. *Liolaemus buergeri* MCN–UNSa 3783–84, 3814, 3828–29. *Liolaemus ceii* MCN–UNSa 3752, 3755, 3758, 3764. *Liolaemus* cf. *ceii* MCN–UNSa 4895, 4897, 4901. *Liolaemus kriegi* MCN–UNSa 690, IBIGEO 7079–80. *Liolaemus kunza* MCN–UNSa 1763–88, 1771,1786; 1859–60,1868–70,1936, 2040, 4376–77, 4380. *Liolaemus mapuche* MCN–UNSa 4800, 4803. *Liolaemus tulkas* IBIGEO 5805–08, 5812. *Liolaemus umbrifer* MCN–UNSa 2865, IBIGEO 5113, 5115, 5228, 5230.

DIET LITERATURE FOR LIOLAEMID LIZARDS

(36 species studied. *Phymaturus*: 6, *Liolaemus* 30)

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